Age Differences in Vestibular Processing: Neural and Behavioral Evidence

by

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DEDICATION

To my parents,
for teaching me to live a virtuous life.

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ABSTRACT

The vestibular system is well known for its role in balance, but its mechanisms of action in this role are not well understood. My dissertation aims to provide a better understanding of vestibular brain function, its correlation with postural control, and its alteration with advancing age. This is an important topic considering that falls are the current leading cause of injuries in older adults in the U.S., and they have negative consequences on wellbeing and independence.

In this dissertation, I first review the conventional methods for studying vestibular function in the human brain, and I evaluate a novel MRI-compatible method, which relies on a pneumatic tapper. This approach successfully induces vestibular responses, while preventing the aversive effects of stimulation that are common in other approaches. Next, I assess age differences in brain responses to pneumatic vestibular stimulation, and find that older adults demonstrate less sensitivity to stimulation. Also, those with better postural control exhibit less deactivation of cross-modal sensory regions (e.g. visual and somatosensory cortices). This greater engagement of non-vestibular sensory regions in older adults with better balance could be a mechanism to compensate for inefficient vestibular processing. Consistent with this hypothesis, the relationship between postural control and deactivation of sensory regions was only evident in tasks of low difficulty (i.e. normal stance) in which compensatory neural recruitment might be most effective.

After assessing the brain responses to vestibular stimulation in terms of activation and deactivation, I examine connectivity of the vestibular cortex with other regions. This last experiment demonstrates that vestibular cortex connectivity increases in response to vestibular stimulation, and young adults exhibit greater connectivity relative to older adults. Also, connectivity predicts postural stability in high difficulty tasks for young adults, and in low difficulty tasks for older adults. Better balance in young adults is associated with less vestibular connectivity (i.e. they engaged vestibular cortex more selectively), whereas better balance in

older adults is associated with higher connectivity (i.e. more recruitment of other sensory regions). These findings reinforce the conclusions from the second experiment, and provide more evidence in support of the compensation related utilization of neural circuits hypothesis (CRUNCH) of neural processing in older adults.

Chapter I

Introduction

i. Vestibular System and its Contribution to Motor and Cognitive Processes

The vestibular system is best known for its role in postural control and balance. The vestibular organs embedded in the inner ear detect the orientation of the head with respect to a gravitational vector as well as linear and angular head accelerations. Awareness of body position in space is essential for spatial navigation and differentiation between active and passive movements. Detection of head motion and translation of this information into compensatory eye movements is the basis of the vestibulo-ocular reflex, which is necessary for stabilizing visual inputs on the retina during movement (Jay M. Goldberg et al., 2012).

Vestibular system functions are not limited to postural control. As Bolmont et al. (Bolmont, Gangloff, Vouriot, & Perrin, 2002) demonstrated, individuals' balance correlates with their cognitive status. Gurvich et al. (Gurvich, Maller, Lithgow, Haghgooie, & Kulkarni, 2013) and Mast et al. (Mast, Preuss, Hartmann, & Grabherr, 2014) published reviews on the growing body of literature on the role of the vestibular system in cognition, mental imagery, sensation of pain, and mood control. Other studies have also shown the effects of caloric vestibular stimulation (CVS) and galvanic vestibular stimulation (GVS) on body representation and hemineglect (potentially via restoration of egocentric representations) (Cappa et al. 1987, Vallar et al. 1995, Ferrè et al. 2013; Lopez et al. 2012; Ronchi et al. 2012). Studies on patients with vestibular dysfunction have also documented performance declines in tasks of spatial memory, egocentric mental rotation, navigation, visual construction, and motor speed (Smith & Darlington, 2013; Smith & Zheng, 2013). This emerging body of literature suggests that vestibular function is broader than originally thought. These findings point to several unexplored territories of vestibular function yet to be discovered. Therefore, in this dissertation I attempt to add to our current knowledge of this complex system by assessing the neural correlates of vestibular processing in relation to age and behavior.

ii. Vestibular Interaction with other Sensory Systems

The successful integration of multiple sensory inputs is essential for postural stability. Visual, auditory, tactile and other proprioceptive information integrates with vestibular signals through a dynamic weighting process. In this process, the sensory modalities are thought to be weighted based on their precision. Van Beers et al. (Van Beers & Gon., 1999) showed that the central nervous system (CNS) weighs the more precise input more heavily, through experience and instant evaluation of sensory signals. They further discussed the underlying mechanisms of multisensory integration, stating that the CNS does not perform an actual probability calculation. Rather, it weights sensory inputs to maximize the signal to noise ratio to produce the least amount of error in perception and action. As Vidal et al. (Vidal PP, Berthoz A, 1982) showed, the CNS integrates all available sensory inputs (even if they are unreliable), but through experience the weighting of these inputs becomes more accurate.

Previously it was suggested that multisensory signals integrate in a hierarchical fashion, meaning that single sensory modalities are processed in specific brain regions and multi modal processing occurs in associative cortical regions (Jones, 1970); however, recent evidence from neuroimaging studies suggests that multisensory convergence can occur in regions known to be involved in primary sensory processing (Macaluso, 2006). For example, occipital cortex can be involved in processing of non-visual signals (e.g. tactile orientation recognition), if visual and non-visual stimuli are presented to the same hemisphere.

Although these findings suggest non-specificity of cortical regions involved in multisensory processing, a few main “integration sites” that contribute greatly to multisensory processing have been identified. In particular, evidence suggests that the right temporoparietal junction (TPJ) is an integration site that regulates the coherent sense of body ownership (Tsakiris, Costantini, &

Haggard, 2008). Many studies have provided support that the TPJ, PIVC, intraparietal cortex, and posterior insula form a vestibular processing network (Cullen, 2012; Dieterich and Brandt, 2008; Eickhoff et al., 2010, 2006; Fasold et al., 2002; Guldin and Grüsser, 1998; Karim et al., 2013; Kirsch et al., 2016; Lobel et al., 1998; Lopez et al., 2012; Lopez and Blanke, 2011; Miyamoto et al., 2007; Schlindwein et al., 2008; Suzuki et al., 2001; zu Eulenburg et al., 2012). Also, Ferrè et al. (Ferrè et al., 2013) reported that vestibular inputs selectively regulated the perception of other sensory modalities (e.g. increasing the threshold for touch sensation and vice versa for pain).

In sum, the literature has provided extensive reports on the interaction of different sensory modalities with vestibular signals; however, how these interactions relate to balance is less understood. In this dissertation, I study how vestibular cortex and other sensory regions respond to vestibular stimulation, and whether their connectivity correlates with quantitative behavioral metrics (i.e. body sway).

iii. Types of Vestibular Stimulation

Studies in humans have used different modes of stimulation to evoke vestibular responses. Here, I discuss the five main types of vestibular stimulation commonly used in clinical and basic science research, and explain which one I will use in my experiments:

- Caloric Vestibular Stimulation (CVS): caloric stimulation comprises the irrigation of cold or warm water into the ear that alters the air temperature within the middle ear canal (Marcelli et al., 2009; M. Suzuki et al., 2001; Wang et al., 2008). Vestibular nystagmus is the vestibular ocular response (VOR) to this stimulation, which stabilizes the visual inputs on the retina during the perceived head movement. One limitation of caloric stimulation is that the evoked vestibular *cortical* activity varies based on the side and temperature of the irrigation (i.e. warm water induced bilateral brain activity, whereas cool water induced a contralateral response, (Karim et al. 2013)). Moreover, caloric stimulation is rather unpleasant for subjects.

- Auditory Tone Bursts/ Auditory Clicks: another common method of vestibular stimulation is high decibel auditory tone bursts, which delivers high decibel clicks that stimulate the otolith organs (mainly the saccule) (Colebatch, Halmagyi, & Skuse, 1994; Schlindwein et al., 2008). This method is also commonly used to induce vestibular evoked myogenic potentials (VEMP) (Ferber-Viart, Dubreuil, & Duclaux, 1999) as a test of vestibular function (Brantberg & Fransson, 2001). The tone burst stimulation method can also be irritating and uncomfortable for subjects due to the high decibel sound required to elicit vestibular responses.

- Galvanic Vestibular Stimulation (GVS): in this method, electric current is used to stimulate the vestibular nerve via electrodes placed over the mastoid bones (Elie Lobel et al., 1998; Wuehr et al., 2016; Yamamoto, Struzik, Soma, Ohashi, & Kwak, 2005). The amplitude and frequency of the GVS is altered to either increase or decrease the signal to noise ratio (enhance or perturb the vestibular function). GVS activates the vestibular nerve (semicircular canals and otolith), whereas CVS only activates the horizontal semicircular canals (Day, Ramsay, Welgampola, & Fitzpatrick, 2011; M. Dieterich, 2003; Stephan et al., 2005). If used supra-threshold, GVS can induce nausea and motion sickness in subjects.

- Transcranial direct current stimulation (tDCS) is another form of electrical stimulation that has been used to modify vestibular cortical excitability, providing another window into vestibular function. Arshad et al. (Arshad et al., 2014) used bilateral tDCS of parietal cortex to modulate the CVS-induced vestibular ocular response, and showed that tDCS interrupts the parietal inter-hemispheric balance, causing asymmetric vestibular responses. Kyriakareli et al. (Kyriakareli, Cousins, Pettorossi, & Bronstein, 2013) also used bilateral tDCS of the temporoparietal junction to lower the threshold for vestibular ocular responses and self-motion perception. Moreover, Inukai et al. (Inukai et al., 2016) showed that cathodal tDCS over the vestibular cerebellum reduced the amount of body sway in healthy young adults. Compared to CVS and auditory tone burst methods, using the electrical current is less irritating for subjects.

- Bone Conduction (vibration): bone conduction has been recently introduced as a method of vestibular stimulation (Krister Brantberg, Westin, Löfqvist, Verrecchia, & Tribukait, 2009). The induction of low-level vibration in the skull is transmitted via bone conduction to vestibular receptors in the inner ear, resulting in stimulation of vestibular receptors. Wackym et al. (Wackym et al., 2012) compared the conventional auditory click/tone burst stimuli with a bone conduction striker system for their ability to elicit vestibular responses. They evaluated VEMP responses, and reported that VEMPs elicited by the bone conduction method were faster and more comfortable for healthy subjects. Also, they found more consistent ocular VEMPs (i.e. recorded from the muscle underneath the eye) elicited by bone conduction stimulation compared to the auditory tone bursts. Curthoys et al. (Curthoys et al. 2009) provided a review of animal and human studies in which they showed that the VEMP characteristics (i.e. n10 component of ocular VEMP) in response to bone conduction stimulation reflect otolithic (mainly utricle) function, rather than semicircular canal function. They suggested that even low amplitude bone-conducted vibration triggers the utricular receptors through a shear wave mechanism that transfers the vibration in the skull (Curthoys et al. 2006a). Brantberg et al. (Krister Brantberg et al., 2009) further supported these findings, showing that lateral bone conducted vibrations induced VEMP responses through vibration and translation mechanisms. Compared to other vestibular stimulation methods discussed above, the bone tapping method is the most comfortable from the subjects' perspective.

In the first experiment of this dissertation, I demonstrate the effectiveness of the bone conduction method in an fMRI setting. This is a novel approach since the previously used methods in the fMRI setting mainly elicit saccule responses –auditory short tone bursts (Schlindwein et al., 2008), or the horizontal semicircular canals --CVS (Fasold et al., 2002), or the entire vestibular nerve –GVS (Stephan et al., 2005). Therefore, the vestibular imaging field can benefit from using this method to better understand the *utricle's* contribution to vestibular neural processing. I use the bone tap method of vestibular stimulation in all of the experiments of this dissertation.

iv. Vestibular Network Imaging

A recent meta-analysis by zu Eulenburg et al. (zu Eulenburg et al., 2012) showed that across 28 neuroimaging studies using different modes of vestibular stimulation, the *parietal opercular* area OP2 showed the most overlapping activation. However, many other regions were also found to be involved in vestibular processing, including inferior parietal cortex, superior temporal gyrus, middle frontal lobe, posterior cingulate, thalamus, cerebellum, and other regions. In another meta-analysis, Lopez et al. (Lopez, Blanke, & Mast, 2012) evaluated 16 neuroimaging studies that used CVS, GVS, or auditory tone burst stimulation. Among 352 foci of activation reported in these studies, only the *retroinsular cortex* was commonly activated by all three stimulation modes. They also found parietal operculum, posterior insula, superior temporal gyrus, sylvian fissure, and cingulate cortex as converging sites for vestibular signals elicited by different stimulation types. In addition to PET and fMRI studies, a few studies have used fNIRS to assess vestibular cortex activity during balance and postural control (Karim et al. 2012) and in response to caloric stimulation (Karim et al. 2013). The *temporal-parietal cortex* was also the main activated region in these studies, matching the results obtained with vestibular stimulation when participants were supine.

In this dissertation, I use functional MRI to assess vestibular function, since it has been shown to successfully detect the brain regions involved in vestibular processing.

v. Aging and Vestibular Function

Similar to other sensory modalities, vestibular function exhibits declines with healthy aging. In a longitudinal study of healthy older adults, Baloh et al. (Baloh, Enrietto, Jacobson, & Lin, 2001) found a significant decline in vestibular function (indicated by changes in VOR) over five years. However, this decline was not associated with changes in balance or postural stability. Peripheral sensation (i.e. proprioception) and in particular the sensation of vibration in the legs has been shown to have a strong correlation with body sway in older adults (Brocklehurst, Robertson, & James-Groom, 1982), and among other age groups (Lord & Ward, 1994). After age 65, reliance on visual inputs for postural control declines and efficient peripheral sensation becomes the most important contributing factor to balance control (Lord & Ward, 1994). However, in a challenging situation with poor visual and peripheral sensation (i.e. standing on an uneven surface in a dark room) vestibular function serves as the main source of equilibrium (Lord & Ward, 1994). Other studies have reported that healthy older adults and patients with vestibular loss exhibit similar reliance on visual inputs and difficulties with sensory reweighting (Barrett et al., 2013; Jeka, Allison, & Kiemel, 2010). Cousins et al. (Cousins et al., 2014) showed that patients with vestibular neuritis rely heavily on visual inputs, which leads to poor behavioral outcomes.

Age-related vestibular declines have also been studied in patient populations: following cochlear implant surgery, older adults are at higher risk of loss of caloric responses (22% chance) compared to young adults (3% chance), which can indicate poorer vestibular plasticity in post-operative recovery (Enticott, Tari, Koh, Dowell, & Leary, 2006). Despite general declines with aging, Allison et al. (Allison, Kiemel, & Jeka, 2006) showed that the multisensory integration and reweighting dynamics of visual and tactile stimuli in older adults with sufficient peripheral sensation are similar to those of young adults (possibly due to higher reliance on somatosensory cues).

The literature seems to be mixed on whether there are age differences in vestibular function and its relative weight compared to other sensory inputs in healthy aging. According to the compensation-related utilization of neural circuits hypothesis (CRUNCH) (Patricia A. Reuter-Lorenz & Cappell, 2008), one would predict that age-related declines in vestibular function and deterioration of vestibular anatomical structures result in patterns of over and under activation, which can be interpreted according to behavior. In particular, CRUNCH predicts that for relatively easy tasks, older adults compensate for their impaired postural stability by recruiting more brain regions and overactivating the regions they recruit. But as task difficulty increases, the ceiling for neural compensation is reached and patterns of under-activation and poor balance become more evident. To the best of my knowledge, CRUNCH has not been tested in relation to vestibular processing and balance control.

In this dissertation, I compare vestibular brain activity and connectivity in young and older adults, to determine the extent to which vestibular neural responses change with age, and how these changes correlate with behavioral metrics of vestibular function. I use a battery of balance assessments to compare the performance when different sensory inputs are compromised (i.e. different levels of difficulty in balance control).

vi. Correlation of neural and behavioral measures of vestibular function

Many studies in healthy individuals and patient populations have documented correlations between neural and behavioral measures of vestibular function. For example, galvanic vestibular stimulation has been used to modulate the activity of vestibular cortex to either enhance or perturb postural stability (Bent, McFadyen, & Inglis, 2002; Mulavara et al., 2015; Pal, …, & 2009, n.d.; Peterka, 2012; Scinicariello, Eaton, Inglis, & Collins, 2001; Yamamoto et al., 2005). Reduced postural stability and increased fall risk among older adults has been associated with more body sway (Bird, Pittaway, Cuisick, Rattray, & Ahuja, 2013; Melzer, Benjuya, & Kaplanski, 2004), less muscle strength (Moreland, Richardson, Goldsmith, & Clase, 2004; Wolfson, Judge, Whipple, & King, 1995), and inefficient muscle recruitment strategies (i.e. excessive co-contraction) (Benjuya, Melzer, & Kaplanski, 2004; Nelson-Wong et al., 2012), but the neural mechanisms involved in such abnormal behavioral patterns are not well understood. The muscle co-contraction in patient population has been linked to atypical recruitment of different brain regions (i.e. patterns of over and under activation relative to healthy individuals) (Ceballos-Baumann et al., 1995; Pujol et al., 2000). Therefore, one might speculate that inefficient neural processing, and in particular dedifferentiation of neural recruitment in older adults (J. a Bernard & Seidler, 2012; Carp, Park, Hebrank, Park, & Polk, 2011) may associate with poorer specificity of muscle recruitment. On the other hand, the co- contraction of ankle muscles has also shown to work as a strategy to increase stability via increased stiffness (Seidler-Dobrin, He, & Stelmach, 1998). The compensation-related utilization of neural circuits hypothesis (CRUNCH) (Patricia A. Reuter-Lorenz & Cappell, 2008) could potentially explain the neural mechanisms underlying these compensatory muscle activations in elderly.

In this dissertation I investigate age differences in brain responses to vestibular stimulation to identify regions that older adults over- or underactivate, compared to young adults. This could identify targets for non-invasive brain stimulation to enhance balance control. Using a battery of balance assessments that have been shown to be reliable and sensitive predictors of falls (Bloem, Grimbergen, Cramer, Willemsen, & Zwinderman, 2001; Franchignoni, Tesio, Martino, & Ricupero, 1998; Mancini & Horak, 2010), I assess brain-behavior correlations for vestibular processing with respect to age. This is of special importance for older adults who cannot benefit from conventional balance training methods to improve muscle strength and postural sway.

vii. Overview of the conducted experiments

In this dissertation, I conducted three experiments to examine vestibular brain responses, differences with age, and associations with postural control:

In experiment one, I validated a new method for stimulating the vestibular cortex inside the MRI scanner. The conventional approaches do not successfully stimulate the utricle, and induce aversive responses due to subjects' discomfort. I also investigated the correlation between postural control and vestibular brain function. My hypothesis was that the pneumatic bone conduction method would activate the canonical vestibular cortex, as it has been successful in inducing the behavioral VEMP response in previous studies. Also, I hypothesized that higher activation of vestibular cortex would reflect greater sensitivity to the stimulus, and would correlate with better postural control.

In my second experiment, I investigated age differences in vestibular brain function, and how they correlate with postural control. Using the vestibular stimulation method of experiment one, I compared neural activation in young vs. older adults. A correlation analysis between measures of postural control and vestibular brain responses sheds light on the extent to which older adults rely on vestibular activation. Based on previous reports in the literature, I hypothesized that young adults would exhibit greater response in canonical vestibular cortex relative to older adults, and the pattern of this activity would be less distinctive in older adults. I expected dedifferentiation of neural patterns, and more recruitment of non-vestibular regions in older adults. Also, I expected that better postural control would be correlated with greater magnitude and more distinctive patterns of vestibular cortex activity, regardless of age.

In the final experiment, I examined age differences in resting state and task-based functional connectivity of the brain regions identified in the second experiment. Moreover, in this experiment I examined the correlation between balance control and vestibular network connectivity strength. I calculated connectivity based on the correlation of average time series between two regions. I hypothesized that young adults would exhibit greater vestibular connectivity relative to older adults, due to being more sensitive to the vestibular stimulation. I also predicted that vestibular connectivity would decrease from resting state to stimulation since vestibular cortex would respond differently to the stimulation than other regions (i.e. less synchronous time series during stimulation). Further, I expected better postural control to be correlated with connectivity patterns, with higher connectivity during rest and lower connectivity during stimulation predicting better balance. Such findings would be consistent with the hypothesis that greater neural specificity in response to stimulation correlates with better balance, especially in balance tasks with the highest reliance on vestibular inputs.

The findings of these three experiments provide neural and behavioral evidence to further expand our knowledge of the aging vestibular system.

viii. References

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Chapter II

Functional Brain Activation in Response to a Clinical Vestibular Test Correlates with Balance

i. Abstract

The current study characterizes brain fMRI activation in response to two modes of vestibular stimulation: skull tap and auditory tone burst. The auditory tone burst has been used in previous studies to elicit either a vestibulo-spinal reflex (saccular-mediated colic Vestibular Evoked Myogenic Potentials (cVEMP)), or an ocular muscle response (utricle-mediated ocular VEMP (oVEMP)). Research suggests that the skull tap elicits both saccular and utricle-mediated VEMPs, while being faster and less irritating for subjects than the high decibel tones required to elicit VEMPs. However, it is not clear whether the skull tap and auditory tone burst elicit the same pattern of brain activity. Previous imaging studies have documented activity in the anterior and posterior insula, superior temporal gyrus, inferior parietal lobule, inferior frontal gyrus, and the anterior cingulate cortex in response to different modes of vestibular stimulation. Here we hypothesized that pneumatically powered skull taps would elicit a similar pattern of brain activity as shown in previous studies. Our results provide the first evidence that using pneumatically powered skull taps can elicit vestibular activity inside the MRI scanner. A conjunction analysis revealed that skull taps elicit overlapping activation with auditory tone bursts in the canonical vestibular cortical regions. Further, our postural control assessments revealed that greater amplitude of brain activation in response to vestibular stimulation was associated with better balance control for both techniques. Additionally, we found that skull taps elicit more robust vestibular activity compared to auditory tone bursts, with less reported

aversive effects, highlighting the utility of this approach for future clinical and basic science research. [1]

ii. Introduction

Recent studies have shown that a vestibular brain network is engaged when participants perform various motor and cognitive processes including sense of balance, postural control, navigation, spatial learning and memory, and autonomic responses to stress (Bigelow & Agrawal, 2015; Thomas Brandt et al., 2005; Diener & Dichgans, 1988; Guidetti, 2013; Hitier, Besnard, & Smith, 2014; Israel, Bronstein, Kanayama, Faldon, & Gresty, 1996; Smith, Darlington, & Zheng, 2010). The imaging of human vestibular cortex has opened a new window to our understanding of the underlying neural mechanisms of these motor and cognitive processes (Fasold et al., 2002; Elie Lobel et al., 1998; Stephan et al., 2005). Neuroimaging meta-analyses have indicated the superior temporal gyrus (STG), retroinsular cortex, and inferior parietal lobule (IPL) as the common cortical regions involved in the vestibular network (C Lopez et al., 2012; zu Eulenburg et al., 2012). Previous neuroimaging studies have used different methods to activate the vestibular cortex in the scanner, including caloric vestibular stimulation (CVS) (Bottini et al., 2001; M. Dieterich, 2003; Emri et al., 2003; Indovina, 2005; Marcelli et al., 2009; M. Suzuki et al., 2001), galvanic vestibular stimulation (GVS) (S Bense, Stephan, Yousry, Brandt, & Dieterich, 2001; Simon B. Eickhoff et al., 2006; Elie Lobel et al., 1998; Stephan et al., 2005), and auditory clicks/short tone bursts (Janzen et al., 2008a; Miyamoto et al., 2007; Schlindwein et al., 2008). In a recent meta-analysis, Lopez et al. (2012) showed that the regions that are commonly activated across these modes of stimulation include insular cortex, parietal operculum, and retroinsular cortex (C Lopez et al., 2012).

Administration of CVS (i.e. irrigation of water into the ear canal) inside an MRI scanner is somewhat challenging, since the vestibular sensation takes up to 15 minutes to disappear (Proctor, 1988), and controlling for susceptibility artifacts between air and water is difficult (E Lobel, Bihan, Berthoz, & Cnrs, 1996). Additionally, the evoked vestibular cortical activity by caloric stimulation varies based on the side and temperature of the irrigation (i.e. warm water

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[1] This work has been published as Noohi et al. 2017, Functional Brain Activation in Response to a Clinical Vestibular Test Correlates with Balance, in Frontiers in Systems Neuroscience (Noohi et al., 2017).

induces bilateral brain activity, whereas cool water induces a contralateral response (Karim et al., 2013), and it shows high inter-individual variability (Fife et al., 2000). Moreover, caloric stimulation is rather unpleasant for subjects (Capps, Preciado, Paparella, & Hoppe, 1973).

Galvanic vestibular stimulation is another common method in which electric current is used to stimulate the vestibular nerve via electrodes placed over the mastoid bones (Elie Lobel et al., 1998; Wuehr et al., 2016; Yamamoto et al., 2005). GVS activates the entire vestibular nerve and thus activates pathways associated with both the semicircular canals and the otoliths, whereas CVS mainly activates the horizontal semicircular canals (Day et al., 2011; M. Dieterich, 2003; Stephan et al., 2005). Although GVS and CVS have been recently implemented as standard methods for imaging vestibular function, neither allows for evaluation of specifically otolithic vestibular processing (i.e. independent from semicircular canals).

Here, we evaluated a novel bone conduction device to elicit vestibular activation inside the MRI scanner (manufactured by Engineering Acoustics, Incorporated) (Iwasaki et al., 2008; Wackym et al., 2012). Curthoys et al. provided a review of animal and human studies in which they showed that the vestibular evoked myogenic potential (VEMP) characteristics in response to bone conduction stimulation reflects the otolith responses (utricles and saccules) independently of canal function (Curthoys et al., 2009). Brantberg et al. further supported these findings, showing that lateral bone conducted-vibrations induce VEMP responses through vibration and translation mechanisms (Krister Brantberg et al., 2009).

Wackym et al. (2102) used bone conduction stimulation to elicit VEMPs, and then compared the response characteristics to those elicited by high decibel auditory tone bursts (Wackym et al., 2012). They showed the effectiveness of this novel device in eliciting typical vestibular responses. In the present study, we investigated whether the bone conduction method activates brain regions characterized in previous studies as playing a role in vestibular processing, and whether this activity correlates with vestibularly mediated balance control.

As Wackym et al. (2012) pointed out, the bone conduction method is more comfortable for subjects and results in more reliable oVEMP responses compared to auditory tone bursts

(Wackym et al., 2012). In addition to subjects' comfort, this novel approach can provide new insights into vestibular utricular function (Curthoys et al., 2009, Manzari et al. 2010), since the previously used methods in neuroimaging studies have mainly indicated otolith responses with short auditory tone bursts (Schlindwein et al., 2008), semicircular canal responses with CVS (Fasold et al., 2002; Gentine, Eichhorn, Kopp, & Conraux, 1990; Elie Lobel et al., 1998), or combined otolith & canal responses with GVS (Angelaki & Perachio, 1993; J. M. Goldberg, Smith, & Fernandez, 1984; Stephan et al., 2005). Similar to GVS studies, a potential drawback of using the bone conduction method is tactile perception and potential co-activation of somatosensory regions (Simon B. Eickhoff et al., 2006).

To replicate the results of Wackym et al. (2012), we used a similar design to compare vestibular activation elicited by skull taps (bone conduction) and auditory tone bursts both outside and inside the MRI scanner, hypothesizing that both stimulation methods would result in similar brain activation patterns. We also hypothesized that acoustic effects of the auditory tone burst stimulation could be differentiated from the vestibular components as previously done by Schlindwein and colleagues (Schlindwein et al., 2008).

