# Older adults demonstrate superior vestibular perception for virtual rotations

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## ARTICLE INFO

## ABSTRACT

Adult ageing results in a progressive loss of vestibular hair cell receptors and afferent fibres. Given the robustness of vestibulo-ocular and vestibular-evoked whole-body responses to age-related deterioration, it was proposed that the vestibular system compensates centrally. Here we examine the potential for central compensation in vestibular sensitivity with adult ageing by using a combination of real and virtual rotation-based psychophysical testing at two stimulus frequencies (0.1 & 1 Hz). Real rotations activate semi-circular canal hair cell receptors naturally via mechanotransduction, while electrical current used to evoke virtual rotations does not rely on mechanical deformation of hair cell receptors to activate vestibular afferents. This two-pronged approach allows us to determine the independent effects of age-related peripheral afferent receptor loss and potential compensatory mechanisms. Older adults had thresholds for discriminating real rotations that were significantly greater than young adults at 0.1 Hz (7.2 vs. 3°/s), but the effect of age was weaker (non-significant) at 1 Hz (2.4 vs. 1.3°/s). For virtual rotations, older adults had greater thresholds than young adults at 0.1 Hz (1.2 vs. 0.5 mA), however, older adults outperformed young adults at 1 Hz (0.6 vs. 1.1 mA). Based on these thresholds, we argue that central vestibular processing gain is enhanced in older adults for 1 Hz real and virtual rotations, partially offsetting the negative impact of normal age-related hair cell receptor and primary afferent loss. We propose that the frequency dependence of this compensation reflects the physiological importance of the 1–5 Hz range in natural vestibular input.

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## 1. Introduction

The vestibular system transduces linear and angular head motion and plays a role in stabilization of the eyes and head, standing balance control and the perception of head motion. Our focus is on the angular rotation signals provided by the 6 semi-circular ducts bilaterally. Much like in other sensory systems, age-related deterioration of the human peripheral vestibular sensory apparatus is well documented (for review see Ishiyama, 2009). Consistently, anatomists report a decline in human hair cell receptor number within the crista ampullaris of the semi-circular ducts by 40% beyond the age of 70. Type 1 receptors in the central crest zone of the crista show a more rapid decline in number than type 2 receptors, which decline at a similar rate across all 10 vestibular sensory end organs (Rosenhall, 1973; Richter, 1980;

Merchant et al., 2000; Rauch et al., 2001; Ishiyama, 2009). Concomitantly, peripheral afferent number decreases by ~40% starting around age 50 (Richter, 1980), being most pronounced for the central crest zone of the crista ampullaris which is primarily innervated by large, irregularly discharging afferent fibres. Neuron counts in Scarpa's ganglion also decline with adult ageing (Richter, 1980), with the reported losses mirroring those in the peripheral branch of the vestibular nerve (Bergström, 1973). Given this, we would expect healthy ageing to lead to a large decrement in the sensitivity to head rotation required for accurate vestibular perception.

However, only small increments in perceptual thresholds have been observed previously with age (Seemungal et al., 2004; Roditi and Crane, 2012), suggesting that an adaptive neural mechanism counteracts the anatomical loss of hair cell receptors and primary afferents. The presence of an age-related central gain enhancement mechanism has previously been proposed for vestibulo-ocular (Peterka et al., 1990; Jahn et al., 2003), and vestibulo-motor (Welgampola and Colbatch, 2002; Dalton et al., 2014) function. Here we investigate the potential for this gain enhancement to influence vestibular perception. Loss of hair cell

receptors would be predicted to result in elevated thresholds for real rotations by increasing the noise in the afferent population response (Goldberg et al., 2012). If older adults are as sensitive as younger adults at detecting real rotary stimuli despite the loss of vestibular hair cell receptors and primary afferents this would imply that the population signal is being enhanced relative to the noise centrally, which could be accomplished through central response gain enhancement in neurons that remain connected to functioning hair cell receptors (Phillips et al., 2015).

Recently, we have deployed a combination of real and virtual rotation-based psychophysical testing to examine peripheral and central contributions to vestibular processing (Peters et al., 2015). Real kinetic rotations activate hair cell receptors within the semi-circular canals via mechanical shearing forces, whereas electrical vestibular stimulation (EVS) used to evoke virtual rotations does not rely on mechanical deformation of hair cell receptors to activate vestibular afferents (Goldberg et al., 1984; Fitzpatrick and Day, 2004; Kim and Curthoys, 2004). Pitching the head down toward the lap brings the net EVS-evoked response vector (Fitzpatrick and Day, 2004) in-line with a rotary chair or platform's earth-vertical axis of rotation, giving rise to the distinct sensation of virtual rotation that is indistinguishable from real kinetic rotation (Wardman et al., 2003; Day and Fitzpatrick, 2005; St. George et al., 2011; Fitzpatrick and Watson, 2015; Peters et al., 2015). We utilize this two-pronged approach of homologous real and virtual rotation testing to examine the differential effects of age-related hair cell receptor loss or dysfunction, and potential adaptive compensatory mechanisms. Given the deterioration of the peripheral vestibular apparatus with age, we hypothesized that older adults would exhibit greater thresholds on real rotation testing relative to young adults. In light of the central gain enhancement mechanism suggested in vestibulo-ocular (Peterka et al., 1990; Jahn et al., 2003) and vestibulo-motor (Welgampola and Colbatch, 2002; Dalton et al., 2014) function, we hypothesized that older adults would exhibit lower discrimination thresholds for virtual rotations relative to young adults.