To validate the vestibular evoked activation inside the scanner, we also recorded vestibular evoked myogenic potentials (VEMPs) elicited by the skull tap device and auditory tone bursts outside the scanner. The ocular vestibular evoked myogenic potential (oVEMP) has been measured in previous studies as an index of vestibular function (Akin et al., 2003). Therefore, we considered the brain activity as reflecting vestibular system activation relative to typical oVEMP characteristics (Nguyen, Welgampola, & Carey, 2010; Welgampola & Colebatch, 2005) in response to the same stimulation outside of the scanner.

Further, we assessed individual differences in balance control ability to examine whether greater activation of vestibular network measured in the scanner is associated with better postural control measured outside of the scanner. Goble et al. (2011) showed that brain activity in response to proprioceptive stimulation of ankle joint muscles inside the scanner is correlated with individual differences in balance performance (Goble et al., 2011). Similarly, here we hypothesized that the magnitude of vestibular brain activity is associated with the ability to maintain balance, and that this association would be similar for both modes of stimulation. Using behavioral assessments we were able to fortify our interpretation of vestibular cortex function and to examine whether brain activation elicited by pneumatic skull tap and auditory tone burst associates differentially with behavioral metrics. Inline with our hypothesis, we found that the performance in balance control tasks (with degraded proprioceptive inputs and absence of vision) correlates with vestibular activity in right and left vestibular nuclei.

This study provides the first evidence of using an MR compatible pneumatic skull tap device to elicit vestibular brain activation inside the scanner. The results of this study indicate the extent to which pneumatic skull tap could be implemented in clinical and basic science research as a reliable method of vestibular otolith stimulation inside the scanner. Moreover, this study shows that vestibular brain activity elicited by pneumatic skull tap can be used as an index of individual differences in balance control and susceptibility to fall.

iii. Methods

Participants

We recruited 16 healthy, right-handed young adults (mean age 20.87 ± 2.55, 7 females) from the University of Michigan student population. The study was approved by the University of Michigan Medical Institutional Review Board; all participants signed a consent form prior to participation. Exclusion criteria comprised history of neurological disorder, vestibular or auditory impairments, or any other major health issues. All participants were right hand dominant. Two participants were excluded from analyses because of incomplete MRI scan coverage of the brain. From the remaining 14 participants who were included in the fMRI analysis, only 10 were included in the balance analyses due to technical errors in the force plate data collection.

Balance Assessments

To assess whether individual differences in balance control are associated with vestibular brain activity, subjects performed 4 different tasks (Romberg, tandem, normal, and single leg stance) in 4 different levels of difficulty (eyes closed/open, yaw/pitch/no head movement, arms crossed/free, & on firm/compliant surface), leading to a total of 22 different tasks. These tests were conducted on a force platform (AMTI Inc, USA) and subjects' movements were captured with a Vicon motion capture system (Nexus, Vicon Inc). We selected two balance tasks for the brain-behavior correlation analyses: Romberg stance (feet together) with eyes closed and sinusoidal head movements (roughly ±20°, 0.6 Hz); and Tandem Romberg stance (heel to toe) on a compliant surface (high density viscoelastic foam; length=45cm, width=45cm, thickness=18cm; Natus Inc.), with eyes open and sinusoidal head movements (roughly ±20°, 0.6 Hz). The tasks were performed once with yaw and once with pitch head movements. We instructed subjects to match their head movements to the beat of a metronome (0.6 Hz) to keep the frequency of movement consistent throughout the trials and across subjects. Subjects maintained a comfortable amplitude with head turns of approximately 20 degrees, however this amplitude was not strictly controlled. The order of tasks was counterbalanced across subjects.

Subjects were instructed to maintain their balance for the whole duration of trial (i.e. 30 seconds) for each task. The experimenter demonstrated the correct performance prior to each trial; however, to capture the individuals' true postural ability and control for the learning effects, they were not given any practice trials. So subjects performed each task for one trial (i.e. 30 seconds), as Whitney and colleagues showed that single trial (as opposed to average of multiple trials) is sufficient for balance assessment (Whitney et al., 2011). The total amount of movement was calculated as the area of an ellipse fit to the 95th percentile confidence interval of center of pressure motion in the anterior-posterior and medial-lateral directions (Sienko, Balkwill, Oddsson, & Wall, 2008). Smaller ellipse areas reflect smaller body sway and better performance. Ellipse areas and balance maintenance times were tested for correlation with vestibular brain activity by entering scores as covariates in a single sample t-test analysis of vestibular activity, using spm8 software (Wellcome Department of Cognitive Neurology, London, UK. (Karl. J. Friston et al., 1995)).

Ocular Vestibular Evoked Myogenic Potentials (oVEMP)

Prior to the MRI scan, we measured vestibular evoked myogenic potentials in ocular muscles in response to both auditory tone bursts and head taps applied outside of the MRI scanner (cf. (Iwasaki et al., 2008; Todd, Rosengren, Aw, & Colebatch, 2007)). First, we performed routine skin preparation using alcohol wipes and Nuprep skin preparation gel. Next, EMG electrodes were placed symmetrically on the skin over the medial inferior oblique muscles, slightly lateral to the pupil directly beneath both eyes (Chihara et al., 2009). We collected ocular EMG data at 1KHz using a Delsys 8-channel Bagnoli EMG system. Subjects were in a supine position, maintaining an approximately 30º upward gaze during the stimulation trials by staring at a fixation point placed on the ceiling. They were instructed to avoid blinking for the duration of each stimulation trial (tap stimulation trials lasted 29 seconds, while tone stimulation trials lasted 20 seconds; first 5 seconds in both trials were baseline when no stimulation applied), and to relax their eyes in between trials. Subjects received auditory tone bursts (~3Hz) via headphones (MR compatible SereneSound auditory system, Resonance technology Inc.) and skull taps (1Hz) via the pneumatic tactile pulse system (MR compatible Pneumatic Tactile Pulse System (PnTPS), Engineering Acoustics Inc.; see supplementary materials for the picture) placed over the lateral cheekbones. The lateral direction of the force of the skull tap served to maximize the shear along the utricular macula, and therefore optimize the oVEMP response that is attributed to utricular-ocular reflex pathway (I S Curthoys, Vulovic, & Manzari, 2012). A self-adhering elastic bandage wrap (Coban, 3M Inc) was used over the subject's head to secure the stimulation devices. We collected five trials of each stimulation type for each subject and visually inspected the data after each trial and adjusted the tapper/headphones as necessary.

Each subject received auditory tone burst stimulation at 130 dB SPL on the left side (5 trials) and right side (5 trials) separately. A pneumatically powered skull tapper was used to deliver low force taps to the left (5 trials) and right (5 trials) cheekbones (Engineering Acoustics Inc). We applied unilateral stimulation since Cornell et al. (2009) reported that bilateral bone conduction vibration activates deeper muscles and eliminates the horizontal eye response (Cornell, Burgess, MacDougall, & Curthoys, 2009). The skull tapper uses compressed air (50 – 55 psi) to power a small piston that delivers an average force of 19.6 N for each tap to the cheekbones. Each tapping trial consisted of 24 taps, delivered at 1 Hz. Each auditory tone burst trial consisted of 45 tone bursts applied at 3.003 Hz. The order of stimulation modes was counterbalanced across subjects. The resting period between trials varied based on the subject's preference, ranging between 10-15 seconds. Stimulation routines were programmed using LabView (National Instruments Inc.).

Functional Magnetic Resonance Imaging (fMRI)

fMRI data were acquired using a 3.0 T MRI scanner (General Electric Medical Systems, DISCOVERY MR750). Using a self-adhering elastic bandage wrap, the experimenter fixed the position of the pneumatic tappers and auditory headphones before the subject entered the scanner. To keep consistent placement of devices, we conducted the oVEMP measurements prior to the scan and did not change the device arrangement (i.e. placement of tappers on the cheekbones) as we proceeded with the scan. Head movement was minimized via a Velcro strap over the forehead and padding placed around the sides of the head. Subjects' physiological responses were collected via pulse oximeter placed on the index finger, and a respirometer wrapped around the subjects' abdomen, and later regressed out of the blood oxygenation level dependent (BOLD) signal.

The scan protocol comprised five sections: a high resolution T1 scan, a resting state functional connectivity scan, vestibular stimulation runs (with auditory and tapper trials counterbalanced across subjects), another resting state functional connectivity scan, and a diffusion tensor scan (DTI). The resting state and DTI scan results are not presented here. Before each section began, the MRI technician notified the subject about the upcoming condition. This way we minimized the potential artifacts of surprise (e.g. involuntary responses to the start of the stimulation) and kept the subject alert.

The structural imaging was conducted using a T1-weighted interleaved echo-planar imaging (EPI) sequence (TR = 12.2 s, TE =5.1 ms, FA= 15°, matrix size= 256 x256, FOV= 260 x260 mm, slice thickness = 1 mm) covering the whole brain and the cerebellum. The functional images were acquired with gradient-echo spiral-pulse sequence (FOV=220 mm, TR=2 s, TE= 30 ms, number of slices=43, voxel size =3.4375x3.4375mm).

The skull tap and auditory tone burst stimulations were applied using the same protocol as was used for oVEMP testing outside of the scanner, with two exceptions: 1) following the auditory tone burst stimulation (130 dB SPL) on the left and right sides separately, there was an additional condition in which subjects received 90 dB SPL auditory tone burst stimulation on both sides simultaneously. By including the 90 dB SPL stimulation we were able to compare and dissociate the neural correlates of acoustic and vestibular processing (Schlindwein et al., 2008); 2) Unlike in the oVEMP testing, there was no subject-determined rest period between stimulation trials. Rather, to identify stimulation-evoked changes in the BOLD signal we implemented a block design in which each functional run comprised five alternating periods of rest (20 seconds) and stimulation (24 seconds). Each run was four minutes, and subjects were asked to keep their eyes closed during each run. The sound of the piston delivering taps to the cheekbones was not detectable over the noise of the scanner, and there was no head motion induced by the taps. All subjects reported feeling a tactile perception of the pneumatic skull taps over the skin.

iv. Data Analysis

Balance analysis

Force plate data were collected at 100 Hz and center of pressure (COP) values were measured analyzed using Vicon software (Nexus, Vicon Inc). The COP signals were low pass filtered with a 2nd order recursive Butterworth filter with a cutoff of 10 Hz (Lee, Kim, Chen, & Sienko, 2012) using Matlab. Subsequently, 95% confidence interval ellipses were fit to the 2 dimensional medial-lateral and anterior-posterior center of pressure trajectories across each 30s balance task. The ellipse area measure was selected due to previous reports showing the reliability of this measure for predicting susceptibility to fall (Bird et al., 2013; Melzer et al., 2004).

In case of a step out, the trial was stopped prematurely, and the balance maintenance time was used as a second representative of subjects' balance ability in addition to the measures of body sway.

oVEMP analysis

We identified the oVEMP EMG response according to the typical waveform described in previous studies (Nguyen et al., 2010; Welgampola & Colebatch, 2005). We parsed the data into responses for each individual tap (from tap-to-tap), and the oVEMPs were averaged on the contralateral stimulation sides. We identified the amplitude and timing of the first peak, followed by the first trough, followed by the second peak of the VEMPs. We used a 2nd order butterworth notch filter to remove 60 Hz noise (59-61 Hz) and the detrend function in Matlab to remove the mean value from the vector. We did all of the above for the auditory tone burst induced oVEMPs as well, but added some additional notch filters for harmonics of electrical noise (harmonics of 60 Hz): 60 Hz, 120 Hz, 240 Hz, 360Hz.

FMRI analyses

The fMRI preprocessing analyses were conducted using spm8 software (Welcome Department of Cognitive Neurology, London, UK (Karl. J. Friston et al., 1995)). The first 10 volumes in each run were discarded to ensure steady state of the MR signal at the beginning of the runs. Functional data were corrected for the physiological responses (i.e. cardiac and respiration data) using the RETROICOR algorithm (Glover, Li, & Ress, 2000). Since the skull vibration induced by the pneumatic taps could be a potential source of motion artifacts during EPI acquisition, the raw data were carefully examined for excessive motion. Head motion correction was implemented; the cut off for trial exclusion was >3mm translation or >5° rotation. The functional images were realigned to the first functional image and the anatomical image. Next, both functional and anatomical images were normalized to the Montreal Neurological Institute (MNI) template (Karl. J. Friston et al., 1995). We normalized the cerebellum to the Spatially Unbiased Atlas Template (SUIT, Diedrichsen and Zotow, 2015; Diedrichsen, 2006; Diedrichsen et al., 2011, 2009). Caret software (Van Essen et al., 2001) was used for hand corrected isolation of the cerebellum and brainstem from the brain. These isolated cerebellar images were subsequently analyzed and are presented separately from the whole brain results. The normalized functional images were spatially smoothed with a Gaussian kernel function (8,8,8 mm). The smoothed functional images were used to design the first level analysis, in which we compared brain activity in each condition to rest.

Next, we used the contrast images (created at the single subject level) for whole group analyses. We applied one-sample t-tests to measure brain activation and deactivation in stimulation trials compared to rest across all subjects. Further, we applied paired t-tests to compare brain activity between different stimulation conditions across all subjects. We applied a threshold of $P \leq 0.001$ (unc.) with a minimum cluster size of 10 voxels (voxel size= 2x2x2 mm) for all contrasts. To find the common brain regions activated by both auditory tone bursts and pneumatic taps, we conducted a conjunction analysis across these two conditions. The threshold for conjunction analyses was determined based on $p^{1/n}$, where p is the individual threshold and n is the number of contrasts in the conjunction (K J Friston, Holmes, Price, Büchel, & Worsley, 1999).

We assessed the correlation between brain activity and balance control using the balance performance parameters (i.e. area of the ellipse & balance maintenance time) as covariates in our group analyses, with a threshold of $p<.001$ (unc.). The correlation analyses were limited to the identified brain regions in the previous step.

We used the MNI atlas (Karl. J. Friston et al., 1995) to localize the significant coordinates resulting from our analyses. The cerebellar coordinates were localized according to the SUIT atlas (Jörn Diedrichsen et al., 2009) using MRIcron. We also applied Automated Anatomical Labeling (AAL, Tzourio-Mazoyer et al., 2002) with a gray matter inclusive mask to filter out activity in the white matter. A small volume correction was also applied to examine activity in regions previously identified as the vestibular nuclei (x = -16/16, y = -36, z = -32) (Kirsch et al., 2015). Deep cerebellar nuclei were identified using the SUIT probabilistic atlas for deep cerebellar nuclei (J Diedrichsen et al., 2011).

Finally, to provide an estimate of the effect size, we used the SPM MarsBaR toolbox to extract the beta values for each significant cluster. We did not report the percent signal change since previous studies showed that MR acquisition parameters (e.g. field strength, scanner sequence, echo time, etc.) could influence this metric (Chen, Taylor, & Cox, 2016; Uludağ, Müller-Bierl, & Uğurbil, 2009). Thus, we reported the beta values for each significant cluster. First, we defined the region of interest (ROI) as a 5mm sphere around the coordinates at the peak value. Next, we reported the mean beta values averaged across the voxels within each ROI (Hein, Silani, Preuschoff, Batson, & Singer, 2010; Kong et al., 2007; Oechslin, Meyer, & Jäncke, 2010).

v. Results

Balance performance results

As shown in table 2.1, all subjects were able to maintain their balance for 30 seconds when performing the Romberg stance with eyes closed and making yaw or pitch head movements. The tandem stance on a compliant surface with eyes open and yaw/pitch head movements was found to be more difficult, as the average balance time in this task did not reach the 30 s cap. In addition, the average amount of body sway was greater in tandem conditions compared to Romberg (see table 1 for details). An example of body sway trajectories (captured in an ellipse) is presented in figure 2.1.

Table 2. 1 List of balance tasks that subjects performed on the force platform.

Mean and standard deviation (in parenthesis) of balance maintenance times and ellipse areas are shown for each task.

Balance Tasks	**Time** $_{Seconds}$	**Ellipse Area** $_{cm^2}$
Romberg stance, eyes closed, firm surface, yaw head movement	30 (0)	8.36 (4.14)
Romberg stance, eyes closed, firm surface, pitch head movement	30 (0)	12.84 (9.39)
Tandem stance, eyes open, compliant surface, yaw head movements	20.05 (12.0)	39.60 (32.53)
Tandem stance, eyes open, compliant surface, pitch head movements	28.11 (3.95)	29.23 (20.25)

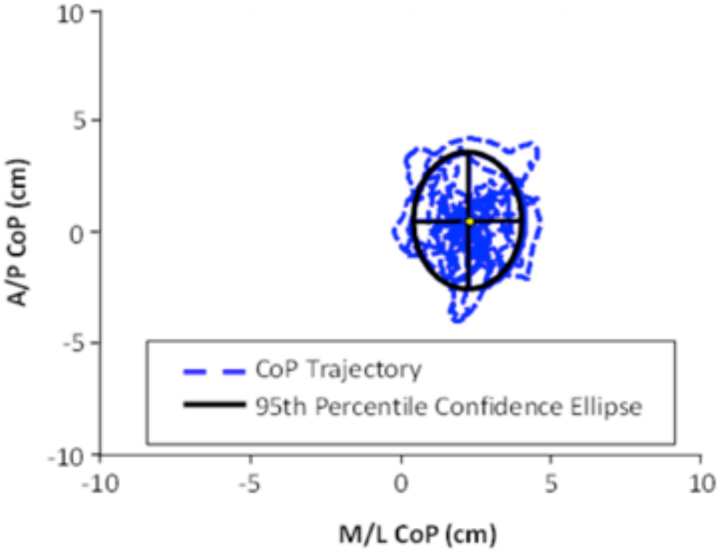

Figure 2. 1 An example of ellipse area.

This example shows the ellipse area calculated based on the center of pressure (CoP) motion in the anterior-posterior (A/P) and medial-lateral (M/L) trajectories in Romberg stance on firm stance, with eyes closed and yaw head movement.

To assess the correlation between balance and vestibularly mediated brain activity, we used the ellipse area measurements of "Romberg stance on firm surface, with eyes closed and yaw/pitch head movements", because the time factor in performing this task was equal for all subjects. Only 10 subjects were included in this analysis due to substandard quality of force plate data for the remaining four subjects. In addition, we used the time measurements of "tandem stance on a compliant surface with eyes open and yaw/pitch head movements", because not all subjects were able to maintain their balance for 30 seconds when performing this task.

oVEMP results

As shown in table 2.2, the overall oVEMP characteristics of our data fit the typical oVEMP response (Iwasaki et al., 2008; Todd, 2010; Wackym et al., 2012), which validates the observed vestibular-evoked activation inside the scanner. There was no significant effect of side/mode of the stimulation on the elicited oVEMP characteristics (Figure 2.2).

Table 2. 2 Latency and amplitude of oVEMP response induced by tap and tone.

Table shows the mean and standard error (in parenthesis) of oVEMPs. The left and right refer to the side of the stimulation, and oVEMPS are the averaged response on the contralateral side (i.e. left tap column represents the right infraorbital eye muscle's response to left side tap stimulation). The latencies of tap-induced responses are corrected for hardware delay. The latencies are presented in milliseconds and amplitudes are in millivolts. Peak to peak amplitude1= change between the amplitude at first peak to the first trough; peak to peak amplitude2= change between the amplitude at first trough to the second peak.

oVEMP characteristics	**Tap-induced response**		**Tone-induced response**	
	Left tap	***Right tap***	***Left tone***	***Right tone***
Peak 1 latency $_{ms}$	13.43(2.04)	14.95(2.01)	9.82(2.36)	12.1(2.65)
Trough 1 latency $_{ms}$	17.63(2.10)	19.83(2.14)	15.19(2.76)	16.77(2.79)
Peak 2 latency $_{ms}$	23.34(2.06)	25.01(2.34)	24.89(3.40)	23.3(2.87)
Peak to Peak Amplitude 1$_{mv}$	3.91 (0.55)	4.36 (1.08)	3.27 (0.72)	2.65(0.59)
Peak to Peak Amplitude 2$_{mv}$	5.39 (1.05)	5.59 (1.35)	3.26 (0.99)	2.86(0.41)

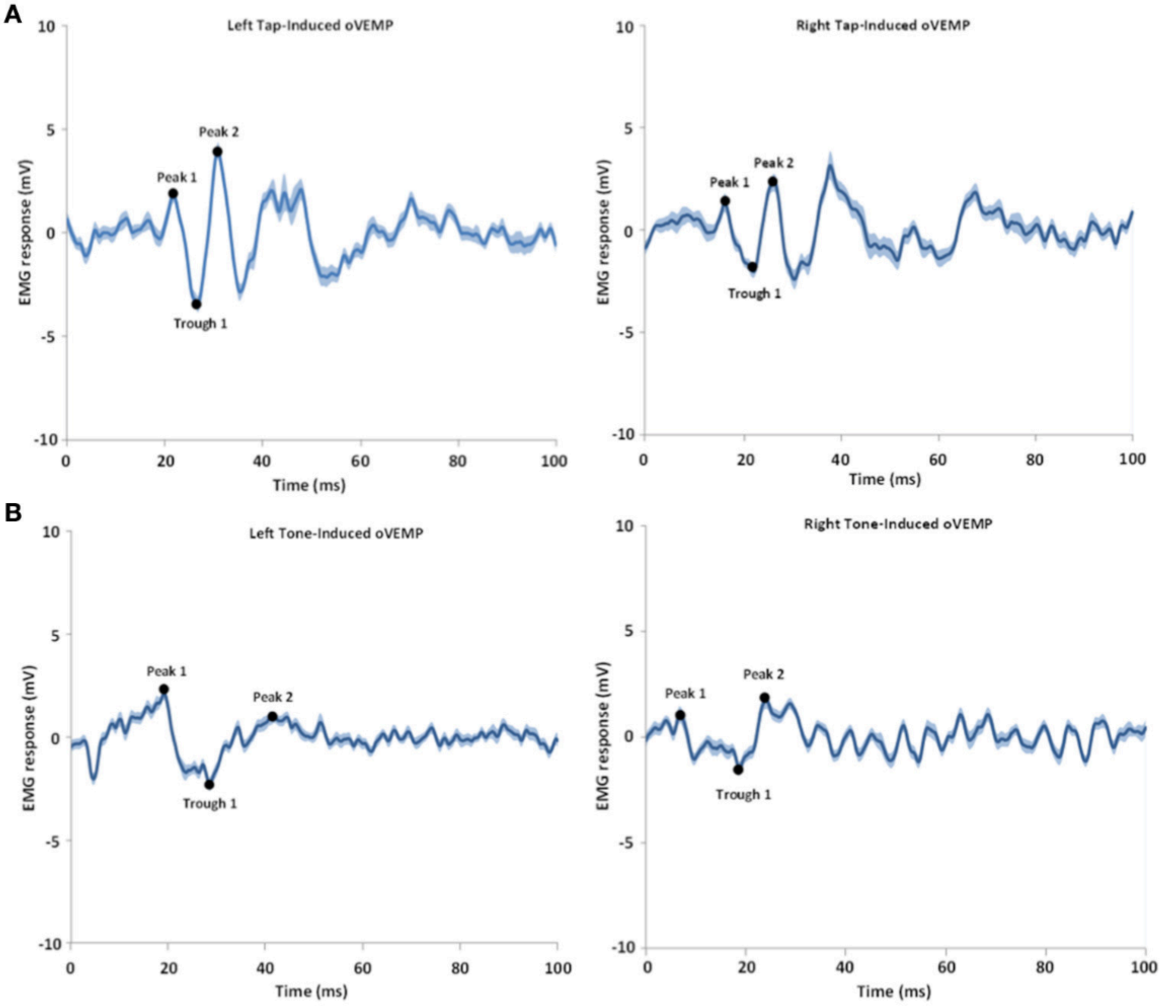

Figure 2. 2 An example of tap-induced (A) and tone-induced (B) oVEMPs for one subject.

The left and right refer to the left and right sides of stimulation; the oVEMPs represent the averaged response on the contralateral side of stimulus delivery. The shaded areas represent the standard error of the mean (SEM). Time 0 indicates the stimulus onset time.

FMRI results

Tap Stimulation versus rest

The results for tap-induced alterations in brain function are presented in table 2.3.

Left side tap stimulation increased the activation of right superior temporal gyrus (STG) and bilateral posterior insula (figure 2.3.a), both portions of the canonical vestibular cortex (zu Eulenburg et al., 2012). Multiple regions exhibited deactivation in response to the left tap, including bilateral cerebellum lobule VI, left cerebellum lobule VIIIA, bilateral brainstem (pons), bilateral precuneus, bilateral fusiform gyrus, and bilateral frontal regions including superior, middle and inferior frontal gyri (figure 2.3.a).

Right side tap stimulation activated the bilateral posterior insula, left postcentral gyrus, and right STG (figure 2.3.b). Similar to the left tap deactivation pattern, the right tap deactivated multiple regions including left cerebellum lobule VI and Crus I, left vestibular nucleus, right cerebellum lobule VIIIA, left temporal lobe sub gyral, left cingulate gyrus, right paracentral lobule, and the right thalamus (figure 2.3.b).

Table 2. 3 Results of activation and deactivation for left and right tap versus rest.

*significant at FWE. P<.05. Mean beta values (β) are represented with %95 confidence interval (CI).

t-contrast	Brain region	MNI coordinates x,y,z	Cluster size	t-value	P-value	β (CI)
Left tap versus rest						
activation						
	Right Superior Temporal Gyrus	58, -30, 14	1118	5.79	0.0002*	.65(±.23)
	Left Posterior Insula	-50, -32, 20	222	5.56	0.0006*	.37(±.14)
	Right Posterior Insula	38, -12, 16	12	3.61	0.0008	.14(±.07)
deactivation						
	Left Fusiform Gyrus	-30, -40, -18	189	4.55	0.0004	-.15(±.05)
	Right Cerebellar Lobule VI	30, -44, -35	152	5.21	0.0001	-.09(±.04)
	Left Cerebellar Lobule VI	-32, -46, -31	37	4.40	0.0001	-.12(±.05)
	Left Precuneus	-22, -84, 44	125	4.56	0.0002	-.20(±.07)
	Right Precuneus	8, -52, 60	93	3.57	0.0004	-.15(±.07)
	Left Middle Frontal Gyrus	-36, 42, 34	39	3.71	0.0004	-.17(±.08)
	Right Inferior Temporal Gyrus	56, -8, -14	21	3.75	0.0004	-.17(±.09)
	Right Inferior Frontal Gyrus	28, 30, -4	21	3.08	0.0008	-.09(±.04)
	Right Fusiform Gyrus	34, -36, -16	16	3.43	0.0008	-.06(±.03)
	Right Middle Frontal Gyrus	22, -12, 58	12	3.12	0.0008	-.08(±.04)
	Left Superior Frontal Gyrus	-20, 52, -4	10	3.43	0.0008	-.11(±.06)
	Right Brainstem, Pons	6, -26, -15	189	4.75	0.0001	-.08(±.05)
	Left Brainstem, Pons	-6, -28, -9	189	6.15	0.0001	-.13(±.07)
	Left Cerebellar Lobule VIIIA	-2, -60, -31	29	4.29	0.0001	-.05(.04)
Right tap versus rest						
activation						
	Left Posterior Insula	-52, -34, 18	682	5.91	0.0002	.41(±.13)
	Left Postcentral Gyrus	-54, -12, 14	682	4.38	0.0002	.25(±.12)
	Right Superior Temporal Gyrus	60, -32, 16	296	5.13	0.0004	.42(±.16)
	Right Posterior Insula	50, -36, 20	296	4.57	0.0002	.36(±.17)
deactivation						
	Left Cerebellar Crus I	-36, -54, -35	640	7.63	0.0001*	-.09(±.03)
	Left Cerebellar Lobule VI	-10, -64, -27	144	5.11	0.0001	-.06(±.04)
	Right Cerebellar Lobule VIIIA	4, -66, -33	144	3.99	0.0010	-.03(±.03)

Left Temporal Lobe, Sub-Gyral	-42, -46, -6	96	6.21	0.0002	-.09(±.02)
Left Cingulate Gyrus	-16, -2, 48	50	5.28	0.0004	-.08(±.03)
Right Thalamus	4, -6, 2	30	5.63	0.0006	-.10(±.04)
Right Paracentral Lobule	16, -40, 50	17	4.93	0.0004	-.07(±.03)
Left Vestibular Nucleus	-22, -44, -31	17	4.89	0.0001*	-.04(±.04)

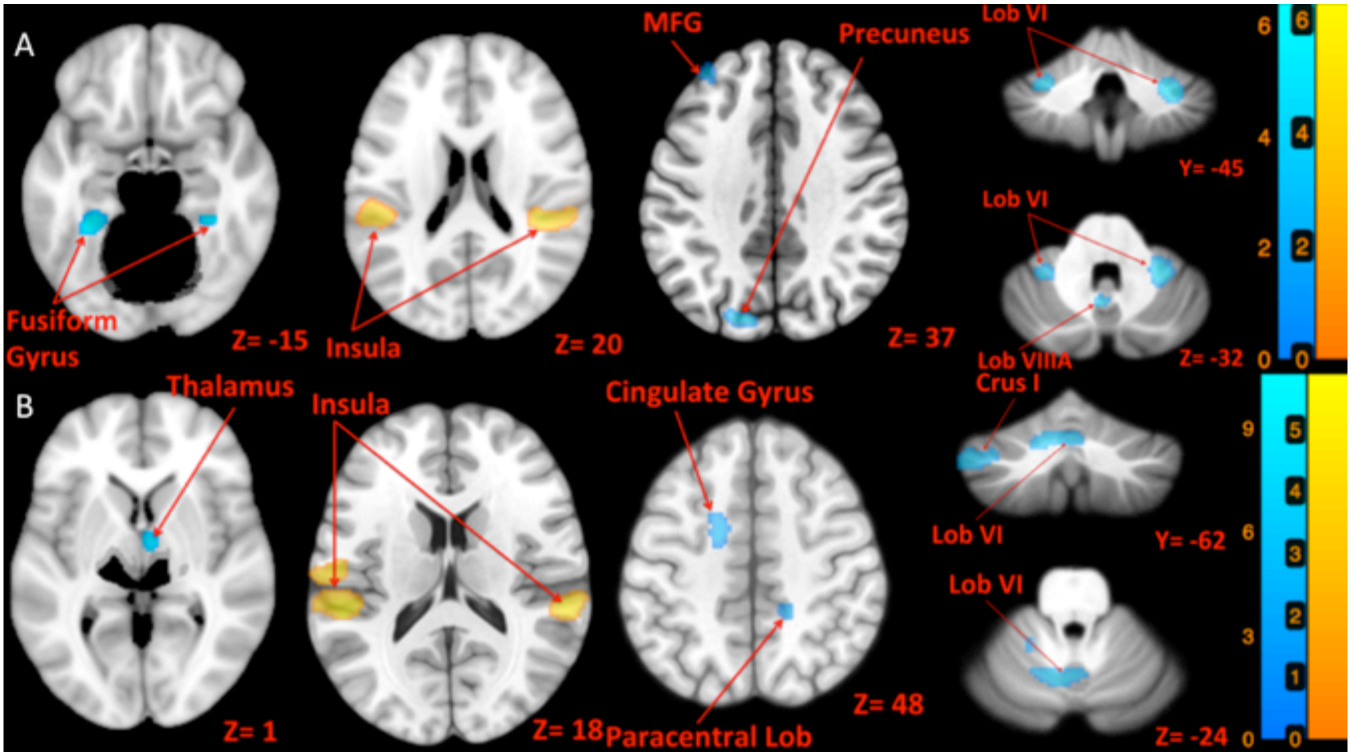

Figure 2. 3 Map of brain activation and deactivation for left (a: Left tap > rest (yellow); Left tap < rest (blue)) and right (b: Right tap > rest (yellow); Right tap < rest (blue)) taps.

The corresponding t-value is presented next to each figure. Left and right sides refer to the left and right sides of the brain, respectively. Note: the cerebellum is depicted separately due to extraction and normalization to the SUIT template. N.S= Non Significant. MFG=Middle Frontal Gyrus.

Auditory Tone Burst Stimulation versus rest

The results for tone-induced alterations in brain function are presented in table 2.4.

Left side tone stimulation (130 dB SPL) mainly activated the right STG. Additionally, it resulted in activation of ipsilateral regions including the left middle frontal and precentral gyrus, left superior and middle temporal gyrus, and left caudate (figure 2.4.a). Left tone stimulation did not result in significant deactivation.

Right side tone stimulation (130 dB SPL) did not result in a significant increase in brain activity compared to rest. However, it deactivated multiple regions including right cuneus, right posterior cingulate, right precuneus, and left insula (figure 2.4.b).

Both sides tone stimulation (90 dB SPL) resulted in activation of multiple regions predominantly in the left hemisphere including the middle temporal gyrus, middle and superior frontal gyri, left inferior parietal lobule, and bilateral activation of the insula (figure 2.4.c). There was a unilateral pattern of deactivation including left parahippocampal gyrus and left temporal lobe sub-gyral (figure 2.4.c).

Table 2. 4 Results of activation and deactivation for left, right, and both sides tone stimulation versus rest.

*significant at FWE. P<.05. Mean beta values (β) are represented with %95 confidence interval (CI).

t-contrast	Brain region	MNI coordinates x,y,z	Cluster size	t-value	P-value	β (CI)
Left tone (130 dB) versus rest						
activation						
	Right Superior Temporal Gyrus	58, -38, 12	614	5.19	0.0002	.51(±.20)
	Left Middle Frontal Gyrus	-44, 26, 16	198	6.76	0.0002	.11(±.03)
	Left Middle Frontal Gyrus	-36, 12, 30	170	4.82	0.0002	.07(±.03)
	Left Superior Temporal Gyrus	-44, -28, 8	152	4.45	0.0006	.25(±.11)
	Left Middle Temporal Gyrus	-68, -40, -8	127	5.72	0.0006	.16(±.05)
	Left Superior Temporal Gyrus	-64, -24, 8	44	4.06	0.0008	.56(±.27)
	Left Precentral Gyrus	-54, -4, 54	17	4.50	0.0008	.21(±.11)
	Left Caudate	-18, 16, 12	13	5.54	0.0002	.06(±.02)
deactivation	No suprathreshold voxels were found					
Right tone (130 dB) versus rest						
activation	No suprathreshold voxels were found					
deactivation						
	Right Cuneus	4, -68, 30	82	5.89	0.0002	-.13(±.04)
	Right Posterior Cingulate	4, -48, 18	40	8.38	0.0002	-.07(±.01)
	Left Insula	-38, -2, 20	19	4.19	0.0004	-.05(±.02)
	Right Precuneus	16, -48, 42	18	4.18	0.0004	-.05(±.02)
Both sides tone (90 dB) versus rest						
activation						
	Left Middle Temporal Gyrus	-70, -14, -18	315	7.67	0.0002*	.14(±.05)
	Left Middle Frontal Gyrus	-30, 24, 58	236	7.14	0.0002*	.15(±.04)
	Left Inferior Parietal Lobule	-52, -52, 54	163	6.03	0.0002	.20(±.10)
	Left Superior Frontal Gyrus	-4, 28, 60	51	6.24	0.0002	.18(±.06)
	Left Insula	-36, 8, 20	17	5.83	0.0004	.04(±.01)
	Left Superior Frontal Gyrus	-14, 46, 30	15	4.74	0.0004	.10(±.04)
	Right insula	36, 10, 20	27	4.47	0.0001	.09(±.04)
deactivation						

Left Parahippocampal Gyrus	-40, -44, 2	17	4.47	0.0004	-.05(±.03)
Left Temporal Lobe, Sub-Gyral	-42, -40, -6	17	3.53	0.0006	-.04(±.02)

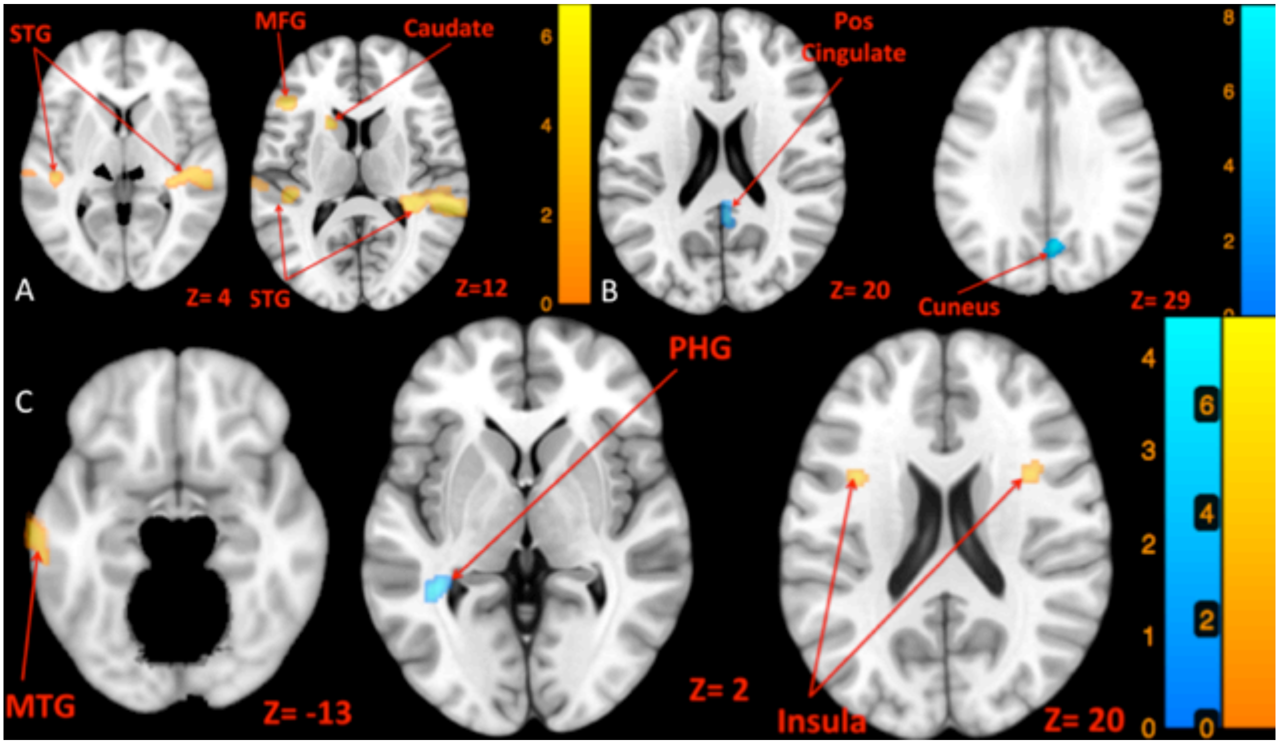

Figure 2. 4 Map of brain activation and deactivation for left (a: Left tone > rest (yellow); Left tone < rest (N.S)), right (b: Right tone > rest (N.S); Right tone < rest (blue)), and both sides (c: Both side tone > rest (yellow); Both side tone < rest (blue)) tone stimulation.

The corresponding t-value is presented next to each figure. Left and right sides refer to the left and right sides of the brain, respectively. N.S= Non Significant. STG=Superior Temporal Gyrus, MFG=Middle Frontal Gyrus, MTG=Middle Temporal Gyrus, PHG=Parahippocampal Gyrus.

Conjunction Results

Using conjunction analyses we were able to locate common regions activated by tap and tone stimulation modes (table 2.5). The results showed that left side tap and left side tone stimulations commonly activated the right and left STG (figure 2.5.a), whereas right side tap and right side tone stimulations commonly activated the left STG (figure 2.5.b).

Since the primary contrasts between stimulation modes and rest revealed a potential laterality effect, we conducted additional conjunction analyses to locate possible common regions activated by the two stimulation modes delivered to opposite sides: left side tap and right side tone commonly activated the left STG (figure 2.5.c); whereas right side tap and left side tone commonly activated the left insula, left STG, and right STG (figure 2.5.d).

Table 2. 5 Conjunction results for commonly activated regions by tap and tone stimuli.

Mean beta values (β) are represented with %95 confidence interval (CI).

t-contrast	**Brain region**	**MNI coordinates x,y,z**	**Cluster size**	**t-value**	**P-value**	**β (CI)_tap**	**β (CI)_tone**
Left tap & left tone	Right Superior Temporal Gyrus	58, -38, 12	39	4.97	0.0001	.48(±.18)	.51(±.20)
	Left Superior Temporal Gyrus	-48, -34, 20	1101	4.33	0.0001	.32(±.12)	.32(±.16)
Right tap & right tone	Left Superior Temporal Gyrus	-50, -32, 14	48	2.78	0.005	.35(±.14)	.19(±.15)
Left tap & right tone	Left Superior Temporal Gyrus	-52, -32, 14	238	2.92	0.004	.34(±.18)	.20(±.15)
	Right Inferior Parietal Lobule	48, -48, 50	16	2.26	0.016	.15(±.12)	.10(±.10)
Right tap & left tone	Left Insula	-50, -36, 18	1525	4.37	0.0001	.31(±.11)	.33(±.15)
	Left Superior Temporal Gyrus	-62, -22, 12	1525	3.52	0.0010	.49(±.28)	.58(±.31)
	Right Superior Temporal Gyrus	58, -36, 14	1139	4.43	0.0001	.43(±.19)	.55(±.23)
	Left Precentral Gyrus	-54, -4, 54	78	3.51	0.0010	.18(±.15)	.21(±.11)

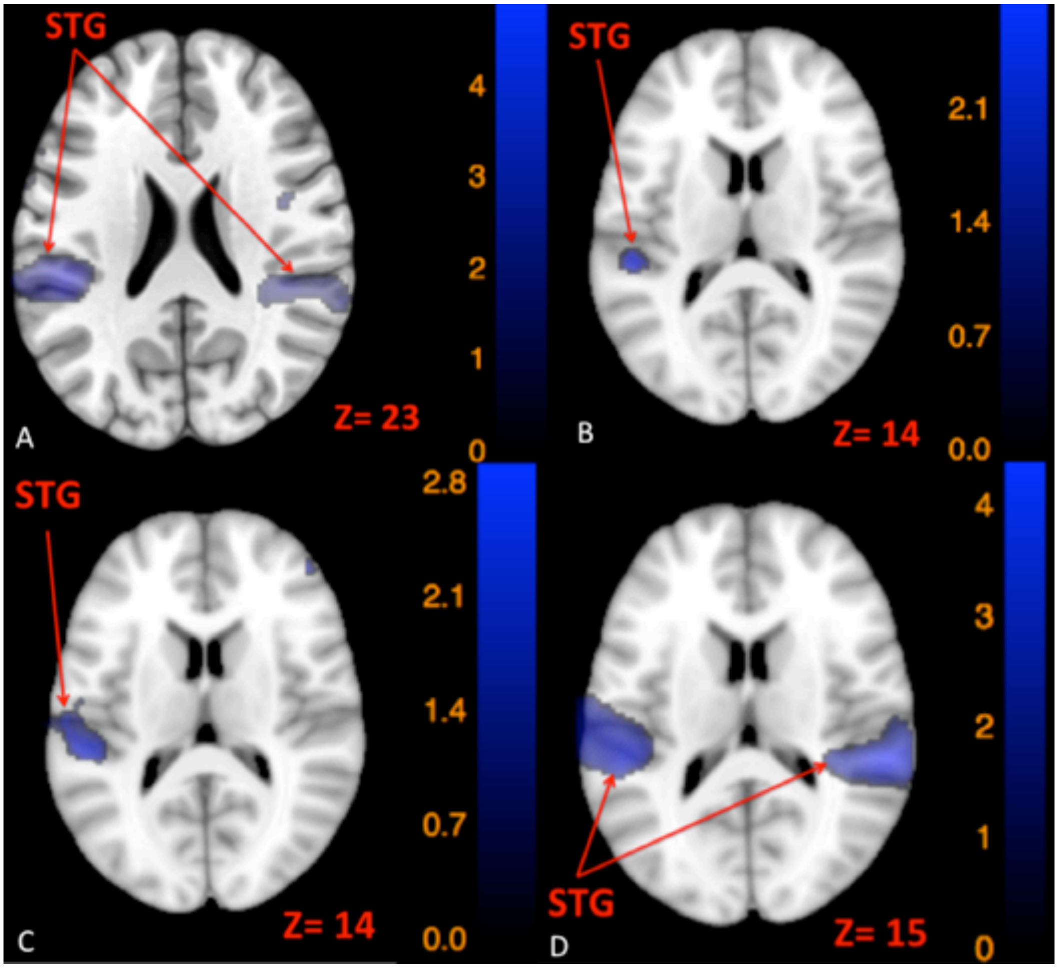

Figure 2. 5 Map of brain regions commonly activated by left tap and left tone stimuli (a), right tap and right tone stimuli (b), left tap and right tone stimuli (c) and right tap and left tone stimuli (d).

The corresponding t-value is presented next to each figure. Left and right sides refer to the left and right sides of the brain, respectively. N.S= Non Significant. STG=Superior Temporal Gyrus.

Correlation between brain activity and balance

The results for correlation between tap-induced brain activity and ellipse area are presented in table 2.6. There was a significant correlation between left side tap-induced brain activity and body sway (in Romberg stance on firm surface, with eyes closed and “yaw” head movement). Greater activation of the left inferior parietal lobule and less deactivation of the left vestibular nucleus were correlated with smaller ellipse area (i.e. less body sway) (figure 2.6.a). The scatterplot of correlation between IPL activity and balance is also included for illustration purposes (figure 2.6.b). Left side tap-induced brain activity was also negatively correlated with body sway in Romberg stance on firm surface, with eyes closed and "pitch" head movement: less deactivation of left cerebellum (lobule VI & VIIIB), and bilateral vestibular nuclei were correlated with smaller ellipse area (figure 2.6.c). This is further illustrated by a scatterplot to illuminate the direction of correlation (figure 2.6.d).

Table 2. 6 Results of correlations between tap-induced brain activity and ellipse area.

*significant at FWE. P<.05. Mean beta values (β) are represented with %95 confidence interval (CI).

t-contrast	Brain region	MNI coordinates x,y,z	Cluster size	t-value	P-value	β (CI)
left tap & ellipse area (Romberg,eyes closed,yaw)						
positive	No suprathreshold voxels were found					
negative	Left Inferior Parietal Lobule	-58, -26, 26	16	8.09	0.0001	.25(±.18)
	Left Vestibular Nucleus	-10, -32, -35	28	4.24	0.0010*	-.02(±.02)
left tap & ellipse area (Romberg,eyes closed,pitch)						
positive	No suprathreshold voxels were found					
negative	Right Vestibular Nucleus	24, -38, -37	93	6.16	0.0001	-.09(±.05)
	Left Cerebellar Lobule VI	-36, -44, -31	75	6.07	0.0001	-.15(±.05)
	Left Vestibular Nucleus	-26, -32, -21	56	5.66	0.0001	-.13(±.07)
	Left Cerebellar Lobule VIIIB	-2, -61, -35	23	5.13	0.0001	-.07(±.06)

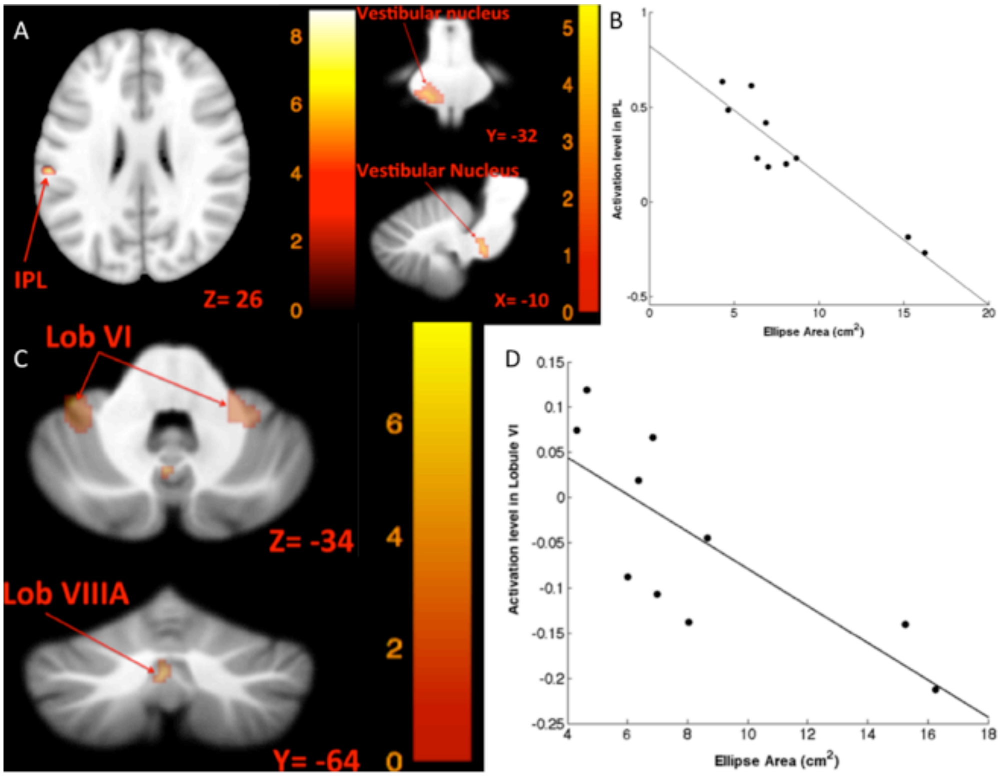

Figure 2. 6 Map of correlation between ellipse area and brain activity induced by left tap.

Left tap correlation with ellipse area in Romberg stance on firm surface, eyes closed, yaw head movement (a); the scatter plot illustrates the correlation between ellipse area and activation in IPL, suggesting that greater activation in IPL was correlated with smaller ellipse area (b); left tap correlation with ellipse area in Romberg stance on firm surface, eyes closed, pitch head movement (c); the scatter plot illustrates the direction of correlation between ellipse area and activation in cerebellar lobule VI, suggesting that less deactivation of cerebellar lobule VI is correlated with smaller ellipse area (d). The corresponding t-value is presented next to each figure. Left and right sides refer to the left and right sides of the brain, respectively. N.S= Non Significant. IPL=Inferior Parietal Lobule.

The results for correlation between tone-induced brain activity and ellipse area are shown in table 2.7. The left side tone-induced brain activity was correlated with balance (in Romberg stance on firm surface, with eyes closed and yaw head movement), as greater activation in right middle temporal gyrus was associated with smaller ellipse area and better balance control (figure 2.7.a). Moreover, higher activation in the right cerebellum (lobule VI), right vestibular nucleus, and left cerebellum (lobule V) during the right side tones was associated with smaller ellipse area during Romberg stance on firm surface, with eyes closed and yaw head movements (figure 2.7.b).

Table 2. 7 Results of correlations between tone-induced brain activity and ellipse area.

*significant at FWE. P<.05. Mean beta values (β) are represented with %95 confidence interval (CI).

t-contrast	Brain region	MNI coordinates x,y,z	Cluster size	t-value	P-value	β (CI)
left tone & ellipse area (Romberg,eyes closed,yaw)						
positive	No suprathreshold voxels were found					
negative	Right Middle Temporal Gyrus	56, -62, 6	19	9.65	0.0001	-.05(±.19)
right tone & ellipse area (Romberg,eyes closed,yaw)						
Positive	No suprathreshold voxels were found					
negative	Right Vestibular Nucleus	22, -36, -23	32	4.19	0.0020*	.02(±.06)
	Right Cerebellar Lobule VI	8, -68, -25	37	5.19	0.0001	-.01(±.05)
	Left Cerebellar Lobule V	-16, -48, -23	17	5.30	0.0001	-.02(±.07)

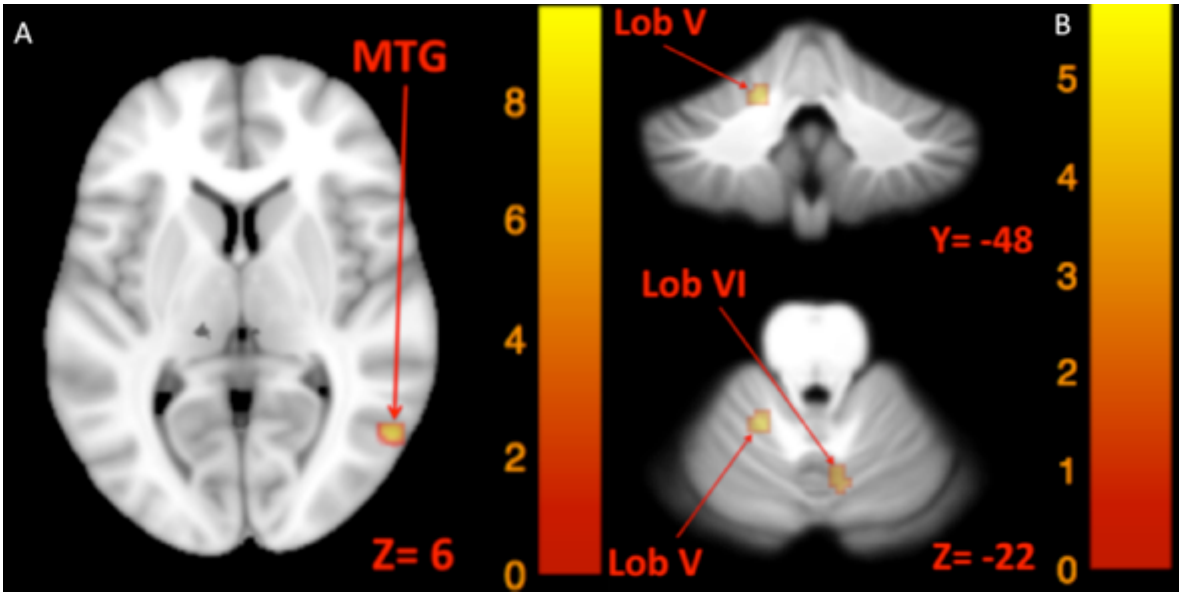

Figure 2. 7 Map of correlation between ellipse area and brain activity induced by left and right tone.

Left tone correlation with ellipse area in Romberg stance on firm surface, eyes closed, yaw head movement (a); Right tone correlation with ellipse area in Romberg stance on firm surface, eyes closed, yaw head movement (b). The corresponding t-value is presented next to each figure. Left and right sides refer to the left and right sides of the brain, respectively. N.S= Non Significant. MTG=Middle Temporal Gyrus.

Table 2.8 shows the results for correlation between tone-induced brain activity and balance maintenance time (i.e. time to step out). Greater activation in left inferior temporal gyrus and right cerebellum (lobule VIIB) were associated with longer balance maintenance time in tandem stance on compliant surface with "yaw" head movement (figure 2.8.a&b). Also, greater activation in right cerebellum (Crus II) in response to left tone was associated with longer balance maintenance time in tandem stance on compliant surface with "pitch" head movement (figure 2.8.c).