## 2. Materials and methods

### 2.1. Participants

Ten healthy older adults (4 men, 6 women) between the ages of 69 and 81 years (mean = 74.6, SD = 3.6), and ten healthy young adults (4 men, 6 women) between the ages of 20 and 30 years (mean = 25.2, SD = 3.6), with no known history of otologic or neurologic diseases or of falling participated in this study. Experimental protocols were explained to each subject and their written, informed consent was obtained. All procedures conformed to the standards of the World Medical Association Declaration of Helsinki and were approved by the University of British Columbia's Clinical Research Ethics Board.

### 2.2. Real kinetic rotations

To deliver whole-body yaw rotations, we used a custom-built rotary chair (see Fig. 1A), which we drove with a real-time motion controller (PXI-7350 Motion Controller, National Instruments, USA; Universal Motion Interface UMI-7774, National Instruments, USA) running in-house LabVIEW software built with the NI Motion programming suite (National Instruments, USA). The motion controller sent torque commands to a servo amplifier (SGDV-200A01A, Yaskawa, Japan), which powered a large AC motor (SGMCS-2ZN3A-YA21, Yaskawa, Japan; encoder angular resolution 0.00034°, continuous torque 200 Nm). Rotation stimuli consisted of raised-cosine bell curves, with the peak angular velocity adaptively adjusted (from 0.1 to 15°/s) across trials. The predicted movement of the cupula that results from this sinusoidal velocity pulse is a sinusoidal monophasic deflection (see rightmost column plots in Fig. 5 from Guedry, 1974). Afferent firing rate will be proportional to cupular deflection, thus showing a monophasic increase/

decrease following such a sinusoidal velocity pulse pattern. To mitigate non-vestibular (somatosensory) cues, additional dual-layer memory foam padding depicted in Fig. 1A was added beneath the participant's socked feet and around their chest, forearms, and shanks, and was secured firmly to the chair using adjustable strapping. The participant was further strapped to the device using a five-point racing harness. Testing was carried out in a dark, electrically shielded room, with the participant blindfolded and wearing earplugs. Before each testing block, 5 to 10 practice trials° were given at clearly discernible stimulus amplitudes for each participant to ensure that they were entirely comfortable with the task.

### 2.3. Electrical vestibular stimuli

Electrical vestibular stimulation was delivered in a binaural bipolar electrode configuration. Carbon rubber electrodes (9 cm²), coated with Spectra 360 electrode gel (Parker Laboratories, USA), were secured over participants' mastoid processes with surgical tape and an elastic headband. Vestibular stimuli were generated on a PC computer using custom LabVIEW software (National Instruments, USA) and were sent to a constant current isolation unit (STMISOLA; Biopac Systems Inc., USA) via a multifunction data acquisition board (PXI-6289; National Instruments, USA). Vestibular stimuli consisted of raised-cosine bell curves, with the peak current amplitude adaptively adjusted (from 0.1 to 5 mA) across trials. We note that the activation of vestibular afferents to real motion (see above) is predicted to be very similar to the activation pattern evoked by a sinusoidal EVS pulse (our virtual stimuli; see Goldberg et al., 2012). Additionally, we have demonstrated that EVS is perceived as an angular velocity signal over the frequency range tested here (Peters et al., 2015). Therefore, the pattern of afferent activation is expected to be similar between stimulus types. As with real rotation testing, before each virtual testing block, 5 to 10 practice trials were given at clearly discernible stimulus amplitudes to ensure that the participant was comfortable performing the task. To minimize any non-vestibular cues associated with skin tingling under the electrodes, we anaesthetized the skin over the mastoid processes bilaterally using AMETOP (Tetracaine HCl Gel 4% w/w; Smith & Nephew Inc., UK), which was applied 30–45 min prior to each experiment. Given the low amplitude of currents applied during sensory testing (~0.5–1.5 mA at peak), tingling under the electrodes was rarely reported, and all participants reported performing the task based on their vivid perception of chair rotation.

### 2.4. Direction discrimination threshold estimation

Participants attempted to discern whether the direction of real or virtual whole-body rotation was to the right or left. Participants were seated comfortably atop the rotary chair with their head facing down toward their lap and immobilized. The experimenter ensured that the head was pitched down 71° aligning the angle of the EVS-evoked rotational vector (Fitzpatrick and Day, 2004) with an earth-vertical axis through the centre of the chair's axis of rotation (see Fig. 1B). Applying electrical vestibular stimulation in a binaural bipolar configuration with the head pitched downward evokes an illusion of whole-body rotation around an earth-vertical axis, providing the sensation of whole-body motion induced by the motor. For this study, the participant's head was held fixed in-place with a helmet (Pro-Tec, China) that was braced firmly to the rotary chair carriage. Correct head pitch was confirmed periodically throughout testing using a protractor.

We asked each participant to complete a series of trials wherein they were given a single-cycle of a raised-cosine bell electrical vestibular stimulation or real angular velocity pulse (with electrode polarity and rotation direction randomized across trials), and were required (forced choice) to indicate which direction they were rotated with a verbal response ("right" or "left"). With electrical vestibular stimulation, participants reported vivid sensations of chair rotation, although the chair