Table 2. 8 Results of correlations between tone-induced brain activity and balance time.

Mean beta values (β) are represented with %95 confidence interval (CI).

t-contrast	**Brain region**	**MNI coordinates x,y,z**	**Cluster size**	**t-value**	**P-value**	**β (CI)**
left tone & balance time (Tandem on foam, yaw)						
positive						
	Left Inferior Temporal Gyrus	-62, -50, -14	20	7.83	0.0001	.15(±.07)
	Right Cerebellar Lobule VIIB	22, -72, -47	73	5.20	0.0001	.08(±.05)
negative						
	No suprathreshold voxels were found					
Left tone & balance time (Tandem on foam, pitch)						
Positive						
	Right Cerebellar Crus II	14, -82, -33	87	5.18	0.0001	.04(±.03)
negative						
	No suprathreshold voxels were found					

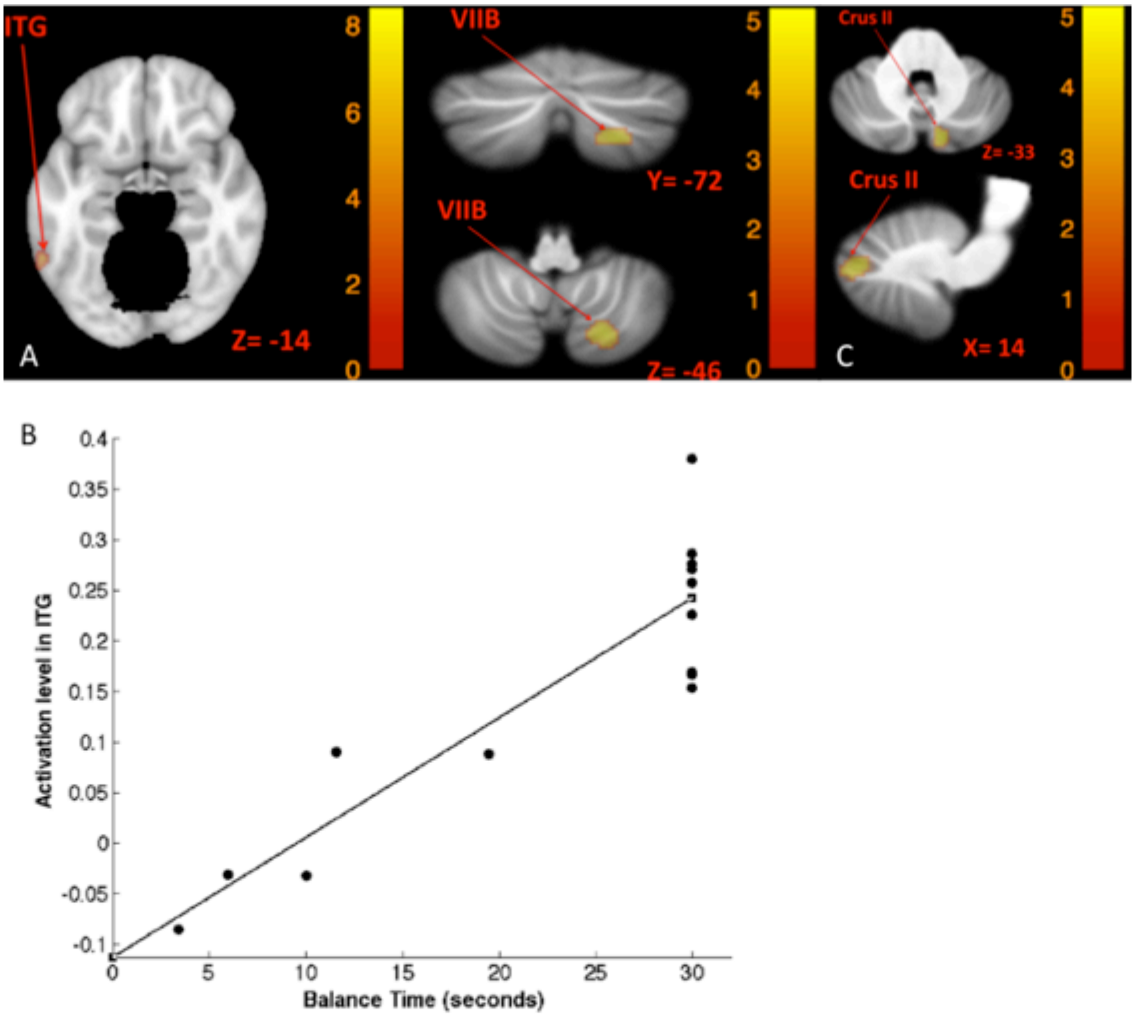

Figure 2. 8 Map of correlation between balance time and brain activity induced by left tone stimulation.

Left tone correlation with balance time in Tandem stance on compliant surface, eyes open, yaw head movement (a); the scatter plot illustrates the correlation between balance time and activation in ITG suggesting that greater activation of ITG is correlated with lengthier balance time (b); left tone correlation with balance time in Tandem stance on compliant surface, eyes open, pitch head movement (c). The corresponding t-value is presented next to each figure. Left and right sides refer to the left and right sides of the brain, respectively. N.S= Non Significant. ITG=Inferior Temporal gyrus.

Left tap versus Right tap

No suprathreshold voxels showed a significant difference between left and right side taps (table 2.9).

Left tone versus Right tone

Right tone resulted in greater activation of the right temporal lobe sub-gyral and left postcentral gyrus than left side tone stimulation (table 2.9, figure 2.9.a).

Left tone versus both sides tone

There was greater activation of left STG with tone stimulation delivered to both sides at 90 dB SPL than to the left side at 130 dB SPL (table 2.9, figure 2.9.b).

Right tone versus both sides tone

There was greater activation of bilateral superior temporal gyri, right precuneus, and right anterior cingulate gyrus with tone stimulation delivered to both sides at 90 dB SPL than to the right side at 130 dB SPL (table 2.9, figure 2.9.c).

Table 2. 9 Results of comparison between left and right side brain activity elicited by tap and tone stimuli.

*significant at FWE. P<.05. Mean beta values (β) are represented with %95 confidence interval (CI).

t-contrast	**Brain region**	**MNI coordinates x,y,z**	**Cluster size**	**t-value**	**P-value**	**β (CI)**
Left tap versus right tap						
left tap > right tap	No suprathreshold voxels were found					
left tap < right tap	No suprathreshold voxels were found					
Left tone versus right tone						
left tone > right tone	No suprathreshold voxels were found					
left tone < right tone	Left Postcentral Gyrus	-62, -22, 14	33	6.56	0.0001	.38(±.28)
	Right Temporal Lobe, Sub-Gyral	42, -24, 0	23	6.21	0.0001	.18(±.15)
Left tone versus both sides tone						
left tone > both tone	No suprathreshold voxels were found					
left tone < both tone	Left Superior Temporal Gyrus	-42, -40, 10	20	7.52	0.0001	.05(±.06)

Right tone versus both sides tone

right tone >both tone	No suprathreshold voxels were found					
right tone< both tone						
	Right Anterior Cingulate	8, 12, 26	15	7.94	0.0001	.005(±.03)
	Right Precuneus	12, -68, 44	23	6.89	0.0001	-.04(±.10)
	Right Superior Temporal Gyrus	64,-18,-0	51	6.30	0.0001	.06(±.12)
	Left Superior Temporal Gyrus	-62, -24, 8	41	5.65	0.0001	.20(±.21)

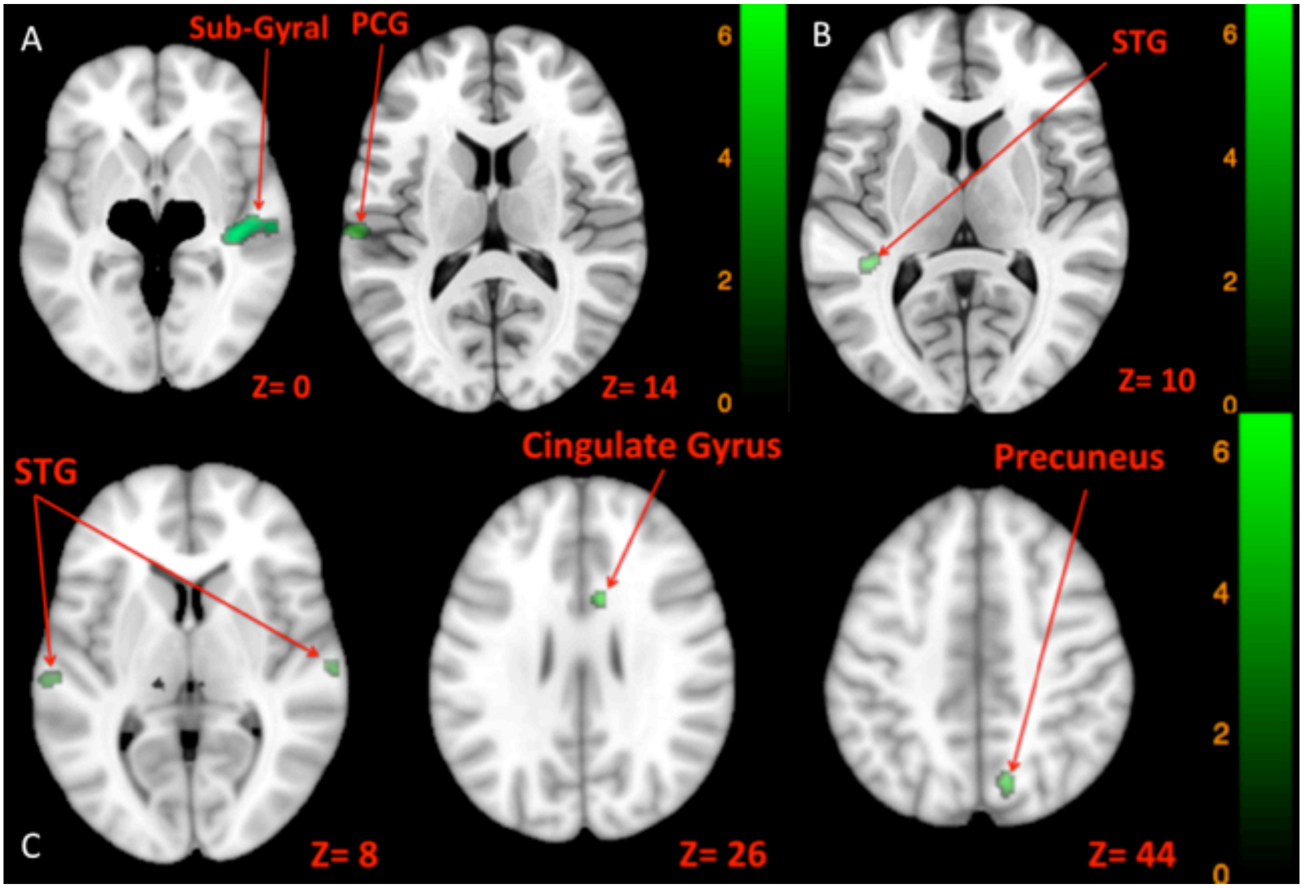

Figure 2. 9 Map of comparison between brain activity elicited by right versus left side tone

(a: Left tone > Right tone (N.S); Left tone < Right tone (green)), left versus both sides tone (b: Left tone > Both side tone (N.S); Left tone < Both side tone (green)), and right versus both sides tone (c: Right tone > Both side tone (N.S); Right tone < Both side tone (green)). The corresponding t-value is presented next to each figure. Left and right sides refer to the left and right sides of the brain, respectively. N.S= Non Significant. PCG=Post Central Gyrus, STG=Superior Temporal Gyrus.

Skull tap versus auditory tone burst stimulation: subjects' perceptions

The majority of subjects found the auditory tone bursts loud and unpleasant. One subject withdrew from the study specifically due to the loudness of the auditory tone bursts. Although we provided padding around the ears to help muffle the scanner noise, the fact that subjects did not have the benefit of earplugs while wearing the headphones inside the scanner was an additional source of discomfort for auditory trials. In some cases subjects had a hard time discerning the auditory tone bursts from the scanner noise, whereas every single subject reported feeling the taps. Subjects reported no discomfort with the skull tap stimulation.

vi. Discussion

Here we provide the first evidence of using skull taps to elicit vestibular fMRI activity. Conjunction analyses revealed that skull taps elicit overlapping activation patterns with auditory tone bursts (i.e. superior temporal gyrus), and both modes of stimulation activate previously identified regions of the vestibular network (Kirsch et al., 2015; C Lopez et al., 2012; zu Eulenburg et al., 2012). Additionally, we found that skull taps elicit more robust activity compared to auditory tone bursts, with brain activation from taps frequently surviving family-wise error corrections. The taps were also better tolerated by subjects than the auditory tones, further supporting their potential use in future clinical and basic science research.

We also provided evidence that individual differences in amplitude of activation and deactivation in vestibular regions in response to vestibular stimulation are associated with better balance and postural control. To our knowledge, the correlation of vestibular brain activity with balance has been addressed only in a few recent fNIRS studies (Huppert, Schmidt, Beluk, Furman, & Sparto, 2013; H. Karim et al., 2012). We showed that not only the quality of balance (indicated by the amount of body sway) but also the ability to maintain balance for a longer time (indicated by the balance time) depends on individuals' brain activation levels, particularly in vestibular cortical regions and the vestibular nuclei. Thus, vestibular brain activity could potentially serve as a predictor of individual differences in susceptibility to falling, and could further be used to index neuroplasticity occurring with balance interventions.

Vestibular cortex response elicited by skull taps and auditory tone bursts

Although there were some discrepancies between the activation patterns elicited by the auditory tone burst versus the skull-tap, these weighed in favor of the skull-tap method being a more specific way of stimulating the vestibular network. While skull tap resulted in consistent activation of the right superior temporal gyrus (STG) and the bilateral insula—areas identified in meta analyses of vestibular cortical activity (Lopez et al., 2012; Eulenburg et al., 2012)—the left side auditory tone burst stimulation only activated the right STG. Right side auditory stimulation did not elicit any significant activation. Moreover, the left side auditory tone burst resulted in a less vestibular-specific activity pattern, activating somatosensory cortices, the frontal gyrus and the precentral gyrus. This could be partly related to the noisier processing of auditory tone bursts over the scanner noise. Considering that subjects had to wear the headphones instead of earplugs inside the scanner the tones could have been difficult to detect. Also, the potential aversive effects of high decibel stimulation could be another source of inconsistency in tone-induced responses.

Interestingly, the skull tap predominantly deactivated the cerebellar lobules VI and VIIIA, along with cortical regions involved in somatosensory processing (e.g. frontal and parietal cortices) and subcortical regions such as thalamus, which relays information between vestibular nuclei and cortex. This may reflect a shift in attention towards vestibular processing and away from other sensory modalities. Similar deactivation of somatosensory and visual cortices has also been reported during vestibular stimulation by Schlindwein et al. (Schlindwein et al., 2008). Skull tap also resulted in deactivation of the contralateral vestibular nucleus, which replicates a known inhibitory projection reported in the animal literature (Shimazu & Precht, 1966) and recently documented in human subjects with diffusion tractography MRI (Kirsch et al., 2015). Also, the deactivation of vestibular nuclei has shown to be related to resolving state estimation errors. Brooks et al. (Brooks, Carriot, & Cullen, 2015) have shown that when there is a mismatch between predicted and actual sensory consequences, the fastigial nuclei's projection to vestibular neurons activates reflex pathways to maintain postural control. However, both the fastigial and vestibular nuclei are generally suppressed during voluntary movement in which efference copy is used to suppress state estimation errors. In our case, we delivered vestibular stimulation in the absence of movement, potentially resulting in sensory conflict. Our finding of less deactivation of vestibular nuclei being correlated with better balance could therefore suggest that a better ability to maintain balance is associated with being better able to resolve prediction errors.

We also found that balance abilities correlated with activation in cerebellar lobules V, VI, and VIII, but only for balance tasks that were performed with eyes closed (i.e. more vestibular reliant). Similar cerebellar regions have also been activated in previous studies using different modes of vestibular stimulation; for instance, auditory short tone burst (Schlindwein et al., 2008) and galvanic vestibular stimulation (Stephan et al., 2005) altered the activation of cerebellar lobules VI, VIIIB, Crus I, Crus II, and the dentate nucleus.

Laterality effects of stimulation modes

We compared the brain activation pattern elicited by left versus right side stimulation for both auditory tone bursts and skull taps. There are some inconsistencies in the literature regarding the laterality of VEMPs. Although these inconsistencies can be partly explained considering the location of VEMP responses (i.e. oVEMPs show the vestibular processing in crossed otolith-ocular pathways, whereas cVEMP reflects the function of uncrossed otolith-spinal pathways (Iwasaki et al., 2007)) and different electrode setups (Ertl et al., 2015), different modes of stimulation have shown to be the main driving factor for different patterns of laterality in VEMPs. We observed that skull tap stimulation resulted in bilateral vestibular cortical activation regardless of the side of stimulation, but specific contralateral deactivation of the vestibular nucleus. Brantberg and colleagues also showed that skull taps elicit bilateral cVEMPs, with a net excitatory response on the ipsilateral side (Krister Brantberg & Tribukait, 2002) and a net inhibitory on the contralateral side (Krister Brantberg et al., 2009). Our finding that skull tap prominently deactivated the contralateral vestibular nucleus is compatible with this previously reported pattern of cVEMPs. Brantberg et al. (2009) suggested that skull taps induce this bilateral response possibly through vibration (more ipsilateral) and translation (more contralateral) mechanisms (Krister Brantberg et al., 2009). The bilaterality of tap-induced cVEMPs is independent of recording location (Krister Brantberg et al., 2009) and it has been confirmed by oVEMP measurements as well (Holmeslet, Westin, & Brantberg, 2011).

As for the auditory tone bursts, our results support a laterality of vestibular processing. Murofushi and colleagues found a dominant ipsilateral cVEMP using short tone bursts and auditory clicks (Murofushi, Ochiai, Ozeki, & Iwasaki, 2004). Likewise, Schlindwein et al. reported a laterality effect using short tone bursts and acoustic stimuli in an fMRI experiment: while the overall brain activation pattern was bilateral, tone burst-induced vestibular processing was predominantly ipsilateral and in the right hemisphere, whereas the lower decibel acoustic stimulus resulted in a contralateral response, more on the left hemisphere (Schlindwein et al., 2008). Our findings also showed a left hemispheric activation pattern resulting from lower decibel acoustic stimulation (table 3: both sides tone, 90 dB versus rest). However, our results for tone-induced brain activation do not entirely overlap with the Schlindwein et al. findings: while left tone predominantly activated the ipsilateral hemisphere (table 3: left tone 130 dB versus rest), the right tone predominantly deactivated the ipsilateral hemisphere (table 3: right tone 130 dB versus rest). Nevertheless, our results support that auditory tone bursts results in a lateralized vestibular evoked response.

The conjunction analyses also revealed a laterality effect of auditory tone burst stimulation; the commonly activated regions by left side tap and left side tone were bilateral STG, and the commonly activated region by right side tap and right side tone was left STG. The further confirmation for the laterality effects came from the results of conjunction between the two stimulation modes in opposite sides: The commonly activated region by left side tap and right side tone was the left STG; whereas the right side tap and left side tone commonly activated the right STG and left insula. The opposite hemispheric effect seems to be mainly related to right auditory tone bursts, because skull taps elicited bilateral vestibular activation and left auditory tone bursts also evoked weak bilateral responses. One possible mechanism could be that tap-induced vibration engages different pathways to travel within the vestibular system than auditory tone bursts (e.g. the vibration caused by skull taps impacts utricular and saccular pathways, whereas tone bursts primarily engage the saccular structure (Holmeslet et al., 2011)).

Correlation between vestibular cortex activity and balance

We observed a correlation between individual differences in balance control and brain activity elicited by both modes of stimulation; however, the correlation predominantly emerged with left side stimulation. This finding could potentially be related to the right hemispheric dominance of vestibular processing (M. Dieterich, 2003; Janzen et al., 2008b). The correlation results suggested that those who exhibited greater vestibular activation in response to left side stimulation (either by skull taps or auditory tone bursts) had better balance control (i.e. less amount of body sway and longer balance stability).

Although balance performance reflects a multisensory integration of visual, vestibular, and proprioceptive signals, we enforced greater reliance on vestibular processing by removing visual input and adding head movements. Thus performance in these tasks mainly represents vestibularly mediated balance control, which we found to be correlated with vestibular brain activity.

The balance time correlation was only evident with auditory tone burst stimulation, and not the skull taps. More specifically, the positive correlation between cerebellar activity and balance time emerged in lobule VIIB and Crus II, which have been previously linked to spatial processing (Stoodley, Valera, & Schmahmann, 2012). One potential reason for the correlation between balance maintenance time and tone stimulation, but not tap stimulation, could be related to the choice of balance task as the covariate. As explained in the results section, we used "tandem stance on compliant surface with yaw/pitch head movement" to assess the balance time correlation with vestibular activity. In this task the visual input was not removed; therefore, there was less dependency on vestibular function compared to "Romberg stance with eyes closed and yaw/pitch head movement", in which there was no visual input. As discussed earlier, our findings suggest that skull taps elicit a more vestibular-specific activation compared to auditory tone bursts. This could potentially explain why brain activation elicited by skull tap was correlated with balance when performance was more vestibularly mediated (i.e. performed with eyes closed); but it failed to show any correlation with balance when the balance performance was less reliant on vestibular inputs (i.e. performed with eyes open).

Overall, these correlations suggest that those with greater vestibular cortex excitability or more efficient transmission within vestibular networks have better balance control. Although the left and right vestibular nuclei were the only clusters surviving the family-wise error correction (FEW) for multiple comparisons in correlation analyses, the remaining clusters fit the previously identified vestibular network in studies of balance assessment in upright stance using fNIRS (Karim et al., 2013). This provides further validation for associating upright balance performance with vestibular activity elicited in a supine position.

Validity of vestibular evoked activation inside scanner

We included the oVEMP assessments to address the validity of our stimulation inside the scanner. Our findings showed that subjects exhibited typical oVEMP characteristics in response to the skull tap and auditory tone burst stimulation outside the scanner. This supports the notion that the brain activation elicited by the same stimulation modes inside the scanner can be interpreted as vestibular signal processing.

Subjective comfort

Based on the anecdotal reports in our sample of 14 subjects, the MR compatible skull tap is well tolerated inside the scanner, whereas auditory tone bursts cause discomfort and distress, similar to what has been previously reported (Wackym et al., 2012). Therefore, using the skull tap stimulation minimizes the potential artifacts of aversive brain activation elicited by auditory tone bursts.

Limitations

The skull taps are perceived by subjects on the facial skin, which could result in somatosensory processing. We did not observe activation in the somatosensory cortex during taps, however; instead the responses were predominately in regions that have been previously linked to vestibular processing. Nevertheless, future studies would benefit from implementing a tactile stimulation control condition.

vii. Conclusion

In sum, we found that the skull tap stimulation results in activation of canonical vestibular cortex as well as cerebellar and brainstem regions known to process vestibular inputs. This supports the skull tap as an effective method for studying human vestibular processing, especially in otolithic pathology. This is of high importance in longitudinal experiments, in which subjects' comfort is essential for minimizing the aversive effects and maintaining enrollment. Further, we provided evidence of the association between quantitative measures of balance control and vestibular brain activation.

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viii. References

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Chapter III

Deactivation of Somatosensory and Visual Cortices During Vestibular Stimulation is Associated with Older Age and Poorer Balance

i. Abstract

Aging is associated with declines in balance. Previous studies have also shown that, similar to other sensory modalities, the vestibular system exhibits peripheral and central declines with age. Here we used functional MRI to investigate age differences in neural vestibular representations in response to pneumatic skull tap stimulation. We also measured the amount of body sway in multiple balance tasks outside of the MRI scanner to assess correlations between individuals' balance abilities and their vestibular neural responses. We found that activation amplitude of the canonical vestibular cortex was correlated with age, with younger individuals exhibiting higher activation. In contrast, deactivation of visual and somatosensory regions was increased with older age and associated with poorer balance. Furthermore, greater consistency of vestibular cortex activity was correlated with better balance, regardless of age. The results demonstrate that brain activations and deactivations in response to vestibular stimuli are correlated with balance, and the pattern of these correlations varies with age. The findings also suggest that older adults exhibit less sensitivity to vestibular stimuli, and may compensate by differentially reweighting visual and somatosensory processes.

ii. Introduction

One third of older adults above age 65 years fall at least once per year (L. Sturnieks, St George, & R. Lord, 2008), impacting quality of life and resulting in significant healthcare costs. Balance control is a complex sensorimotor-cognitive process, requiring perception and integration of visual, somatosensory, and vestibular inputs. Age effects on the vestibular system have been more extensively studied in recent years (Zalewski, 2015; Allen et al. 2017; Smith 2016). Several studies have documented degeneration of vestibular neurons and hair cells with age. For example, Matheson et al. (Matheson, Darlington, & Smith, 1999) reported that up to 40% of vestibular cells are lost by age 90. Moreover, neurons in the vestibular nuclei are lost at a rate of about 3% per decade after age 40 (Lopez, Honrubia, & Baloh, 1997). Despite these reports, studies have generally not reported associations between these peripheral vestibular changes and functional measures of balance.

Recent fMRI experiments have mapped out central vestibular processing networks (cf. Schlindwein et al., 2008). Two meta-analyses have shown that many brain regions are involved in vestibular processing, including the superior temporal gyri, inferior parietal cortex, middle frontal lobe, posterior cingulate, thalamus, and cerebellum (zu Eulenburg et al., 2012 Lopez, Blanke, & Mast, 2012). The *parietal opercular* area OP2 and *retroinsular cortex* were the most commonly activated regions by different vestibular stimulation modes.

Central cortical responses to vestibular inputs are also affected by age (Allen, Ribeiro, Arshad, & Seemungal, 2016). Karim et al. (Helmet T Karim et al., 2014) used an MR compatible force platform to simulate an active balance task while acquiring fMRI data. They found that older adults showed activation in the bilateral middle temporal gyri and fusiform gyri when performing the balance task inside the scanner. However, the authors only tested older adults in this study, precluding an analysis of age differences; in addition, the task likely engages multiple sensory systems. In another study the same group used fNIRS during upright balance assessments and reported that older adults exhibited greater bilateral activation in the superior temporal gyri in response to caloric vestibular stimulation in comparison to young adults (Karim et al., 2013). Lin and colleagues (Lin, Barker, Sparto, Furman, & Huppert, 2017) also used fNIRS to examine brain activity during upright balance tasks and found greater activation in occipital and frontal regions for older adults compared to middle aged adults. In contrast with these reports of age-related increases in cortical response, Cyran et al. (Cyran, Boegle, Stephan, Dieterich, & Glasauer, 2016) found that vestibular network functional connectivity (measured during galvanic vestibular stimulation) declines with age, and this decline is independent of changes in white matter microstructure measured with diffusion MRI (dMRI). The authors also found that age differences in task-based vestibular connectivity were associated with a decrease in BOLD signal amplitude and an increase in its variability. However, they did not measure balance and thus the behavioral implications of their findings remain unclear.

Some studies have examined the functional impact of age differences in vestibular processing by correlating MRI measures of brain structure or function with balance measured outside of the scanner. For example, Sullivan et al. (Sullivan, Rose, Rohlfing, & Pfefferbaum, 2009) showed that age-related increases in body sway were associated with increased white matter hyper-intensities and enlargement of the ventricles and sulci. Another study by Impe et al. (Impe, Coxon, Goble, Doumas, & Swinnen, 2012) used dMRI and showed that white matter integrity was predictive of postural stability when different sensory modalities were compromised during a sensory organization test (SOT), but only in older adults. Furthermore, Yuan et al. (Yuan, Blumen, Verghese, & Holtzer, 2015) showed that greater resting state functional connectivity (between sensorimotor, visual, vestibular, and left fronto-parietal cortical areas) is associated with higher walking speed in older adults (with the latter measured outside of the scanner). However, the authors did not provide a comparison between young and older adults.

Other researchers have examined age differences in neural distinctiveness, that is, the specificity of neural activation patterns. A number of studies have found that neural activation patterns in response to different stimuli are more distinctive or distinguishable in young adults compared with older adults (D. C. Park & Reuter-Lorenz, 2009). For example, Park and colleagues (D. C. Park et al., 2004) found that activation patterns in ventral visual cortex in response to faces, places, and words were significantly more similar (less distinctive or specific) in older adults than in younger adults. Age differences in the digit symbol, trail making, dot comparison, and verbal fluency tasks were correlated with decreased neural specificity (J. Park, Carp, Hebrank, Park, & Polk, 2010). Carp et al. (Carp, Park, Hebrank, et al., 2011) reported that motor cortical distinctiveness is also reduced in older adults. They used a simple finger tapping design to assess whether older adults show less distinct patterns of activation in response to left and right finger movements. However, there was no report of possible correlation between the age-related changes in performance and neural distinctiveness. It remains unclear as well whether there are age differences in distinctiveness of vestibular representations and if so, how they relate to balance. Since no previous studies have examined the vestibular distinctiveness in young adults, in this work we first assessed the distinctiveness of left and right vestibular responses in young adults, and then investigated possible age differences in distinctiveness.

Thus, the literature documents that older adults recruit more brain regions than young adults for balance and vestibular processing, while the connectivity of these regions is weaker than in young adults. This is generally similar to what has been reported for age differences in cognitive task performance (P. A. Reuter-Lorenz & Park, 2010; Patricia A. Reuter-Lorenz & Cappell, 2008) and motor task performance (Heuninckx, Wenderoth, & Swinnen, 2008). In general, previous reports of age differences in neural responses suggest a complex pattern of over- and under-activation (Eyler, Sherzai, Kaup, & Jeste, 2011; Li et al., 2015). Oftentimes the greater activation in older adults is interpreted as compensatory because it is correlated with better task performance (Cabeza, Anderson, Locantore, & McIntosh, 2002; R. D. Seidler et al., 2010). However, greater neural activation in older adults has also been viewed as dedifferentiation when it is associated with poorer performance (P. A. Reuter-Lorenz & Park, 2010).

In the current study we used fMRI during central vestibular processing to examine age differences in neural activation and neural distinctiveness and their associations with balance abilities. We stimulated the vestibular system in the MRI scanner using a head tapper device (previously validated in Noohi et al., 2017) and measured postural stability outside of the scanner to test for associations between vestibular brain responses and balance with respect to age. Furman and Redfern (Furman & Redfern, 2001) have suggested using alternative vestibular stimulation methods for older adults that are more sensitive and tolerable, since the current clinical methods are not always sensitive enough to detect age differences. In our previous report with young adults (Noohi et al., 2017) we found the tapper stimulation to be well tolerated;

moreover, activation in several brain regions was correlated with balance abilities. Here, we hypothesized that healthy older adults would show an overall increase in vestibular brain activation in response to vestibular stimulation compared to young adults, and decreased distinctiveness as suggested by the studies reviewed above. We also expected that the magnitude and pattern (e.g. distinctiveness and laterality) of vestibular neural responses would correlate with individual differences in postural stability and balance control. These findings would parallel what has been reported for age effects on other sensory and motor systems (Carp, Park, Hebrank, et al., 2011; Carp, Park, Polk, & Park, 2011).

iii. Methods

Participants

We recruited 15 healthy, right-handed older adults (65-80, $\bar{x}$ =71.2 ± 4.14, 10 females) and 18 healthy, right-handed young adults (18-35, $\bar{x}$ =21 ± 2.44, 8 females) from the University of Michigan clinical studies website. All subjects signed the consent form approved by the University of Michigan Medical Institutional Review Board. Subjects were screened prior to participation in the study and were excluded if they had any neurological, vestibular, or postural disorder or contraindications for MRI scanning. Individuals with scores of <26 on the Montreal Cognitive Assessment (MOCA) were excluded from the study (Nasreddine et al., 2005). All subjects underwent the fMRI scan, but only a subset of subjects participated in the behavioral balance assessments. The number of participants in each behavioral task is reported in the results section.

Balance Assessments

Center of Pressure (CoP) measures

Participants underwent a series of balance assessments on a force platform (AMTI Inc, USA) and center of pressure was captured via a Vicon motion capture system (Nexus, Vicon Inc). The balance tasks were categorized into four conditions: romberg, tandem, normal, and single leg stance, with multiple levels of difficulty: eyes closed/open, yaw/pitch/no head movement, arms crossed/free, & on firm/compliant surface. Each of these conditions served to challenge postural stability by degrading or removing a particular sensory input: closing the eyes removed the visual inputs, head movements challenged the vestibular system, crossing the arms served to prevent compensatory strategies, and the compliant surface degraded the somatosensory/tactile inputs.

The yaw and pitch head movements consisted of sinusoidal movements (roughly ±20°, 0.6 Hz). Subjects were instructed to match their head movement to the beat of a metronome (0.6 Hz) that was used consistently for all subjects, within their comfort level. High-density viscoelastic foam was used as the compliant surface (length=45cm, width=45cm, thickness=18cm; Natus Inc.). The order of the tasks was counterbalanced across subjects. Two spotters stood by the subjects to provide support in case of a fall.

The amount of body sway in these tasks reflected individual differences in postural stability. We calculated the amount of body sway as the area of an ellipse fit to the 95th percentile confidence interval of center of pressure motion in the anterior-posterior and medial-lateral directions (Sienko et al., 2008). Better postural stability was reflected as less body sway and smaller ellipse size. The center of pressure measures have been validated in previous studies and showed to be highly correlated with measures of sensory organization test (Jayakaran, Johnson, & Sullivan, 2013).

For each task, we instructed subjects to maintain their balance for 30 seconds. The task was stopped prematurely if they lost their balance and was not included in the analysis. The measures of body sway were later used to assess the correlation between behavioral and neural metrics of vestibular function. Four tasks were selected for these correlation analyses:

1- Normal (feet apart) stance on firm surface with eyes open (baseline measure, reliance on visual, vestibular and somatosensory inputs)
2- Romberg (feet together) stance on firm surface with eyes closed (removed visual inputs, reliance on vestibular and somatosensory inputs)

3- Romberg (feet together) stance on compliant surface with eyes closed (removed visual inputs, degraded somatosensory inputs, greater reliance on vestibular inputs)

4- Single leg stance (left foot) on firm surface with eyes open (degraded somatosensory inputs, greater reliance on visual and vestibular inputs)

These four tasks were selected because: 1) All subjects were able to complete these tasks for 30 seconds (this was not the case for other conditions); 2) Ruhe et al. (Ruhe, Fejer, & Walker, 2010) reviewed the reliability of CoP measures and found no specific task to be more reliable than the others; 3) they represented a relatively step-wise increase in degradation of sensory modalities and difficulty in balance maintenance; and 4) they were reported previously to be reliable predictors of fall in older adults (Bloem et al., 2001; Chun-Ju Chang, Yu-Shin Chang, & Sai-Wei Yang, 2013; Maki, Holliday, & Topper, 1994).

Clinical Tests of Functional Mobility

In addition to CoP measures, we administered two clinical tests of balance and gait: the Modified Dynamic Gait Index (MDGI) (Matsuda, Taylor, & Shumway-Cook, 2014) and the Timed Up and Go (TUG) test (Shumway-Cook, Brauer, & Woollacott, 2000). Both tests have high test-retest reliability (Huang et al., 2011).

Timed Up & Go (TUG)

As described by Podsiadlo & Richardson (Podsiadlo & Richardson, 1991), the TUG test requires subjects to stand up from a chair, walk for 10 ft, turn around, walk back to the chair, and sit down. The time for completing this task (under 20 seconds for healthy older adults) is considered an index of functional mobility and balance control. The TUG-manual task is a modified version of this task, in which subjects are performing the task while carrying a cup of water; we administered this version as well. Lower TUG scores (i.e. less time needed to finish the tests) indicate better functional mobility and balance.

Modified Dynamic Gait Index (MDGI)

As described by Shumway-cook et al. (Shumway-Cook, Taylor, Matsuda, Studer, & Whetten, 2013), the MDGI is a modified scoring index for the DGI, which evaluates three facets of walking performance: time, gait pattern, and level of assistance. This clinical measure indicates the ability of subjects to adjust their gait according to complex walking situations. The test comprises a set of 8 tasks; the first is the baseline gait measure (low-challenged, self-paced). The other 7 tasks are designed to challenge the subject to respond to 4 different forms of environmental conditions (change in speed, change in direction, obstacle avoidance, & climbing stairs). Higher MDGI scores indicate better ability to maintain balance.

Functional Magnetic Resonance Imaging (fMRI)

The fMRI acquisition was conducted at the University of Michigan functional MRI laboratory, using a 3.0 T MRI scanner (General Electric Medical Systems, DISCOVERY MR750). The scanning protocol consisted of a high-resolution T1 structural scan (SPGR), a resting state connectivity scan, and fMRI during vestibular stimulation.

The structural MRI acquisition comprised a T1-weighted ascending sequential echo-planar scan (TR = 12.2 s, TE =5.1 ms, FA= 15°, matrix size= 256 x256, FOV= 260 x260 mm, slice thickness = 1 mm, number of slices=124) covering the whole brain and the cerebellum. A gradient-echo spiral sequence with ascending sequential slice ordering (FOV=220 mm, TR=2 s, TE= 30 ms, slice thickness = 1 mm, number of slices=43, voxel size =3.4375x3.4375mm) was used to acquire the functional images.

We minimized head movement using a Velcro strap over the forehead, and by placing foam padding on the left and right sides of the head. The padding also provided extra hearing protection (in addition to ear plugs) from the scanner noise. Furthermore, we placed a pulse oximeter over the subjects' index finger and wrapped a respirometer belt around the subjects' abdomen to collect physiological responses, which were later corrected by using the RETROICOR algorithm (Glover et al., 2000).

Stimulation of the vestibular system inside the scanner

We used a pneumatic skull tapper (MR compatible Pneumatic Tactile Pulse System (PnTPS), Engineering Acoustics Inc.) to stimulate the vestibular system inside the scanner (Noohi et al., 2017). The skull tapper delivered low force (19.6 N), compressed air taps (50 – 55 psi) to the lateral cheekbones, stimulating the otolith organs through bone conduction mechanisms (Cornell et al. 2009; Curthoys et al., 2011; Curthoys et al. 2006; Curthoys et al. 2009; Iwasaki et al., 2008; Nguyen, Welgampola, & Carey, 2010; Wackym et al., 2012). We applied five stimulation trials on each side; each trial consisted of 24 taps delivered at 1Hz. This was implemented in a block design with five alternating periods of rest (20 seconds) and stimulation (24 seconds). The right and left side stimulations were administered in separate runs.

Before beginning each trial, the MRI technician reminded subjects to keep their eyes closed (to eliminate the effects of visual inputs on vestibular processing). After the completion of each trial, the MRI technician asked subjects to report the side of the stimulation to make sure they felt the taps on the correct spot. This also helped with keeping the subjects alert and communicative.

iv. Data Analyses

Balance performance analysis

Center of Pressure (CoP) analysis

We used the Vicon software (Nexus, Vicon Inc) to analyze the center of pressure (CoP) data that were collected at 100 Hz on the force platform. The force platform channels were plugged into a data acquisition board and the data were recorded using the Vicon Nexus software, which then automatically calculated CoP data from the raw channel data. The CoP data were then exported from Vicon Nexus software and outcome measures were calculated. As shown in previous studies (Lee et al., 2012; Sienko et al., 2008), we applied a low pass filter with a 2nd order recursive Butterworth filter with a cutoff of 10 Hz. For each balance trial, we fitted a 95% confidence interval ellipse to the anterior-posterior and medial-lateral trajectories. The area of the ellipse was calculated for correlation with individual differences in vestibular brain activity.

Functional Mobility tests

We recorded the time of performance of TUG and TUG-manual tests, and used the average performance time over three repetitions of each task. For the MDGI, we used the ordinal scaling system to score the subjects' performance (with the highest possible score of 64).

FMRI data analyses

Preprocessing

We used SPM12 software (Welcome Department of Cognitive Neurology, London, UK (Karl. J. Friston et al., 1995)) to analyze the fMRI data. To ensure the steadiness of the MR signal, we discarded the first 10 seconds of each run. The University of Michigan Functional MRI Laboratory applies the RETROICOR algorithm (Glover et al., 2000) to the raw data to account for physiological responses (e.g. respiration and cardiac signals). We carefully examined the raw data for any potential movement confounds. Additionally, we used the ARTifact detection toolbox ("NITRC: Artifact Detection Tools (ART): Tool/Resource Info," Whitfield-Gabrieli) to detect any volumes with >2mm translational or >2° rotational movement; movement parameters were later used as covariates of no interest in the first level design matrix. Next, we applied slice-timing correction, and then co-registered the functional images with the anatomical image. The images were then normalized to the Montreal Neurological Institute (MNI152) template (Karl. J. Friston et al., 1995). We normalized the cerebellar volumes separately using the Spatially Unbiased Infra-tentorial Template (SUIT, Diedrichsen and Zotow, 2015; Diedrichsen, 2006; Diedrichsen et al., 2011, 2009). Next, we applied a Gaussian kernel function (8,8,8 mm) to spatially smooth the normalized images.

Comparing brain activity within and between young & older adult groups

The first level analysis was designed to compare the brain activity between rest and stimulation blocks, using the smoothed images. The resulting contrasts from the first level analysis were subsequently used in second level (group) analyses. We used SnPM13 software (http://warwick.ac.uk/snpm) to apply non-parametric permutation tests for statistical inferences (Nichols & Holmes, 2002). We applied a one sample t-test to assess the within group effects collapsed across age, a two-sample t-test to compare the brain activity between young and older adult groups, and simple regression to assess the correlation between brain activity and behavioral performance or age. A false discovery rate (FDR) correction (p<.05) was applied to account for multiple comparisons.

Localization

The results from the above analyses were mapped to the MNI atlas (Karl. J. Friston et al., 1995) to localize the corresponding brain regions, using the Harvard-Oxford maximum probability atlas of the bspmview toolbox ("BSPMVIEW|bspmview,"Spunt.B) in SPM12. The cerebellar results were separately localized using the SUIT atlas (Diedrichsen et al., 2009).

Signal to Noise Ratio analysis

We calculated the fMRI signal to noise ratio, following the methods of Bernard et al. (J. A. Bernard et al., 2013) in order to assess potential age differences in variability of vestibular activation.

Laterality Index analysis

We used the Laterality Index (LI) toolbox of SPM 12 (Wilke & Lidzba, 2007; Wilke & Schmithorst, 2006) to assess whether there is a hemispheric dominance in vestibular processing, and whether that is influenced by age. We applied the bootstrapping method to minimize the potential effects of outliers, and performed the analysis on whole brain gray matter, superior temporal gyri, and the cerebellum. The analyses were conducted for each subject, and the LI scores were then compared between the age groups using a two-sample t-test.

Neural distinctiveness analysis

We used freesurfer v6.0.0 ("FreeSurferMethodsCitation - Free Surfer Wiki") to apply the reconstruction algorithm (i.e. recon) to the anatomical images. The functional analysis was done using the FSFAST (FreeSurfer Functional Analysis Stream) algorithm. We applied the same method as Carp et al. (Carp, Gmeindl, & Reuter-Lorenz, 2010) to measure neural distinctiveness: a correlation distance metric (Haxby et al., 2001) was used to assess the distinctiveness of activation patterns in response to the left tap condition and the right tap condition within the region of interest (ROI). The distinctiveness score was defined as mean correlation across beta values within the same condition (e.g., left tap with left tap, right tap with right) minus the mean correlation across beta values between different conditions (e.g., left tap with right tap). The closer distinctiveness scores were to zero, the less distinct the activation patterns resulting from the left and right taps were. The details of the process are as follows.

We created an anatomical mask of the bilateral superior temporal gyri using FreeSurfer's label files that were generated at the cortical parcellation step of the recon algorithm. Within the anatomical mask for each subject, the vertices were first sorted based on the level of activation in response to the left taps, and then based on the level of activation in response to the right taps. In order to include the activated vertices from both left and right stimulation conditions equally, we alternated between the two sorted lists and defined the functional ROI as the most active vertex from left stimulation, then the most active vertex from right stimulation, then the next most active vertex from left stimulation, and so on, until we reached a functional ROI with 2000 vertices.

Following Haxby et al. (Haxby et al., 2001), the *within* correlation index was defined as the average correlation between left stimulation patterns across all left stimulation blocks, and the average correlation between right stimulation patterns across all right stimulation blocks (i.e. within score; indicator of consistency of neural representations within a condition). The *between* correlation index was defined as the average of the correlation between left and right tap conditions across all blocks. For each subject, the neural distinctiveness score was defined as the difference of the average within score and the average between score for that subject. Thus, a positive neural distinctiveness score suggests that the activation patterns between the two stimulation conditions are distinct, and zero or negative scores suggest that the activation patterns resulting from the left and right stimulation are not distinctive from each other.

Correlation analyses

Based on the results from the activation analyses, we created a combined ROI of all regions that were active with vestibular stimulation at an uncorrected $P<.001$ in either young or older adults (i.e. the activation ROIs for the young adults and the old adults were calculated separately, and then added together to create one set of ROIs). These ROIs were later used in a correlation analysis (with FDR correction level of $p<. 05$) in order to find the regions of the brain where activity was associated with age and balance performance.

Correlation between age and brain activity measures

We used participants' age as a covariate in an SnPM simple regression analysis to determine how brain activity varies with respect to age.

Correlation between balance measures and brain activity measures

We used the area of the ellipse, TUG, and MDGI scores as covariates in SnPM simple regression analyses to determine how brain activity varies with respect to measures of postural control.

Conjunction analyses

We performed conjunction analyses to identify regions of the brain where activity was associated with both age and balance performance. We applied the max function in the imcalc toolbox of SPM12, using the results of statistical inference from SnPM13 as the input images. A positive direction for conjunction of the two correlation analyses indicated that greater brain activity was associated with greater age and poorer balance (greater CoP & TUG measures/ smaller MDGI scores). A negative direction for the conjunction of the two correlation analyses indicated that greater brain activity was associated with younger age and better balance.

Correlation analyses for laterality index, signal to noise ratio, and distinctiveness/within scores

We conducted a simple regression to determine whether an individual's balance measures were associated with their laterality index. Similarly, we conducted a simple regression to determine whether individual differences in postural control are associated with differences in signal to noise ratio. Lastly, in order to evaluate whether individual differences in balance control were associated with the distinctiveness of brain activation patterns for vestibular processing, we conducted a simple regression to assess the correlation of balance measures with distinctiveness scores.

v. Results

Balance assessment results

Center of Pressure (CoP) measures

We found a significant difference between young and older adults' performance in single leg stance (SLS) with eyes open (t= -2.69, p= 0.01, df= 23, CI: -105.88, -13.95), documenting poorer balance performance (greater ellipse area) for older adults. The other CoP measures were not significantly different between young and older adults (Figure 3.1).

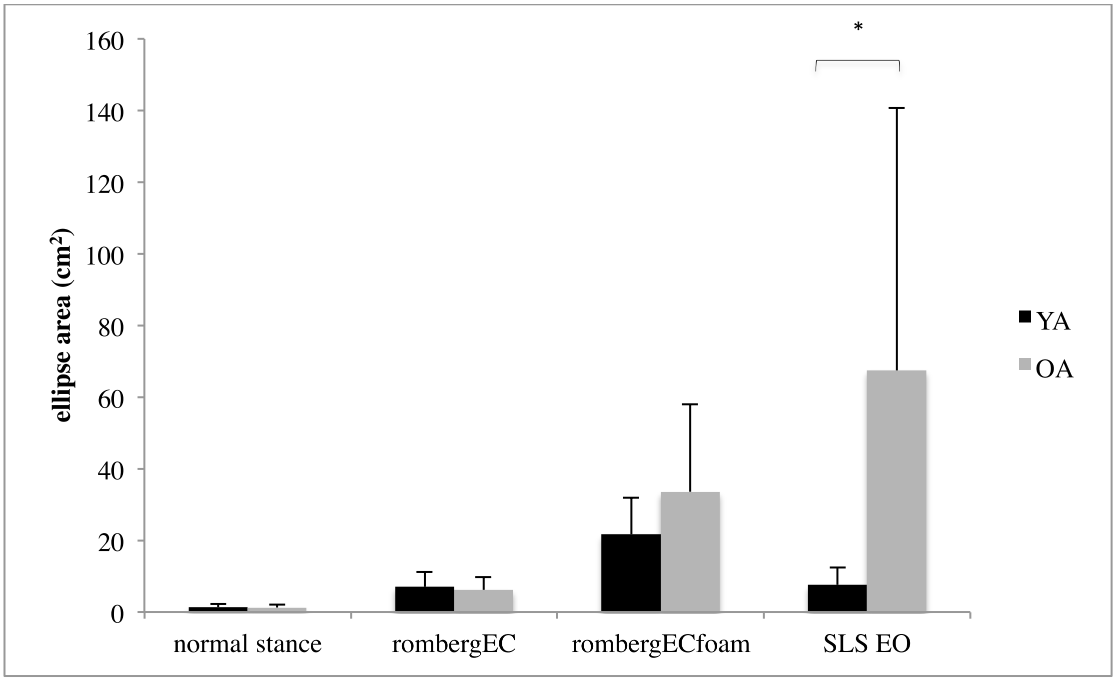

Figure 3. 1 Performance of young and older adults in four balance tasks with different degrees of difficulty.

Task difficulty increases from left to right. Smaller ellipse area reflects less body sway (i.e. better balance). Error bars represent standard error. EO: Eyes Open, EC: Eyes Closed, SLS: Single Leg Stance, YA: Young Adults, OA: Older Adults; N= 12 YA, 14 OA.

Clinical Tests of Functional Mobility

As shown in figures 3.2 and 3.3, there was no significant difference between young and older adults' MDGI and TUG scores.

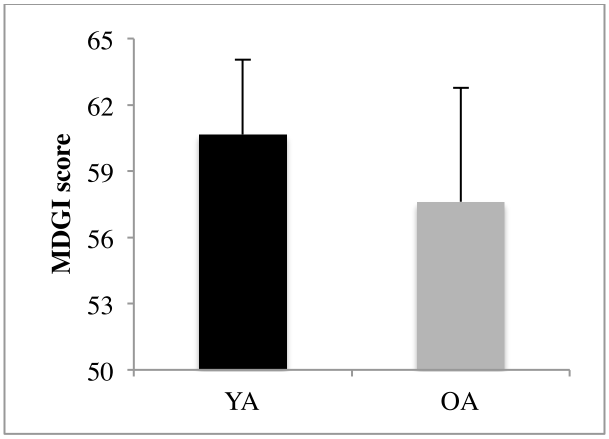

Figure 3. 2 Performance of young and older adults in series of gait assessment tasks (MDGI).

The higher MDGI score reflects better gait and balance. Error bars represent standard error. YA: Young Adults, OA: Older Adults; N= 6 YA, 14 OA

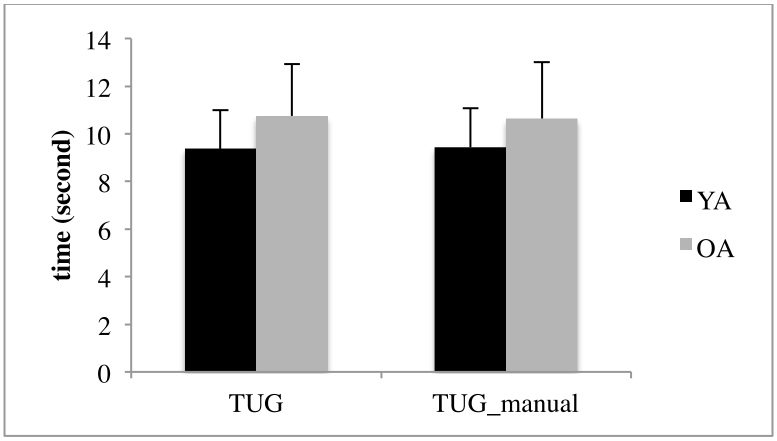

Figure 3. 3 Performance of young and older adults in TUG and TUG-manual tasks.

The lower scores reflect better gait and balance. Error bars represent standard error. YA: Young Adults, OA: Older Adults; N= 6 YA, 14 OA

FMRI results

First we compared the activation patterns elicited by left and right taps, regardless of age. We found no significant difference between activity patterns or laterality index between the left and right tap conditions. Thus, to increase the power of our analyses, we pooled the two conditions together. Results are presented at $p<.05$ with FDR correction, unless otherwise specified.

Comparing brain activity between young & older adult groups

The results from comparison between the brain activation and deactivation of young versus old adults did not survive the FDR p<.05 corrections. The analyses conducted within the cerebellum after normalization to the SUIT template also showed no significant differences between young and older adults.

Signal to Noise Ratio analysis

We found no significant difference in signal to noise ratio between young and older adults.

Laterality Index analysis

We found no significant difference between young and older adults in the laterality index of vestibular brain activity.

Neural distinctiveness analysis

We found no significant difference in neural distinctiveness between young and older adults. It should be noted however that the left and right tap were not very distinctive in the young adults (0.07 – 0.78) in comparison to what has been reported for other tasks. Thus there was little room for the older adults to exhibit less distinctiveness relative to the young.

Associations between brain activity with age and balance

Correlation of brain function and age

There was a negative correlation between age and activation in the left parietal operculum (figure 3.4, table 3.1), with younger subjects exhibiting greater activation than older ones. There was also a positive correlation between age and deactivation of the left intracalcarine cortex and the right temporal pole (figure 3.5, table 3.2), reflecting that older adults deactivated these regions more than younger subjects. Cerebellar results for activation and deactivation did not show any significant correlations with age.

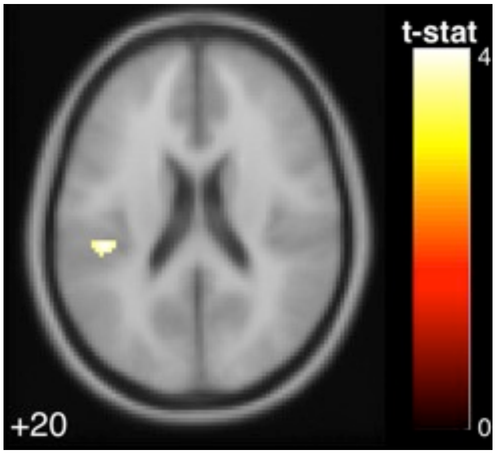

Figure 3. 4 The parietal operculum cortex exhibited a negative association with age in the pooled young and older adults group.

Table 3. 1 The simple regression results of activated regions with significant negative correlation with age.

Table shows all local maxima separated by more than 20 mm. Although this result did not survive FDR correction, it survived a more stringent correction of P<.05 FWE. Regions were automatically labeled using the HarvardOxford max probability atlas. x, y, and z = Montreal Neurological Institute (MNI) coordinates.

			MNI Coordinates		
Region Label	Extent	t-value	x	y	z
Parietal Operculum Cortex	40	4.096	-44	-30	20

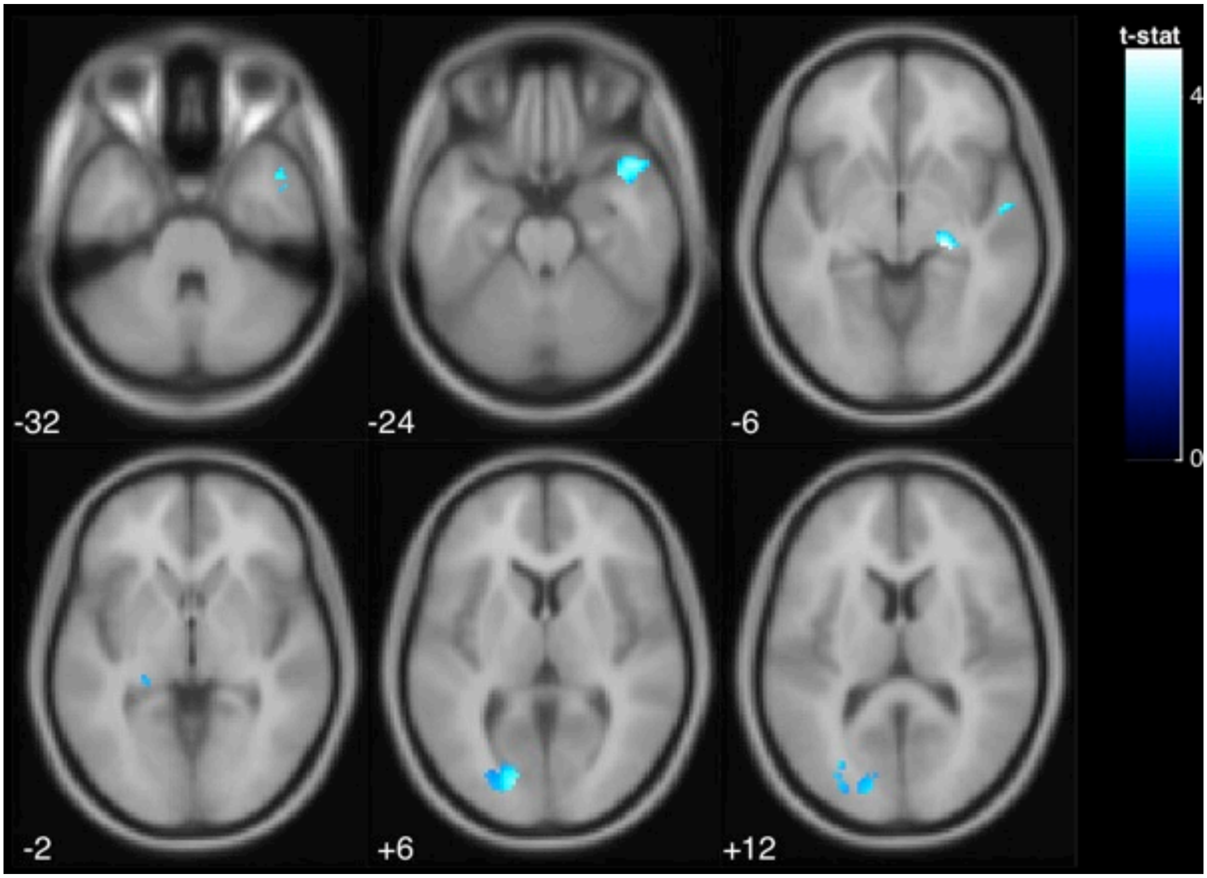

Figure 3. 5 The intracalcarine cortex and temporal pole exhibited a positive association between age and deactivation level in the pooled young and older adults group.

Table 3. 2 The simple regression results of deactivated regions with significant positive correlation with age.

Table shows all local maxima separated by more than 20 mm (P<.05 FDR corrected). Regions were automatically labeled using the HarvardOxford max probability atlas. x, y, and z =Montreal Neurological Institute (MNI) coordinates.

			MNI Coordinates		
Region Label	Extent	t-value	x	y	z
Temporal Pole	221	4.083	46	14	-24
Intracalcarine Cortex	212	3.968	-16	-84	6
Anterior Superior Temporal Gyrus	16	3.623	54	-6	-6

Correlation of brain function and behavior

As shown in figure 3.6, there was a positive correlation between balance performance in normal stance (indicated by area of ellipse) and deactivation of the postcentral gyri and temporal pole, reflecting that those subjects who had a larger ellipse area in normal stance showed higher deactivation of these regions, regardless of age (table 3.3).

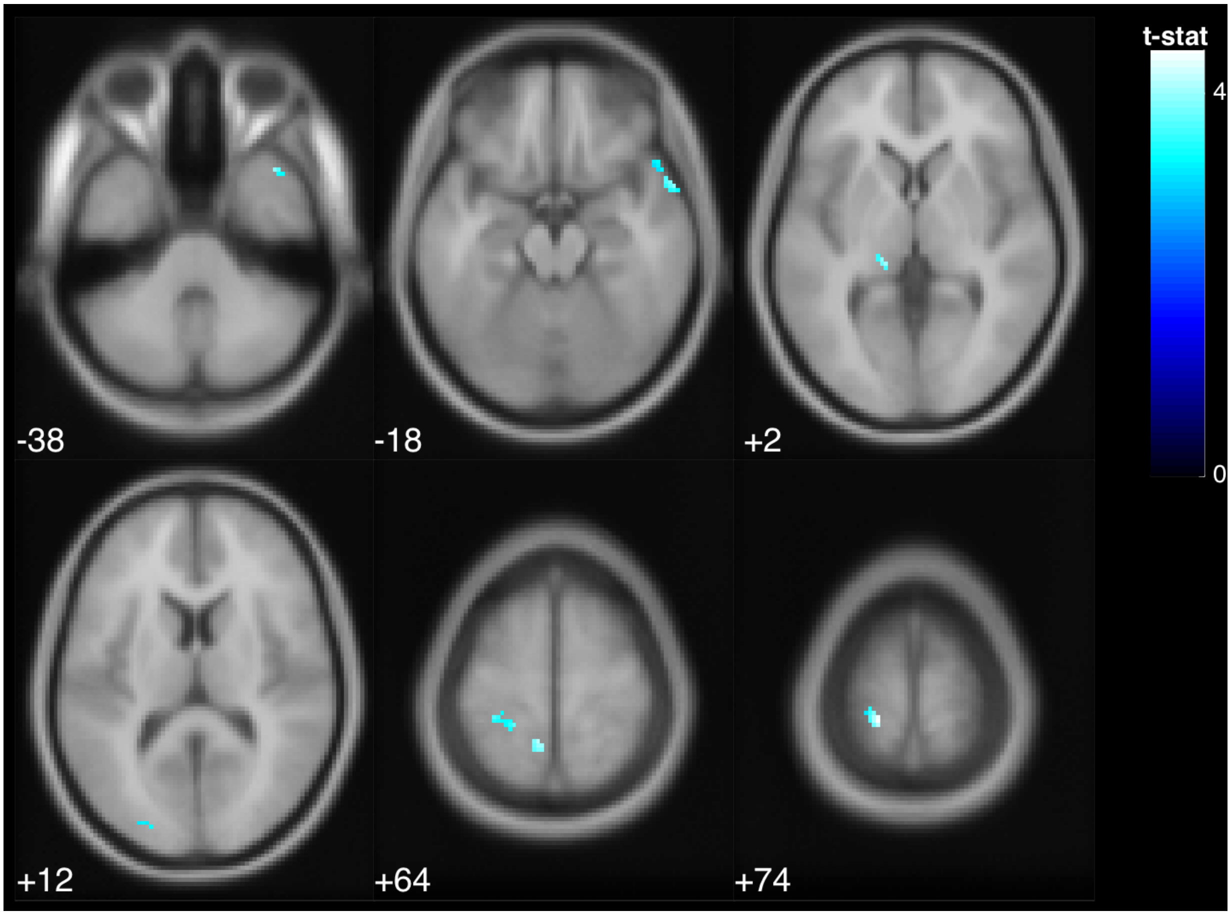

Figure 3. 6 Regardless of age, greater deactivation of the postcentral gyrus and temporal pole was associated with poorer balance.

Table 3. 3 The simple regression results of deactivated regions with significant positive correlation with performance.

Table shows all local maxima separated by more than 20 mm (P<.05 FDR corrected). Regions were automatically labeled using the HarvardOxford max probability atlas. x, y, and z =Montreal Neurological Institute (MNI) coordinates.

Region Label	Extent	t-value	MNI Coordinates x	y	z
Postcentral Gyrus	121	4.452	-18	-38	74
Postcentral Gyrus	20	4.143	-8	-48	64
Temporal Pole	32	3.987	40	16	-38
Temporal Pole	48	3.938	60	8	-18
Lingual Gyrus	10	3.570	-30	-52	-4
Occipital Pole	12	3.328	-22	-90	12

Besides normal stance, no other balance measures were associated with brain activity at FDR p< .05.

As for the cerebellar analyses, we found that performance in single leg stance was negatively correlated with deactivation of the brainstem, cerebellar lobule VI and Crus I, reflecting that those who performed better in single leg stance exhibited greater deactivation of these regions, regardless of age (figure 3.7, table 3.4).

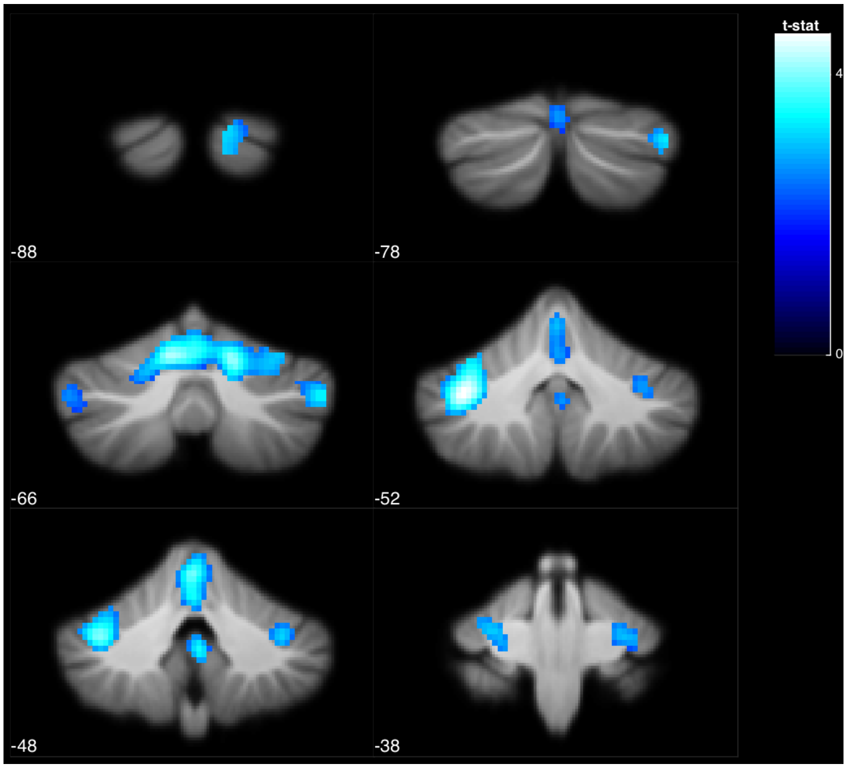

Figure 3. 7 The brainstem and cerebellar lobule VI and Crus I exhibited a negative association between deactivation levels and balance performance in single leg stance (indicated by area of ellipse).

Table 3. 4 The simple regression results of deactivated regions with significant negative correlation with performance.

Table shows all local maxima separated by more than 20 mm (P<.05 FDR corrected). Regions were automatically labeled using the SUIT atlas. x, y, and z =Montreal Neurological Institute (MNI) coordinates in the left-right, anterior-posterior, and inferior-superior dimensions, respectively.

			MNI Coordinates		
Region Label	Extent	t-value	x	y	z
Crus I	2227	4.587	-36	-52	-35
Lobule VI	2227	4.401	16	-64	-23
Lobule VI	2227	4.289	-10	-64	-21
Brain-Stem	58	3.472	2	-48	-37
Crus I	200	3.381	50	-66	-37
Brain-Stem	90	3.274	-4	-22	-13
Crus II	98	3.143	14	-88	-31

Conjunction analyses

Next, we conducted a conjunction analysis across the results from the brain activity – age and the brain activity – balance performance correlations. The results reflect brain regions where activation or deactivation was commonly associated with both age and behavior.

We found that deactivation of left postcentral gyrus, intracalcarine cortex, and right temporal pole was positively correlated with both age and balance performance in normal stance (Figure 3.8); that is, those subjects who were older, and those subjects who performed more poorly in normal stance commonly deactivated these regions more than the other subjects (table 3.5).

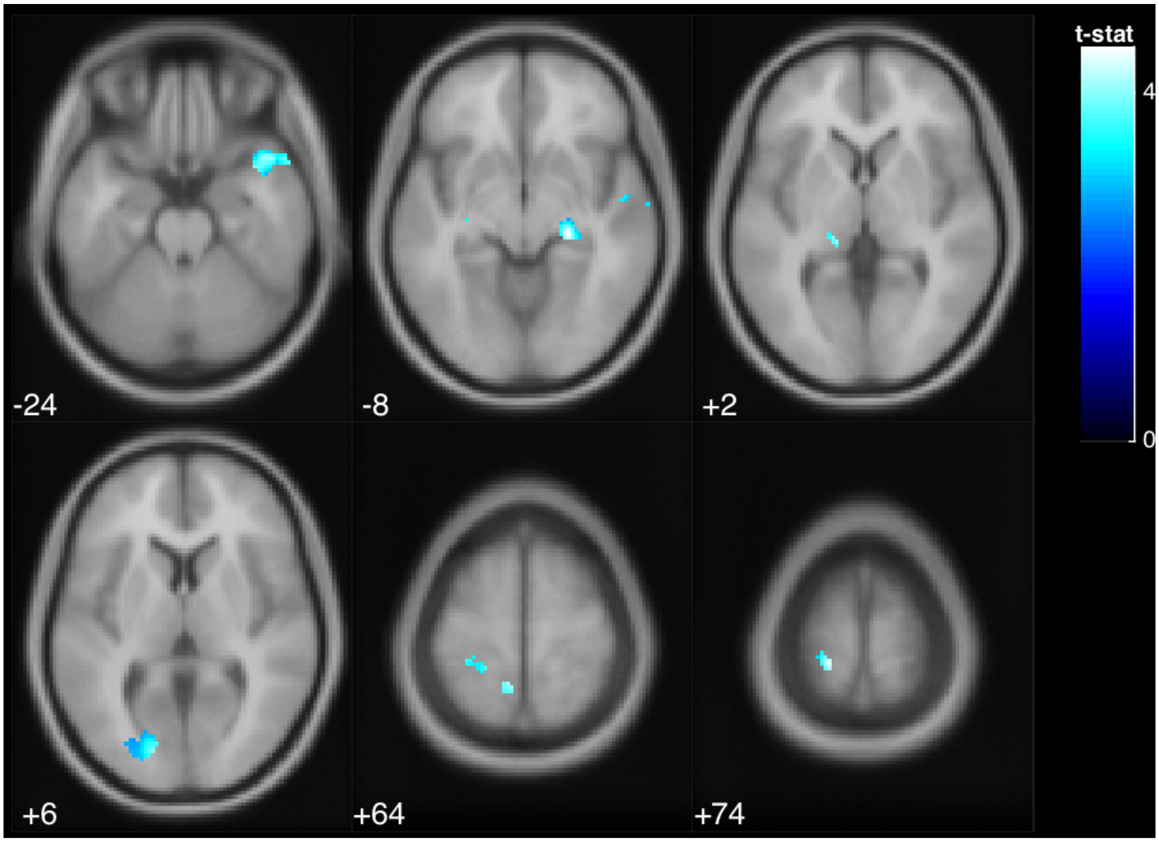

Figure 3. 8 The deactivation of postcentral gyrus, intracalcarine cortex, and temporal pole was positively correlated with age and balance performance in normal stance (indicated by area of ellipse).

Table 3. 5 The multiple regression results of deactivated regions with significant positive correlation with age and performance.

Table shows all local maxima separated by more than 20 mm (P<.05 FDR corrected). Regions were automatically labeled using the HarvardOxford max probability atlas. x, y, and z =Montreal Neurological Institute (MNI) coordinates in the left-right, anterior-posterior, and inferior-superior dimensions, respectively.

			MNI Coordinates		
Region Label	Extent	t-value	x	y	z
Postcentral Gyrus	121	4.452	-18	-38	74
Postcentral Gyrus	20	4.143	-8	-48	64
Temporal Pole	298	4.083	46	14	-24
Intracalcarine Cortex	215	3.968	-16	-84	6
Anterior Superior Temporal Gyrus	16	3.623	54	-6	-6
Lingual Gyrus	10	3.570	-30	-52	-4

None of the other whole brain or cerebellar conjunction analyses were significant.

Correlation of laterality index and behavior

We found no significant associations between laterality index and measures of balance.

Correlation of signal to noise ratio and behavior

We found no significant associations between signal to noise ratio and measures of balance.

Correlation of distinctiveness/within scores and behavior

We found no significant correlation between distinctiveness scores and measures of balance. However, there was a significant negative correlation between individuals' within scores and their performance in normal stance (r = -0.47, p = 0.02), reflecting that better balance was correlated with more consistent neural representations of vestibular activity within a condition, regardless of age.

vi. Discussion

In response to vestibular stimulation both young and older adults exhibited activation of the canonical vestibular cortex (i.e. bilateral parietal operculum). However, as evident by regression analysis, younger adults activated the vestibular cortex more strongly than older adults. In general, brain regions that process other sensory inputs (i.e. somatosensory cortex, visual cortex, and the cerebellum) exhibited deactivation, which—in contrast to the activation patterns—varied with age. The level of deactivation in these regions was correlated with both age and balance; as older age and poorer balance in the normal stance task were associated with greater deactivation of visual and somatosensory cortices and the temporal poles.

Consistent with these findings, other studies have documented similar cross modal sensory inhibition patterns. For example, Bense et al. (S Bense et al., 2001) showed that in response to galvanic vestibular stimulation, somatosensory and visual cortices were deactivated. Deutschlander et al. (Deutschländer et al., 2002a) demonstrated that with unimodal vestibular stimulation, visual cortex exhibited deactivation, and using unimodal visual stimulus resulted in deactivation of vestibular cortex. Laurienti et al. (Laurienti et al., 2002a) reported that auditory stimulation resulted in activation of the auditory cortex and deactivation of the visual cortex; meanwhile the opposite pattern was observed in response to visual stimulation. Similarly, Uludağ et al. (Uludağ et al., 2004) used a flickering checkerboard to induce activation in the visual cortex, and found that simply closing the eyes resulted in deactivation of the visual cortex.

Relative reliance on vestibular, visual and somatosensory inputs varies within individuals. Studies have shown that, in comparison to young adults, older adults seem to rely more strongly on vision for balance control (Costello & Bloesch, 2017). They also rely more on proprioception (Anson et al., 2017; Pasma et al., 2015), which can be shifted towards vestibular reliance with active balance training (Bao et al., 2018; Wiesmeier et al., 2017). Wiesmeier and colleagues showed that balance training improved balance performance for older adults, and made them more reliant on vestibular inputs and less so on proprioceptive inputs, which was more similar to the pattern for young adults. We found that younger adults showed greater vestibular activity and older adults exhibited more deactivation of the somatosensory and visual cortices. It seems that when vestibular information is the most dominant sensory modality (as in our design), the suppression of other sensory systems (i.e. somatosensory and visual) enhances the allocation of neural resources in favor of vestibular processing, and more strongly in older adults. Greater deactivation in these regions was also an indicator of poorer balance in the normal stance task, in which all sensory modalities are available. Therefore, less engagement of visual and somatosensory cortices that occurs in response to unimodal vestibular stimulation is associated with poorer performance in this multisensory task. On the other hand, one might argue that these patterns of brain deactivation in correlation with balance should be interpreted in light of age differences in muscle response. As an adaptive strategy, older adults exhibit greater co-contraction of muscles in normal stance compared to young to maintain their balance (Nelson-Wong et al., 2012). One might speculate that older adults with better postural control may be better at implementing these adaptive strategies, and therefore exhibit less inhibition (i.e. higher recruitment of multiple regions, which is linked to muscle co-contraction).

Moreover, our finding of overall stronger brain responses in young adults parallels previous reports (Hesselmann et al., 2001; Kannurpatti, Motes, Rypma, & Biswal, 2010). For example, Burki et al. (Bürki et al., 2017) showed an overall lower magnitude of brain activation in older adults performing an fMRI gait assessment task.

Our selected method for stimulating the vestibular pathways (i.e. skull tap) induced bilateral activation in both the young and older adults; the left and right tap activation patterns were also not distinctive in young adults, which potentially explains the lack of age differences in these two measures. However, the consistency of activity within a condition (indicated by the "within" scores) showed a significant association with better balance in the normal stance condition. That is, more consistent brain activity across repeated runs of vestibular stimulation was associated with better balance.

Our current results support that pneumatic skull taps elicit vestibular neural activation in older adults, while being tolerable, fast, and easy to conduct, as we reported previously for young adults (Noohi et al., 2017). Thus, this method could be implemented as a novel approach for studying vestibular function and its correlation with balance in a range of populations. By using fMRI we were able to assess the function of vestibularly stimulated subcortical structures (e.g. brainstem, cerebellum, and thalamus) in addition to cortical regions that would be captured with more portable neuroimaging techniques such as fNIRS.

Limitations

The main limitation of this study was the small number of participants per group. Further, the technical constraints of neuroimaging methods warrant a careful interpretation of upright balance measures in correlation with supine brain measures. Moreover, introducing a unimodal vestibular input induces sensory reweighting processes, in which attention can modulate the observed patterns of activations/deactivations and their correlation with balance. Since we did not control for the role of attention, caution should be taken in interpretation of these findings.

vii. Conclusion

We found that both age and balance performance are related to consistency of vestibular neural processing and deactivation of the somatosensory and visual cortices. Considering the high prevalence of falls among older adults, mortality of fall-related injuries, and costs of rehabilitation and healthcare (Center for Disease Control & Prevention), a better understanding of the aging vestibular system may lead to important, new approaches to balance interventions.

Acknowledgments

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Chapter IV

Functional Connectivity in response to Vestibular Stimulation and its Relationship to Postural Control

i. Abstract

The functional connectivity of default mode network and primary sensory regions (e.g. visual and auditory) has shown to decline with age. However, less is known about age effects on vestibular functional connectivity. To better understand the role of aging vestibular cortex in postural control, we assessed age differences in the connectivity of vestibular cortex with other sensory regions involved in postural control. We investigated resting state functional connectivity, as well as connectivity during vestibular stimulation, and compared the connectivity patterns across young and older adults. We found no significant age differences in vestibular network connectivity patterns at rest. During vestibular stimulation, connectivity was significantly increased from the resting state. Connectivity was higher in young relative to older adults. Moreover, we found that the relationship between task-based connectivity and balance differed in young and older adults, but that the relationship between resting state connectivity and balance did not. Specifically, young adults who exhibited higher task-based connectivity also had higher body sway in more challenging tasks, but in the older adults these correlations were present for the easier tasks, not the harder tasks. One potential interpretation of these results is that as task difficulty increases, the available neural resources for compensation in older adults are at ceiling level. Thus we found that in the presence of vestibular stimulation, connectivity of the vestibular cortex with other sensory regions predicts postural stability in a manner that differs with age and task demands.

ii. Introduction

In humans, the vestibular network comprises multiple cortical and subcortical regions that communicate with each other to process vestibular inputs. These regions include (but are not limited to) the parieto-insular vestibular cortex (PIVC), the vestibular nuclei, the thalamus and the cerebellum. Many studies have looked at the functional and anatomical connectivity of these regions using fMRI and diffusion tensor imaging (DTI) techniques. Kirsch et al. (Kirsch et al., 2016) provided evidence that functional connectivity among vestibular regions mirrors anatomical connectivity. Specifically, they showed that bilateral vestibular nuclei and bilateral insular cortex are both functionally and anatomically connected. In a recent study by Eickhoff et al. (Eickhoff et al., 2010), distinct connectivity patterns for core vestibular cortical regions were further identified. The operculum parietale (OP) showed functional and anatomical connectivity with regions of higher order somatosensory processing (anterior inferior parietal cortex, intraparietal sulcus, ventroposterior lateral and inferior nuclei of thalamus). Like Kirsch et al. (Kirsch et al., 2016), their results supported the overall congruency between functional and anatomical connectivity maps, but they also found some discrepancies that could be related to the fact that co-activation of different brain regions can occur independently from their anatomical connections. Also, in their previous work (Simon B. Eickhoff et al., 2006), they found no anatomical asymmetry between left and right OP, whereas there was significant functional asymmetry in vestibular processing. Along the same lines, zu Eulenburg et al. (zu Eulenburg et al., 2012) conducted a meta-analysis in which they showed OP as the core region of the vestibular network. They further implemented a connectivity analysis with OP as the seed region, which revealed functional connectivity of right OP with temporo-parietal cortex, premotor cortex, and the midcingulate gyrus.

Despite the research identifying the vestibular network's core regions and their connectivity, to the best of our knowledge, only one study has investigated the effects of healthy aging on vestibular network connectivity. Cyran et al. (Cyran et al., 2016) recently reported age differences in functional connectivity of the vestibular network during galvanic vestibular stimulation. Their findings suggest that vestibular network connectivity was reduced in older adults, whereas the somatosensory network showed no age differences in functional connectivity. Moreover, they showed that these differences in vestibular network functional connectivity were independent of age-related structural alterations, and were associated with declines in magnitude of the BOLD response. They did not conduct any balance assessments to determine the functional consequences of these age differences in vestibular connectivity, however.

Reports of age differences in functional connectivity in other sensory networks can suggest hypotheses about the vestibular system. For example, Mowinckel et al. (Mowinckel, Espeseth, & Westlye, 2012) found reduced resting state connectivity within the visual and default mode networks for older versus young adults. Yang et al. (Yang et al., 2014) also showed that with advancing age, the precuneus network merged with the default mode network, and specific functional connectivity patterns became less distinguishable between the two. Roski et al. (Roski et al., 2013) reported that older adults had reduced resting state sensorimotor and visual network connectivity. In a study of age effects on auditory cortex functional connectivity, Peelle et al. (Peelle, Troiani, Wingfield, & Grossman, 2010) found that older adults exhibit less activity in speech comprehension core regions and reduced connectivity between these areas.

Here we assessed age differences in vestibular functional connectivity during both the resting state and during vestibular stimulation. Based on the studies just reviewed, we hypothesized that younger individuals would exhibit greater connectivity during both the rest and vestibular stimulation blocks.

A number of previous studies have also shown that in the presence of a unimodal sensory input, there is a general cross-modal deactivation of other sensory areas (Sandra Bense, Stephan, Yousry, Brandt, & Dieterich, n.d.; T Brandt, Bartenstein, Janek, & Dieterich, 1998; Deutschländer et al., 2002b; Laurienti et al., 2002b). We therefore hypothesized that during vestibular stimulation the connectivity of vestibular cortex with other sensory regions would decline.

Yuan et al. (Yuan et al., 2015) showed that greater resting state functional connectivity (between sensorimotor, visual, vestibular, and left fronto-parietal cortical areas) is associated with higher walking speed in older adults (with the latter measured outside of the scanner). We therefore hypothesized that individuals who exhibit greater connectivity between vestibular and other sensory regions at rest would have better postural stability.

Our hypothesis for task-based connectivity associations with balance was formed based on the findings of Pleger et al. (Pleger et al., 2006). They applied excitatory rTMS to primary sensory cortex, and found increased connectivity from the somatosensory to primary motor cortex, which was correlated with behavioral improvements in tactile discrimination. Therefore, we hypothesized that better balance would be correlated with increased connectivity of the vestibular network during vestibular stimulation.

iii. Methods

Participants

We recruited 32 healthy adults (15 old: 65-80, $\bar{x}$ =71.2 ± 4.14, 10 females & 18 young: 18-35, $\bar{x}$ =21 ± 2.44, 8 females) from the University of Michigan clinical studies website. All subjects were right handed. The exclusion criteria were defined as any vestibular, neurological, auditory, or postural disorders. In addition to the Montreal Cognitive Assessment (MOCA), a typical MRI screening was conducted. The University of Michigan Institutional Review Board approved the study, and all subjects signed the consent form prior to participation.

Balance Assessments

Subjects underwent a series of balance assessments in four conditions (Romberg, tandem, normal, and single leg stance), at four degrees of difficulty (eyes closed/open, yaw/pitch/no head movement, arms crossed/free, & on firm/compliant surface). Each of these conditions served to challenge postural stability by degrading or removing a particular sensory input: closing the eyes removed the visual inputs, head movements challenged the vestibular system, crossing the arms served to prevent compensatory strategies, and the compliant surface degraded the somatosensory/proprioceptive inputs.

The yaw and pitch head movements consisted of sinusoidal head movements (roughly ±20º, 0.6 Hz). Subjects were instructed to match their head movement to the beat of a metronome (0.6 Hz) that was used consistently for all subjects. Subjects were asked to move the head approximately 20 degrees, within their comfort level. A high-density viscoelastic foam was used as the compliant surface (length=45cm, width=45cm, thickness=18cm; Natus Inc.). The order of the tasks was counterbalanced across subjects.

The amount of body sway in these tasks reflected individual differences in postural stability. We calculated the amount of body sway as the area of an ellipse fit to the 95th percentile confidence interval of center of pressure motion in the anterior-posterior and medial-lateral directions (Lee et al., 2012; Sienko et al., 2008). Better postural stability was reflected as less body sway and smaller ellipse size.

For each task, we instructed participants to maintain their balance for 30 seconds. The task was stopped prematurely if participants lost their balance.

FMRI data acquisition

Magnetic resonance images were acquired using a 3.0 Tesla MRI scanner (General Electric Medical Systems, DISCOVERY MR750). The parameters of the acquisition for structural images included a T1-weighted 3D IR Prepped FSPGR (TR = 12.2 s, TE =5.1 ms, FA= 15°, matrix size= 256 x 192, FOV= 260 x 260 mm, slice thickness = 1 mm, #slices=152) covering the whole brain and the cerebellum. A gradient-echo plane ascending sequential sequence (FOV=220 mm, TR=2 s, TE= 30 ms, number of slices=43, voxel size =3.4375x3.4375mm) was used to acquire the resting state and functional images.

Head motion was restricted using a Velcro strap over the forehead. Pads were placed around the head to protect hearing (in addition to ear plugs) and to further limit head movements. To collect physiological responses (cardiac and respiration rates), a pulse oximeter was placed on the subjects' index finger and a respirometer belt was wrapped around the abdomen.

The acquisition protocol was as follows: high-resolution T1 structural scan (SPGR), resting state connectivity, and vestibular stimulation. Subjects were instructed to keep their eyes open during the connectivity runs, while keeping their gaze on a fixation point presented to them on the screen. They were instructed to close their eyes during the vestibular stimulation runs to minimize visual processing that could interact with the vestibular system. The resting state connectivity run lasted 10 minutes, and the vestibular stimulation run lasted 4 minutes. The stimulation was applied in the form of pneumatic taps delivered over the left cheekbone, in five alternating blocks of stimulation (24 seconds) and rest (20 seconds).

iv. Data analysis

Balance performance analysis

We used Vicon's Nexus software to analyze the center of pressure (COP) data that were collected at 100 Hz on the force platform. The force platform channels were plugged into a data acquisition board and the data were recorded using the Nexus software, which then automatically calculated COP data from the raw channel data. The COP data were then exported from the Nexus software and outcome measures were calculated. Similar to previous studies (Lee et al., 2012; Sienko et al., 2008), we applied a low pass filter with a 2nd order recursive Butterworth filter with a cutoff of 10 Hz. For each balance trial, we fitted a 95% confidence interval ellipse to the anterior-posterior and medial-lateral trajectories. The area of the ellipse was calculated and used for correlation with individual differences in brain connectivity patterns.

As described in the previous chapter, four tasks were selected for balance assessment analyses:

1- Normal (feet apart) stance on firm surface with eyes open (baseline measure, reliance on visual, vestibular and somatosensory inputs)
2- Romberg (feet together) stance on firm surface with eyes closed (removed visual inputs, reliance on vestibular and somatosensory inputs)
3- Romberg (feet together) stance on compliant surface with eyes closed (removed visual inputs, degraded somatosensory inputs, greater reliance on vestibular inputs)
4- Single leg stance (left foot) on firm surface with eyes open (degraded somatosensory inputs, greater reliance on visual and vestibular inputs)

The COP data was analyzed for a subgroup of subjects who were able to complete the 30 seconds of performance in these tasks (i.e. 12 young and 14 older adults).

FMRI analysis

We used SPM12 software (Welcome Department of Cognitive Neurology, London, UK (Karl. J. Friston et al., 1995)) and the CONN functional connectivity toolbox v14 (Whitfield-Gabrieli & Nieto-Castanon, 2014) to preprocess and analyze the data. The preprocessing steps were completed using the conn toolbox default preprocessing pipeline: 1) Structural segmentation (gray matter, white matter, CSF) and normalization to the Montreal Neurological Institute (MNI152) template (Karl. J. Friston et al., 1995). 2) Functional realignment, slice timing correction, outlier detection (ART-based), segmentation (gray matter, white matter, CSF) and MNI normalization. We segmented and normalized the cerebellum separately using the Spatially Unbiased Infra-tentorial Template (SUIT, Diedrichsen and Zotow, 2015; Diedrichsen, 2006; Diedrichsen et al., 2011, 2009).

We estimated functional connectivity between regions identified in the previous chapter as activated by vestibular stimulation, including the Parietal Operculum, Intracalcarine Cortex, Postcentral Gyrus, Temporal Pole, Brainstem, Cerebellar Lobule VI, and Crus I. We created a 10mm sphere around the corresponding coordinates (5mm sphere for brainstem), and functional connectivity data was derived from unsmoothed data to avoid spillage from neighboring voxels.

A denoising procedure was applied to remove the effects of confounding factors (white matter, CSF, motion, main task effects). A band pass filter threshold of [0.008 inf] was applied to both resting state and stimulation runs. A first level analysis was then performed using a General Linear Model (GLM) for the resting state data and a general Psycho-Physiologic Interaction (gPPI) model for stimulation blocks. The bivariate correlation measures resulting from the GLM represented the connectivity during rest (e.g. a positive correlation indicated a positive association between the time series of two ROIs during rest, and negative correlation represented anti-correlations between the time series of two ROIs during rest). Whereas, the bivariate correlation measures resulting from the gPPI analysis indicated the change in connectivity during stimulation compared to an implicit baseline condition (i.e. rest blocks). So positive correlations reflected higher connectivity during stimulation relative to baseline and negative correlations reflected lower connectivity during stimulation relative to baseline.

Next, a ROI to ROI analysis was performed to quantify connectivity. The correlation between each ROI and all of the others was calculated during the rest and vestibular tap stimulation conditions. We applied the false discovery rate (FDR) error correction to correct for multiple comparisons. The results were considered significant if they reach the p<.05 (FDR) at the peak voxel level. We conducted the analysis for resting state and stimulation runs separately at the first level, and then analyzed the alterations and age differences in the connectivity pattern using t-tests at the second level.

We extracted the average time series of all voxels within each ROI and conducted correlation analyses to compare the average time series of selected ROIs during rest and stimulation. We selected the parietal operculum (i.e. vestibular cortex) as the seed ROI and compared its average time series with the other ROIs. Positive connectivity of the vestibular cortex with any of the other ROIs suggests a synchronous pattern of their time series (i.e. activation and deactivation at similar times) and does not necessarily reflect an overall increase in the BOLD signal. Lastly, we assessed the relationship between such correlations and individual differences in age and balance. The Fisher r-to-z transformation is used to assess the significance of the difference between two correlation coefficients.

v. Results

Balance assessment results

As shown in the previous chapter (figure 3.1), we found a significant difference between young and older adults' performance in single leg stance (SLS) with eyes open (t= -2.69, p= 0.01, df= 23, CI: -105.88, -13.95), documenting poorer balance performance (greater ellipse area) for older adults. The other CoP measures were not significantly different between young and older adults.

Functional connectivity results

For all the results, we report the combined average times series of the Crus I and lobule VI ROIs as the cerebellum ROI, since their timecourses were strongly correlated with each other (r>.9).

Resting-state functional connectivity

First, we assessed whether functional connectivity of the vestibular cortex during rest differed across the two age groups. The two-way ANOVA for age and ROI showed no significant main effects or interaction, suggesting that at rest, there was no significant age difference in connectivity of the vestibular cortex with the other ROIs. Figure 4.1 illustrates a positive trend for correlation of vestibular cortex with all of the other ROIs, with the exception of the visual cortex in older adults (Figure 4.1).

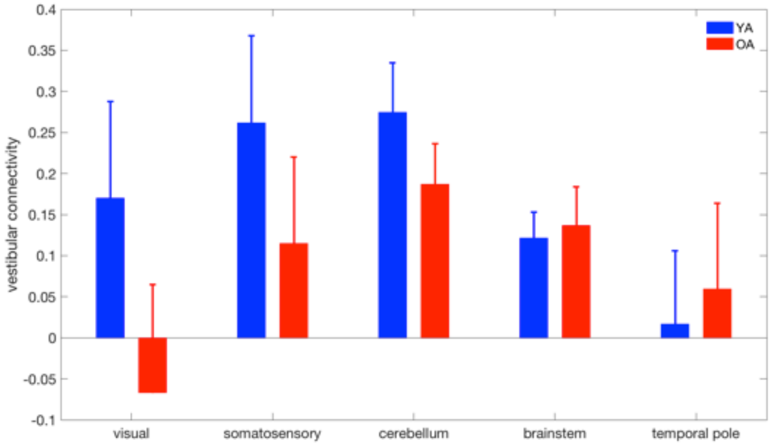


Figure 4. 1 Resting state functional connectivity of the vestibular cortex (no significant main effects of age or ROI).

Error bars represent standard error. YA=young adults, OA=older adults

Task-based functional connectivity

Next, we assessed whether functional connectivity of vestibular cortex during stimulation differed for the two age groups. The two-way ANOVA for age and ROI again showed no significant main effects or interaction. During vestibular stimulation, the vestibular cortex activity was positively correlated with that of all of the other ROIs (Figure 4.2).

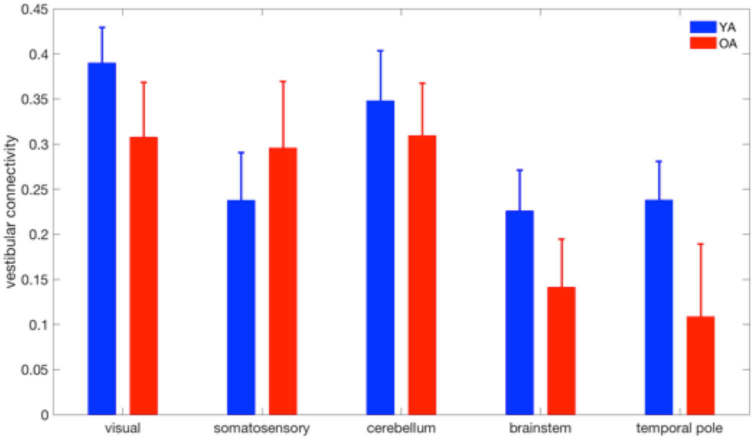
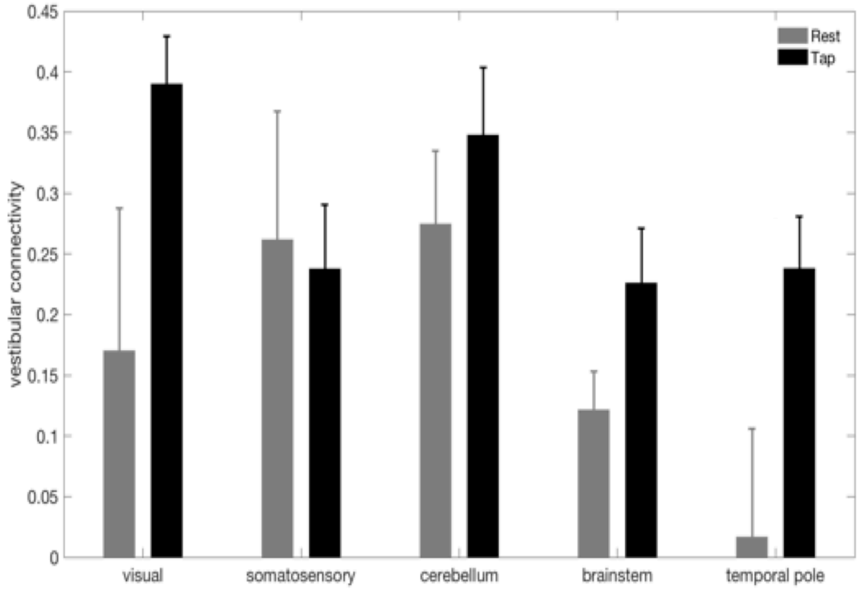


Figure 4. 2 Functional connectivity of the vestibular cortex during vestibular stimulation (no significant main effects of age or ROI). Error bars represent standard error. YA=young adults, OA=older adults

Comparisons of resting-state and task-based functional connectivity

Next, we assessed whether functional connectivity of the vestibular cortex changed from rest to stimulation, and whether this effect differed for young and older adults. A three-way ANOVA of age, ROI, and condition (i.e. rest vs. stimulation) showed a significant main effect of age (F=3.91, p=0.04), condition (F=14.84, p=0.0001), and a significant age by condition by ROI interaction (F=2.33, p=0.04). The young adults exhibited overall greater connectivity than older adults (regardless of condition), and connectivity was higher during vestibular stimulation relative to rest (regardless of age). A follow up two-way ANOVA of age and condition for each ROI revealed a main effect of condition for the visual ROI, suggesting that vestibular-visual connectivity was significantly greater during stimulation than rest (F=9.85, p=.002) (Figure 4.3). The three-way interaction was driven by the increase in vestibular connectivity with temporal pole from rest to stimulation; which was only evident in young adults (F=5.03, p=.03).

a)



b)

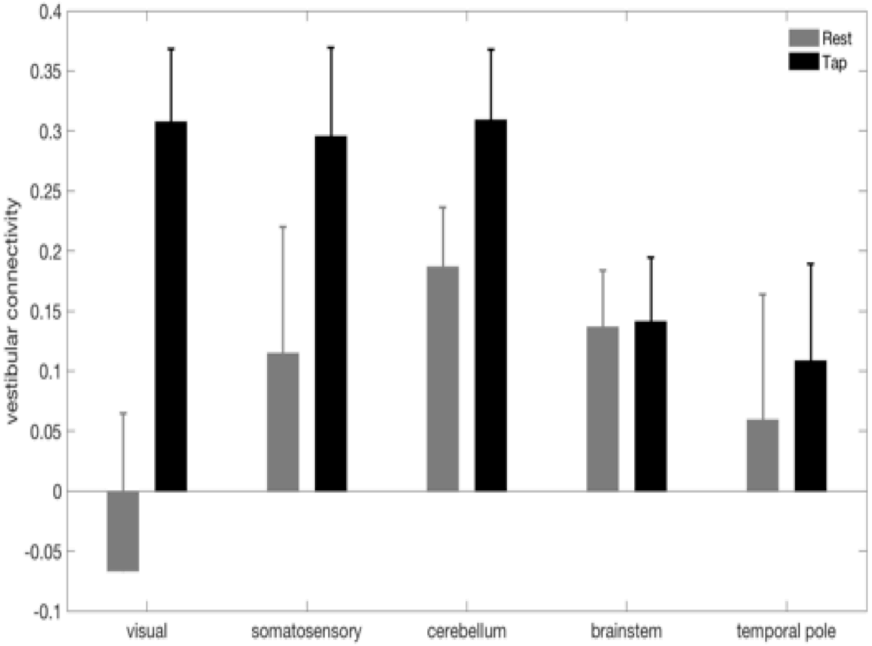


Figure 4. 3 Functional connectivity of vestibular cortex during rest and tap stimulation, for a) young and b) older adults (significant main effects of age, condition, and age by condition by ROI interaction).

Error bars represent standard error.

Functional connectivity association with balance

Next, we assessed whether functional connectivity of vestibular cortex predicts postural control.

For each individual, the correlation values between the vestibular cortex and the other ROIs were analyzed to evaluate associations with individual differences in postural control. Based on visual inspection, we selected the second half of the stimulation run (~last two minutes of a 4 minute run) for the correlation analyses (see Figure 4.4 for an example). The timecourses exhibited much stronger differences between good and bad performers in the second half, suggesting an adaptation to the novel vestibular stimulation that might have functional implications on balance control.

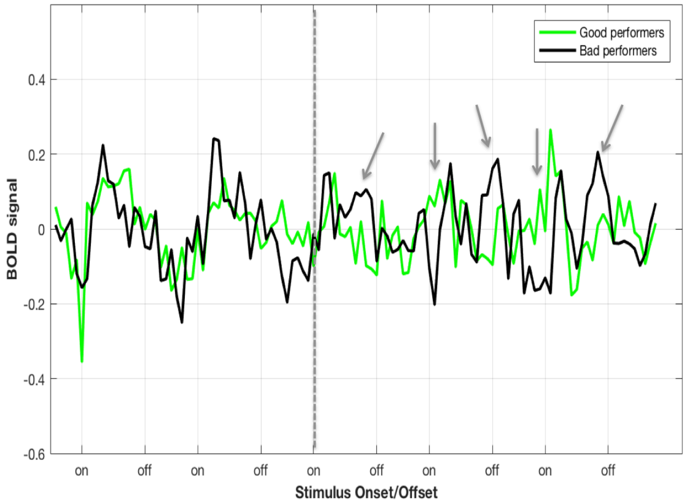
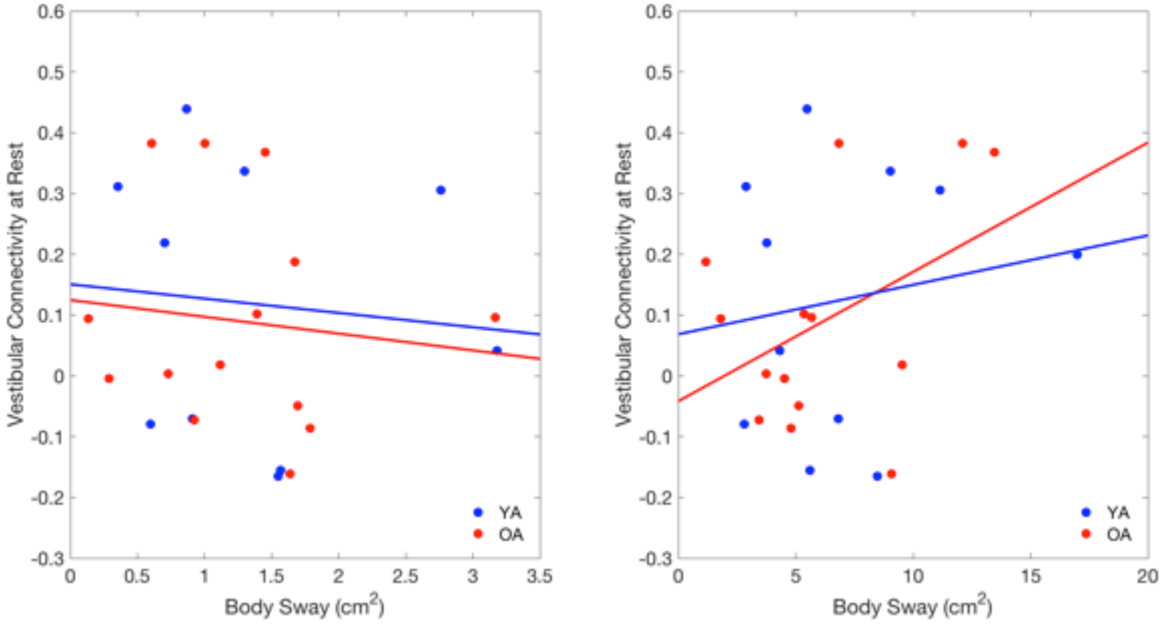


Figure 4. 4 An example timecourse extracted from the vestibular cortex ROI.

This example shows the group average timecourse of vestibular signals for the older adults, parsed by performance in Romberg on Foam task.

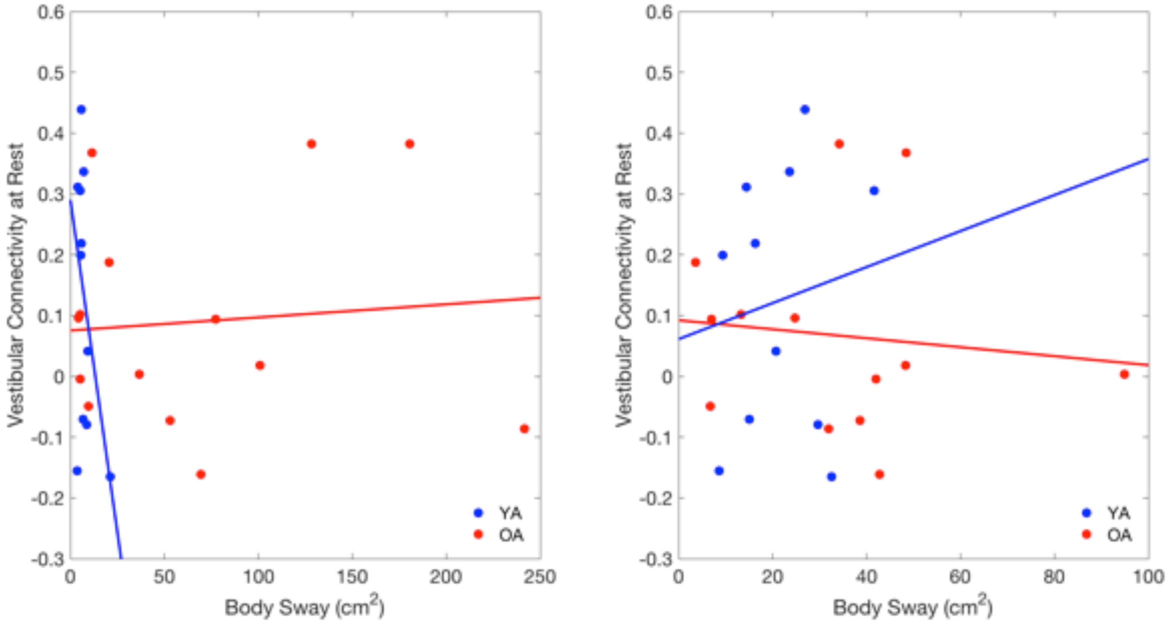
Resting state functional connectivity association with balance

First we assessed whether resting state functional connectivity of the vestibular cortex predicts postural control, and whether this effect is modulated by age and task difficulty. Figure 4.5 depicts the correlation between vestibular cortical connectivity and performance in each of the four balance tasks. For each task, the measures of body sway are presented on the x-axis and the connectivity of vestibular cortex with other ROIs (i.e. correlation of their timecourses) is shown on the y-axis.



a) Normal Stance

b) Romberg



c) Single Leg Stance

d) Romberg on Foam

Figure 4. 5. Correlation of vestibular connectivity during rest with performance in a) normal stance, b) Romberg, c) Single Leg Stance, and d) Romberg on Foam tasks.

Panels a to d are placed in order of lowest to highest difficulty. The correlation values for young adults (YA) were -.09, .15, -.48, & .13 in normal stance, Romberg, Single Leg Stance, and Romberg on Foam; respectively. The correlation values for older adults (OA) were -.11, .43, .08, & -.10 in normal stance, Romberg, Single Leg Stance, and Romberg on Foam; respectively. None were significant.

The overall resting state functional connectivity of vestibular cortex did not predict postural stability in young or older adults. However, the ROI-specific connectivity was a predictor of balance in the Romberg on Foam task for young adults, revealing that higher vestibular-cerebellar connectivity was associated with higher body-sway (r=.61, p=.04).

Further, there was no significant age difference in how performance was associated with vestibular connectivity during rest. However, the ROI-specific correlations revealed a significant age difference in correlation of vestibular-brainstem connectivity with performance in normal stance (z=-2.03, p=.02). This was a positive correlation in the young adult group and negative in the old, revealing that higher connectivity of the vestibular cortex with the brainstem was associated with better performance in the older adults and poorer performance in the young adults. Also, the age difference in association of balance with vestibular connectivity did not change as task difficulty increased. The correlation between performance and vestibular connectivity at rest is summarized in table 4.1.

Table 4. 1 Correlation of vestibular connectivity during rest with performance in a) normal stance and Romberg (low difficulty tasks) and b) Single Leg Stance and Romberg on Foam (high difficulty tasks).

Corresponding p-value to each r and z is shown in parenthesis. *significant at p<.05 (two-tailed)

a)

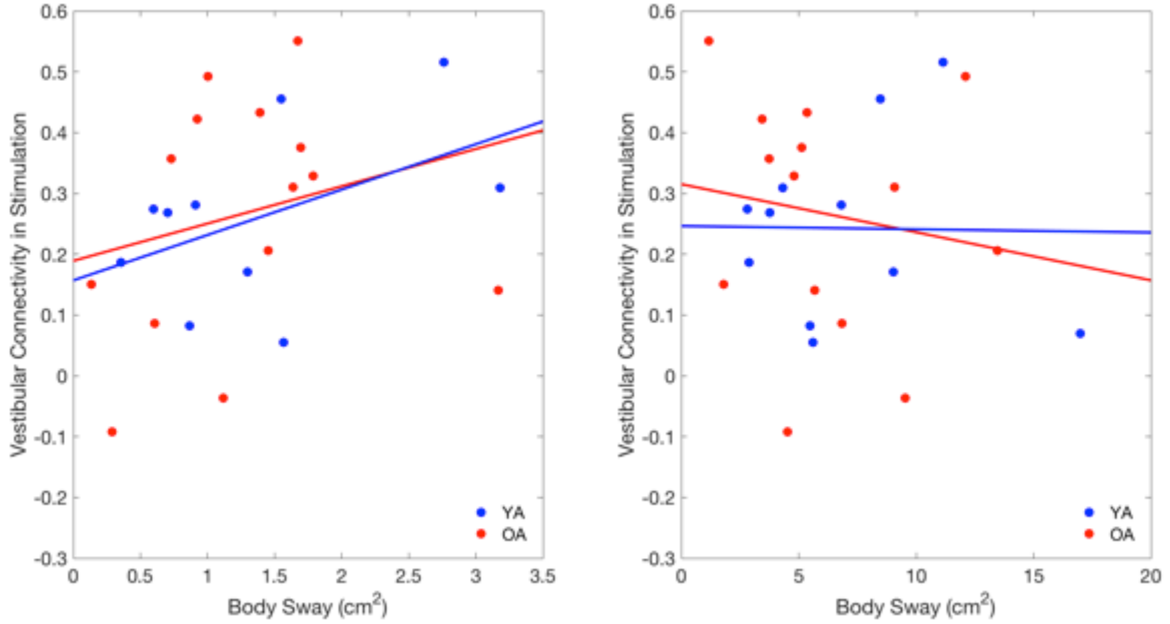
Resting-state Connectivity	**Normal Stance**			**Romberg**		
	Young r (p)	**Old** r (p)	***Age difference*** *z (p)*	**Young** r (p)	**Old** r (p)	***Age difference*** *z (p)*
Vestibular-All ROIs	-.09 (.79)	-.11 (.68)	*.04 (.96)*	.15 (.64)	.43 (.12)	*-.66 (.50)*
Vestibular-Visual	-.35 (.30)	-.09 (.73)	*-.59 (.55)*	.10 (.76)	.22 (.43)	*-.27 (.78)*
Vestibular-Somatosensory	-.09 (.79)	.14 (.63)	*-.5 (.61)*	.19 (.56)	.16 (.56)	*.07 (.94)*
Vestibular-Temporal pole	.05 (.87)	-.09 (.75)	*.3 (.76)*	.18 (.58)	.27 (.33)	*-.2 (.84)*
Vestibular-Cerebellum	.17 (.63)	.03 (.89)	*.3 (.76)*	-.05 (.87)	.44 (.11)	*-1.12 (.26)*
Vestibular-Brainstem	.44 (.20)	-.44 (.11)	***-2.03 (.02)****	-.04 (.90)	.002 (.99)	*-.09 (.92)*

b)

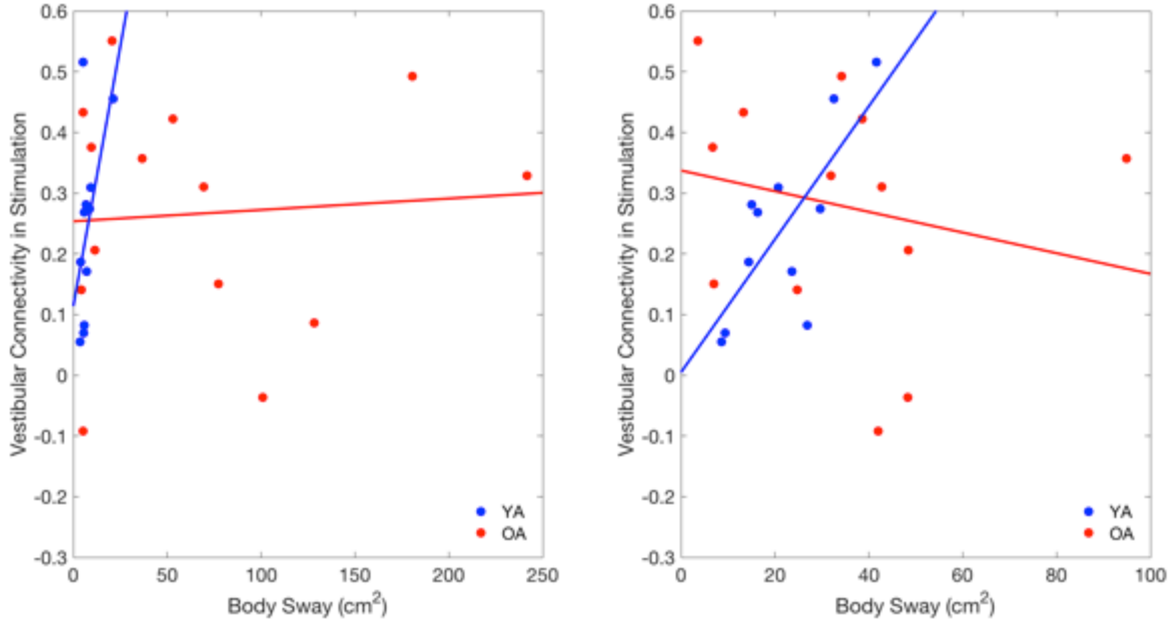
Resting-state Connectivity	Single Leg Stance			Romberg on Foam		
	Young r (p)	**Old** r (p)	***Age difference*** *z (p)*	**Young** r (p)	**Old** r (p)	***Age difference*** *z (p)*
Vestibular-All ROIs	-.48 (.12)	.08 (.76)	*-1.3 (.19)*	.13 (.68)	-.10 (.72)	*.50 (.61)*
Vestibular-Visual	-.38 (.23)	-.06 (.83)	*-.73 (.46)*	-.08 (.81)	-.26 (.38)	*.40 (.68)*
Vestibular-Somatosensory	-.46 (.15)	.18 (.51)	*-1.46 (.14)*	-.05 (.86)	-.11 (.71)	*.13 (.89)*
Vestibular-Temporal pole	-.57 (.06)	.02 (.93)	*-1.44 (.14)*	-.005 (.98)	.25 (.4)	*-.56 (.57)*
Vestibular-Cerebellum	-.03 (.92)	-.17 (.55)	*.3 (.76)*	**.61 (.04)***	.02 (.92)	*1.48 (.13)*
Vestibular-Brainstem	.37 (.25)	.28 (.31)	*.22 (.82)*	.35 (.28)	-.04 (.89)	*.87 (.38)*

Task-based functional connectivity association with balance

Next, we assessed whether functional connectivity of the vestibular cortex during vestibular stimulation is associated with postural control, and whether this effect is modulated by age and task difficulty. Figure 4.6 depicts the correlation between vestibular cortical connectivity and performance in each of the four balance tasks. For each task, the measures of body sway are presented on the x-axis and the connectivity of vestibular cortex with other ROIs (i.e. correlation of their timecourses) is shown on the y-axis.


a) Normal Stance

b) Romberg


c) Single Leg Stance

d) Romberg on Foam

Figure 4. 6 Correlation of vestibular connectivity during stimulation with performance in a) normal stance, b) Romberg, c) Single Leg Stance, and d) Romberg on Foam tasks.

Panels a to d are placed in order of lowest to highest difficulty. The correlation values for young adults (YA) were .47, -.01, .55, & .74 in normal stance, Romberg, Single Leg Stance, and Romberg on Foam; respectively. The correlation values for older adults (OA) were .23, -.14, .07, & -.21

in normal stance, Romberg, Single Leg Stance, and Romberg on Foam; respectively. YA correlation for Romberg on Foam was significant (p=.008).

The results showed that overall functional connectivity of vestibular cortex during stimulation was associated with postural stability in young adults performing the Romberg on Foam task (r=.74, p=.008) (i.e. higher connectivity between the vestibular cortex and all the other regions was associated with a higher amount of body sway). The ROI-specific connectivity association with balance was only significant in young adults, and only in tasks of high difficulty. Higher vestibular-visual connectivity predicted more body sway in Single Leg Stance (r=.74, p=.008), and higher vestibular-somatosensory connectivity and vestibular-cerebellar connectivity predicted more body sway in the Romberg on Foam task (r=.73, p=.009 & r=.66, p=.02; respectively).

Further, there was a significant age difference in the association between overall vestibular connectivity with performance in the Romberg on Foam task (z=-2.5, p=0.006). Vestibular connectivity with other regions was significantly associated with performance in young but not older adults. The ROI-specific correlations revealed a significant age difference in the correlation of vestibular-brainstem connectivity with performance in normal stance (z=-1.91,p=.02). This was a positive correlation in the young adult group and negative in the old, revealing that higher connectivity of the vestibular cortex with the brainstem was associated with better performance in the older adults and poorer performance in the young adults. The vestibular-cerebellar connectivity association with performance in the Romberg task was also significantly different between the young and older adults (z=-2.63,p=.008), revealing that higher connectivity in young adults was associated with better performance. This was the only case in which higher connectivity was associated with *less* body sway in young adults. The vestibular-visual connectivity association with performance in the Single Leg Stance conditions was also significantly different between young and older adults (z=-1.59,p=.05), revealing that young adults with higher vestibular-visual connectivity exhibited a greater amount of body sway. The vestibular-visual and vestibular-somatosensory connectivity association with performance in the Romberg on Foam task (z=1.65, p=.04 & z=2.37, p=.008; respectively) was also significantly different between the young and older adult groups. Higher connectivity was associated with more body sway in young but not older adults. The pattern of results indicates that age differences in the association of balance with task-based vestibular connectivity were influenced by task difficulty (i.e. there were no age differences in associations between balance and overall vestibular connectivity in the lower difficulty tasks). The correlation patterns between performance and vestibular connectivity during stimulation are summarized in table 4.2.

Table 4. 2 Correlation of vestibular connectivity during stimulation with performance in a) normal stance and Romberg (low difficulty tasks) and b) Single Leg Stance and Romberg on Foam (high difficulty tasks).

Corresponding p-value to each r and z is shown in parenthesis. *significant at p<.05 (two-tailed)

a)

Task-based Connectivity	**Normal Stance**			**Romberg**		
	Young r (p)	**Old** r (p)	***Age difference*** *z (p)*	**Young** r (p)	**Old** r (p)	***Age difference*** *z (p)*
Vestibular-All ROIs	.47 (.16)	.23 (.40)	*.59 (.55)*	-.01 (.96)	-.14 (.61)	*.28 (.77)*
Vestibular-Visual	.03 (.93)	.15 (.59)	*-.26 (.79)*	-.03 (.91)	-.06 (.83)	*.06 (.95)*
Vestibular-Somatosensory	.40 (.25)	.41 (.14)	*-.03 (.97)*	.05 (.86)	-.01 (.94)	*.13 (.89)*
Vestibular-Temporal pole	.41 (.22)	.16 (.58)	*.59 (.55)*	.44 (.17)	-.38 (.17)	*1.88 (.06)*
Vestibular-Cerebellum	.16 (.65)	.21 (.57)	*-.11 (.91)*	-.46 (.15)	.62 (.07)	***-2.63 (.008)****
Vestibular-Brainstem	.48 (.15)	-.35 (.35)	***-1.91 (.02)****	-.03 (.91)	-.03 (.93)	*0 (1)*

b)

Task-based Connectivity	**Single Leg Stance**			**Romberg on Foam**		
	Young r (p)	**Old** r (p)	***Age difference*** *z (p)*	**Young** r (p)	**Old** r (p)	***Age difference*** *z (p)*
Vestibular-All ROIs	.55 (.07)	.07 (.81)	*1.18 (.23)*	**.74 (.008)***	-.21 (.48)	***-2.5 (0.006)****
Vestibular-Visual	**.74 (.008)***	.21 (.46)	***-1.59 (.05)****	.41 (.2)	-.32 (.27)	***1.65 (.04)****
Vestibular-Somatosensory	.50 (.10)	-.04 (.88)	*1.27 (.2)*	**.73 (.009)***	-.17 (.57)	***2.37(.008)****
Vestibular-Temporal pole	.19 (.57)	.02 (.92)	*.37 (.71)*	.33 (.30)	-.32 (.28)	*1.45 (.14)*
Vestibular-Cerebellum	.28 (.40)	.28 (.46)	*0 (1)*	**.66 (.02)***	.14 (.73)	*1.40 (.16)*
Vestibular-Brainstem	.34 (.30)	-.01 (.96)	*.78 (.43)*	.31 (.34)	.33 (.41)	*-.05 (.96)*

Rest to task alterations in functional connectivity and their association with balance

Next, we assessed whether associations between functional connectivity and postural control changed from rest to stimulation, and whether any such changes were modulated by age and task difficulty. The results reveal that the association between balance and connectivity significantly changed from rest to stimulation, in that only task-based connectivity predicted performance for the young adults, and only in tasks of high difficulty (i.e. Single Leg Stance (z=-2.28, p=,02) and Romberg on Foam (z=-1.64, p=.05)). The ROI-specific correlations revealed that the connectivity of vestibular cortex with visual, somatosensory, and temporal pole during stimulation and not at rest (z=-2.7, p=.003; z=-2.09,p=.01; z=-1.68,p=.4; respectively) significantly predicted young adults' performance in Single Leg Stance. Also, the connectivity of vestibular cortex with visual cortex during stimulation and not at rest (z=-1.96,p=.02) predicted young adults' performance in the Romberg on Foam task. Table 4.3 depicts the correlation between performance in each of the four balance tasks and changes in vestibular connectivity from rest to stimulation.

Table 4. 3 The difference in association of performance with functional connectivity from rest to stimulation. The z values represent the difference in correlation coefficients of rest and stimulation.

Corresponding p-value to each z value is shown in parenthesis. *significant at p<.05 (two-tailed)

	Normal Stance		**Romberg**		**Single Leg Stance**		**Romberg on Foam**	
	Young z (p)	**Old** z (p)	**Young** z (p)	**Old** z (p)	**Young** z (p)	**Old** z (p)	**Young** z (p)	**Old** z (p)
Vestibular-All ROIs	-1.2 (.23)	-.81 (.41)	.32 (.74)	1.41 (.15)	**-2.28 (.02)***	.02 (.98)	**-1.64 (.05)***	.26 (.79)
Vestibular-Visual	-.79 (.42)	-.57 (.56)	.26 (.79)	.67 (.50)	**-2.7 (.003)***	-.64 (.52)	-1.03 (.30)	.15 (.88)
Vestibular-Somatosensory	-1.03 (.30)	-.69 (.49)	.28 (.77)	.4 (.68)	**-2.09 (0.01)***	.52 (.6)	**-1.96 (.02)***	.14 (.88)
Vestibular-Temporal pole	-.77 (.44)	-.59 (.55)	-.58 (.56)	1.59 (.11)	**-1.68 (.04)***	0 (1)	-.70 (.48)	1.38 (.16)
Vestibular-Cerebellum	.02 (.98)	-.43 (.66)	.89 (.37)	-.59 (.55)	-.64 (.52)	-1.08 (.28)	-.17 (.86)	-.28 (.77)
Vestibular-Brainstem	-.1 (.92)	-.25 (.80)	-.02 (.98)	.08 (.93)	.07 (.94)	.7 (.48)	.09 (.92)	-.90 (.36)

vi. Discussion

In this study we investigated age differences in connectivity of the vestibular cortex with other sensorimotor regions, previously identified to be involved in processing vestibular information. We assessed vestibular connectivity in the resting state, during vestibular stimulation, and alterations from rest to stimulation. Lastly, we examined the relationship between individuals' balance and their functional connectivity patterns.

We found that vestibular connectivity during the resting state was not significantly different between young and older adults, and it did not predict individual differences in balance. There was also no significant age difference in vestibular connectivity during stimulation, but connectivity patterns were predictive of balance performance, depending on age and task demands.

Regardless of condition (i.e. rest or stimulation), young adults generally exhibited greater connectivity than older adults. Considering the higher magnitude of vestibular activation in the young relative to older adults reported in the previous chapter, this finding could be related to a greater sensitivity of young adults to vestibular stimulation. This is also in line with the findings of Cyran et al. (Cyran et al., 2016) who showed higher vestibular network connectivity in young adults. This suggests a distinction between how young and older adults modulate vestibular brain regions, with the young exhibiting stronger, more synchronous neural responses between vestibular cortex and other sensorimotor brain regions. Moreover, we found a significant increase in overall vestibular connectivity from rest to stimulation, predominantly in connectivity of vestibular and visual cortex.

By including the balance metrics and assessing the correlation of behavior with neural responses we were able to interpret the functional consequences of the observed age differences in connectivity patterns. We found that there was largely no significant age difference in correlation of balance with resting state vestibular connectivity (i.e. vestibular connectivity at rest was not a predictor of balance performance for either young or older adults). The only exception was for vestibular-brainstem connectivity, which was negatively correlated with body sway in the older adults, and positively in young adults. This was only true in the normal stance task, which suggests that older adults engage subcortical structures for vestibular processing (i.e. the vestibular nuclei) to perform equally as well as the young adults. That is, this may reflect a compensatory network connectivity pattern.

Unlike in the resting state, vestibular connectivity during stimulation was correlated with individuals' balance performance, and this correlation varied based on age and task demands. In tasks of low difficulty such as normal stance and Romberg, the pattern of correlation was similar between young and older adults. However, in more challenging tasks such as Romberg on foam and single leg stance, the pattern of correlation for young adults was similar to that observed for older adults on the easier balance tasks. In less demanding tasks young adults do not exhibit strong correlations between connectivity and performance, but with increases in difficulty, those young adults who activated the vestibular cortex more strongly and selectively (i.e. they had less connectivity with other ROIs) were the ones who performed better. This doesn't seem to be the case for older adults; they seem to exhibit less efficient processing of the vestibular signals, since more involvement of other regions is beneficial for their performance (i.e. more connectivity with other ROIs). Also, they may alter connectivity with regions outside of our selected ROIs (e.g. frontal cortex), for performing high demand tasks.

These current findings could be interpreted in light of the compensation-related utilization of neural circuits hypothesis (CRUNCH), proposed by Reuter-Lorenz & Cappell (Patricia A. Reuter-Lorenz & Cappell, 2008). According to this theory, at lower task demands, older adults may compensate for their inefficient neural processing by engaging more brain regions compared to the young (e.g. higher connectivity with the brainstem correlated with better balance in normal stance). However, as the task difficulty increases, both performance and the remaining available neural resources for older adults decline. As the current findings show, for example in the single leg stance task, the older adults' performance cannot be predicted by their vestibular connectivity patterns, whereas young adults' performance is strongly correlated with their vestibular connectivity patterns. The lower connectivity (i.e. more specificity of processing vestibular information) showed to benefit the young adults' performance when the task demanded the highest reliance on vestibular input (e.g. Romberg on foam).

Our findings are in general agreement with previous studies suggesting that older adults exhibit an overall decline in functional connectivity compared to young (Cyran et al., 2016; Mowinckel et al., 2012; Peelle et al., 2010; Roski et al., 2013; Yang et al., 2014). However, in contrast with our initial hypothesis of de-synchronization (i.e. less functional connectivity) of vestibular and non-vestibular regions in the presence of vestibular stimulus (T Brandt et al., 1998; Deutschländer et al., 2002b; Laurienti et al., 2002b), we found a general increase in connectivity from resting state to stimulation. Considering that the current results reflect the average timecourse of BOLD signal, the overall greater BOLD amplitude during stimulation compared to resting state may explain the observed effect.

Langan et al. (Langan et al., 2010) showed that reduced resting state interhemispheric connectivity was associated with over-recruitment of non-dominant hemisphere during motor task performance for older adults, which was correlated with longer reaction time in motor performance. Similarly, Seidler et al. (R. Seidler et al., 2015) showed that greater resting state connectivity between motor cortex, putamen, insula and cerebellum was associated with better motor performance in older adults. These studies suggest that higher resting state functional connectivity in older adults was associated with better motor performance. We only found a trend for similar pattern in our data, showing that higher resting state functional connectivity of vestibular cortex and brainstem was correlated with better performance of older adults in normal stance.

Many studies have used non-invasive brain stimulation methods such as tDCS (Callan, Falcone, Wada, & Parasuraman, 2016; Cummiford et al., 2016; Keeser et al., 2011; Kunze, Hunold, Haueisen, Jirsa, & Spiegler, 2016; Polanía, Paulus, & Nitsche, 2012; Sehm, Kipping, Schäfer, Villringer, & Ragert, 2013) and TMS (Eldaief, Halko, Buckner, & Pascual-Leone, 2011; Grefkes et al., 2010; Horacek et al., 2007; Paus, Castro-Alamancos, & Petrides, 2001; Pleger et al., 2006; Vercammen et al., 2009) to modulate functional connectivity of different brain regions. Cai et al. (Cai et al., 2018) used GVS to enhance the deficient connectivity of pedunculopontine nucleus in

Parkinson's disease patients. These studies suggest that functional connectivity of different brain regions could be modulated by non-invasive brain stimulation. According to the current findings, older adults show an overall lower connectivity of vestibular cortex, and those older adults with more connectivity exhibit a trend for better postural stability (i.e. good performers). The brain regions identified in the present study could be potential targets of brain stimulation to modulate the functional connectivity patterns of older adults bad performers and make them more similar to older adult good performers. The behavioral outcomes of such neural modulation could be especially beneficial for older adults who cannot benefit from conventional balance training interventions.

Limitations

The small sample size and lack of power analysis are the most significant limitations of our study. Also, we did not control for other contributing factors in neural and behavioral processing, such as 1) age-related structural differences in gray matter volume and white matter integrity; 2) age differences in peripheral sensory processing, specifically the strength and recruitment strategy in ankle joint muscles; 3) role of attention and cognitive abilities; and 4) fear of fall. Further, the inability to measure the neural vestibular processing simultaneously with balance could be an additional source of variance in our data. Lastly, the older adults who participated in this study represent a relatively high functioning population. As evident by the lack of age difference in clinical tests of gait and balance (i.e. TUG and MDGI), our findings may not properly translate to a more typical population of older adults with balance issues.

vii. Conclusion

This study is the first to document age differences in the relationship between functional connectivity of the vestibular cortex and individual differences in balance. The current findings suggest that young adults who exhibit better balance are those who respond more strongly and selectively to vestibular inputs. This pattern is absent in older adults except in easier tasks, in line with CRUNCH.

Acknowledgments

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viii. References

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Concluding Remarks

Big Picture Findings

In this dissertation I examined the neural mechanisms underlying vestibular processing, how those mechanisms are related to postural control, and how they change with age.

In the first chapter, I provided a general background on the role of the vestibular system, the alterations of vestibular function with healthy aging, and the significance of investigating the vestibular brain network and its correlation with behavioral indexes of vestibular processing (i.e. balance).

In the second chapter, I evaluated a novel method for stimulating the vestibular cortex inside the MRI scanner. I established the validity of my method by showing that it successfully activated the vestibular cortex in a fashion similar to more conventional approaches and that it resulted in vestibular evoked myogenic potentials. This is important because this method prevents aversive responses caused by subjects' discomfort (which is common in other stimulation methods), and the method is fast and easy to implement. I also showed that higher activation of the vestibular cortex and cerebellar lobule VI was correlated with better balance in a visually degraded balance task for young adults.

In the third chapter, I investigated age differences in the neural processing of vestibular inputs and how age differences in neural activity relate to age differences in balance. I found that young adults show higher sensitivity to vestibular stimulation, evidenced by greater responses in the canonical vestibular cortex. Also, I found that vestibular stimulation results in deactivation of other sensory cortices such as visual and somatosensory cortex. Deactivation of these other sensory regions was correlated with greater body sway (i.e. worse balance) in a normal stance task, perhaps due to the multisensory nature of this task. This correlation was stronger in older adults perhaps due to less efficient compensatory mechanisms. I also found that the more reliability of activation patterns in response to stimulation was correlated with better balance, regardless of age.

In the fourth chapter, I assessed age differences in connectivity of the vestibular cortex with other sensory regions, and its correlation with balance. I investigated this connectivity during rest, during vestibular stimulation, and also examined the change from resting state to stimulation. I found that there were no significant age differences in vestibular connectivity at rest. During vestibular stimulation, the connectivity between the vestibular cortex and other ROIs was significantly increased relative to the resting state. The overall connectivity of vestibular cortex was higher in young relative to older adults. Considering the higher magnitude of response in young compared to older adults, this finding could be related to more sensitivity of young adults to vestibular stimulation. Although resting state connectivity was generally not a predictor of balance, connectivity during vestibular stimulation often was. Young adults with higher connectivity exhibited more body sway in more challenging tasks, which suggested that less specificity of vestibular processing was associated with poorer balance. Such strong correlations were absent in older adults performing the difficult tasks, which could be interpreted based on the CRUNCH model of aging. That is, with increases in task difficulty, the available neural resources of older adults declines and the usual compensatory mechanisms used in performing easier tasks (e.g. engaging the brainstem to perform as well as young adults in the normal stance task) become ineffective. Taken together with the findings of chapter three, in performance of easy tasks such as normal stance, good balance in older adults was associated with the following neural patterns: 1) less deactivation of cross modal sensory regions, which indicates less need for neural allocation to vestibular cortex. This could potentially suggest that good performers are more young-like in that they are more sensitive to vestibular inputs, showing expected patterns of *vestibular activation and visual-somatosensory deactivation* (as opposed to excessive visual-somatosensory deactivation); 2) less connectivity of vestibular cortex with other regions, suggesting less synchronized patterns of neural response (i.e. *vestibular activation and visual-somatosensory deactivation*) and more specificity of response to vestibular inputs. In performance of more challenging task such as Romberg on foam, there was no significant correlation between neural response and behavior, suggesting a deterioration of neural resources with increase in task demands (i.e. CRUNCH).

In sum, I have provided evidence for 1) the validity of a new vestibular stimulation method in the fMRI setting, 2) age differences in response to vestibular stimulation, and association of these vestibular neural responses with balance, and 3) age differences in connectivity of vestibular cortex with other sensory regions and its relation to balance. These findings suggest that older adults are overall less sensitive to vestibular stimulation. Also, better balance is associated with stronger activation of vestibular cortex in young adults (second chapter), less deactivation of visual and somatosensory regions in older adults (third chapter), and less connectivity of vestibular cortex with other sensory regions in young adults (fourth chapter).

Limitations

The main limitation of the experiments presented in this dissertation is the relatively small sample size. Caution should therefore be taken in generalizing the findings to a broader population. However, considering similar published work in this field with ≤15 subjects per group (S Bense et al., 2001; T Brandt et al., 1998; Cyran et al., 2016; Simon B. Eickhoff et al., 2006; Fasold et al., 2002; Frank & Greenlee, 2014; H. T. Karim et al., 2013; Elie Lobel et al., 1998; Ruffieux et al., 2018; Mikio Suzuki et al., 2001), it's not unreasonable to consider the current findings as a platform to form hypothesis for future research. Another potential limitation lies with the logistical constraints associated with neuroimaging. In particular, brain function was always measured in the supine position, but I then associated neural activity and connectivity with upright postural control. One may argue that more mobile neuroimaging techniques such as functional near infrared spectroscopy (fNIRS) could be a better fit for assessing the brain function in relation to balance. On the other hand, fNIRS does not have the spatial resolution of fMRI. Furthermore, fNIRS can only estimate activity in cortical regions. The current work and the literature suggest a strong role of subcortical structures in balance, which is not possible to examine using fNIRS. Lastly, like many neuroimaging studies, all of the findings reported in this dissertation are correlational and therefore cannot be interpreted as evidence for causal relationships between age, brain function, and postural control.

Future directions

Additional research needs to be conducted to illuminate the role of cognitive status in the observed effects. In particular, additional cognitive assessments are needed to clarify the extent to which age differences are mediated by attention. Moreover, future research should evaluate the age differences in peripheral sensory processing and how it contributes to the age differences in performance and neural processing at CNS level. Including other measures of body sway such as mean velocity in addition to ellipse area can further illuminate age differences in response to postural perturbation. Further, using the brain regions identified in the present work, future studies could move beyond correlation to causation by modifying the function and connectivity of these regions. Using non-invasive brain stimulation methods such as GVS, TMS, and tDCS would further illuminate the role of these brain regions in balance control, and whether the effect would differ by age. Also, considering that many older adults are unable to meet the suggested exercise requirements for their age, future studies are needed to evaluate the effectiveness of brain stimulation methods to improve the postural stability in these older adults. In particular, instead of using the balance data of completed tasks, future research may focus on percentage of trials completed prior to step out (i.e. fall) and whether they can be modified by brain stimulation.

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