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Visual, Vestibular, and Proprioceptive Contributions

to the Subjective Perception of Vertical

A dissertation submitted in partial satisfaction of the

requirements for the degree Doctor of Philosophy

in Psychology

by

Chéla Rae Willey

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ABSTRACT OF THE DISSERTATION

Visual, Vestibular, and Proprioceptive Contributions

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Professor Zili Liu, Chair

The perception of gravitational vertical is determined by estimates from visual, vestibular and proprioceptive sensory cues. This dissertation investigates the various ways in which these three sources of cues interact to produce a final estimate of the perception of vertical. Specifically, I utilize and validate verticality estimates made in virtual reality and exploit the adaptability of this methodology to probe visual contributions to vertical biases. I then explore the use of a novel methodology using galvanic vestibular stimulation to understand the effects of vestibular influences on verticality. In addition, I validate a vestibular-based orientation discrimination method that uses one's body orientation to estimate the direction of vertical. I then explore the potential influences neck and body proprioceptive cues have on the visual and vestibular-based estimates made in the current investigations. Using the principles of Bayesian cue combination, I then test the optimal integration of verticality estimates based on single-cue estimates of vertical. Finally, I discuss the ways in which these interactions between sensory cues impact the susceptibility and propensity of particular disorders and ailments that result from maladaptive sensory integration.

The dissertation of Chéla Rae Willey is approved.

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DEDICATION

This dissertation is dedicated to my supportive and loving husband, Andrew Forney.

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LIST OF ACRONYMS

GVS	–	Galvanic Vestibular Stimulation
RFT	–	Rod and Frame Task
SV	–	Subjective Vertical
VOR	–	Vestibule-Ocular Reflex
VR	–	Virtual Reality

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1 CHAPTER 1: Introduction

1.1 Overview

The understanding of one's own body orientation within the 3D concept of space is one of the most fundamental aspects to human cognition and movement about the environment. Orientating oneself in an environment is one of the oldest evolutionary feats across organisms. Humans, and other animals, must use informative sensory cues extracted from the environment to determine our own orientation in the environment. These sensory mechanisms that utilize these cues differ based on the goals and evolutionary history of the organism, but remarkably many organisms tend to use the same underlying cues for orientation. Even in the plant kingdom, the main cue for orientation is through the use of light cues (Darwin, 1880). Given that the sun shines from above, plant organisms can determine which direction to grow their roots. Humans and other animals that necessarily must move within the environment in order to survive have more complex sensory cues that inform about their orientation and about their own movements in space. Due to the complexity of human movement, humans utilize many redundant cues from our environment in order to constantly update our sense of orientation in millisecond precision. This redundancy comes at the advantage of the ability to enhance the accuracy of the percept (Ernst, 2006). The source of these cues come from mainly three sensory systems: visual, vestibular, and proprioception. These systems work together to come up with estimates about how the body is situated in space. They are thought to be combined to produce a subjective reality of the position of the body in comparison to other environmental objects. For example, visual cues such as the orientation, contours and natural lighting of environmental objects help to visually identify the direction of gravity (Harris, Jenkin, Dyde, & Jenkin, 2011). Movement of the head and body allow for the vestibular system to detect acceleration and deceleration of motion in contrast with the force of gravity. The angle of the support surface in which one is standing upon facilitates understanding of the direction of gravity through the differentiated pressure of person's weight on their feet (Maurer, Mergner, Bolha, & Hlavacka, 2000; Maurer, Mergner, & Peterka, 2006). Redundant with the orientation of the one's head, proprioceptive cues in the neck during head tilts can also aid in proprioceptive estimates of vertical (Clemens, De Vrijer, Selen, Van Gisbergen, & Medendorp, 2011). Using isolated cues, each system can directly or indirectly produce its own estimate of gravitational vertical and one's body orientation. In order to maintain an updated sense of orientation, an internal model of the body's orientation and subjective vertical must be fed with reliable and relevant estimates from these independent sources.

Subjective vertical (SV) is used to describe the subjective perception of the direction of true vertical (i.e. the direction of gravity). Body orientation can be directly calculated from one's subjective vertical given the ego-centric cues the senses pick up from the environment. Thus, in this manuscript, I will discuss both body orientation and SV as if they are determined from the same underlying internal model and sensory cues. While there are some important nuances between body orientation and subjective vertical, particularly in the role of self-motion, the main investigation here will be concerned with the how people locate SV within an environment. In the coming chapters, I will discuss each sensory system and its available cues involved in SV and body orientation estimates in detail. For now, it is important to recognize that these sensory systems can be viewed as independent estimators of SV. However, in everyday environments, the end SV estimates will almost always be a weighted average of the inputs from visual, vestibular, and proprioceptive systems.

In the upright static position, body orientation should be perceived in the same direction as gravitational vertical. Thus, for investigation of body orientation in this context, we can utilize the same tools to understand the direction of vertical. SV estimates in these experimental contexts are estimates about the direction of gravity. These estimates have mainly been made in the visual domain and are a result of multisensory cues. For example, a popular visual SV task used in clinical setting, named the bucket test, is one in which participants or patients place their head in a horizontally orientated bucket while standing or sitting. Participants will look down the cylinder of the bucket towards the back surface in which a straight line is painted at center. The bucket is rotated by the experimenter until the participant believes that the painted line is at true vertical. The error away from vertical is then recorded. This simple test allows experimenters to quickly estimate a person's underlying internal visual model of subjective vertical, without the presence of strong outside visual indicators of vertical, such as environmental contours, as the circular view through the bucket provides no cues to true vertical. When performing this task while standing, it can be a good indicator of the functioning of vestibular and proprioceptive systems on determining vertical (Chetana & Jayesh, 2015). This visual task has been adapted many times to other mediums, such as projecting the line in total darkness on a wall in front of the participant or presenting the line on a computer with the edges of the computer screen blocked out. However, due to the visual nature of the task, one may also be gathering indirect visual cues from the painted line itself. For example, the initial orientation and the rotational movement of the rod could allow for some visual cues to aid in estimation. Thus, this kind of SV estimate may be very different than an estimate gathered using another sensory modality. This conflict will be discussed in detail in Chapter 3. Regardless, of whether or not the goal is to isolate unisensory cues, this simple test can provide a base estimate of SV.

While most studies that have investigated SV have used a visual SV estimation method, there have been a handful of studies that have developed and used haptic methods. For example, in one popular haptic SV task, participants utilize a handheld rod or other object (Bauermeister, Werner, & Wapner, 1964; Bringoux et al., 2009; Lejeune, Thouvarecq, Anderson, & Jouen, 2004). Without using vision, participants are either asked to rotate the rod to their perceived direction of vertical or touch the rod for an allotted amount of time and then determine if it was tilted clockwise or counterclockwise from vertical over repeated trials. In many situations depending on head and body orientation, this type of haptic task will yield different estimates than those made using vision (Fraser Makooie, & Harris, 2015). While this type of task attempts to understand SV estimates from another modality other than vision, in everyday environments, haptic cues are not usually used in this way. Comparatively, visual SV estimates are slightly more ecologically sound as participants use are using a commonly-used visual cue (straight lines) in order to determine the direction of gravity as they do in every day environments. A hand touching the side of the wall or holding a railing in the dark may help to stabilize a person's balance due to its solid features, but it is unclear if information about the orientation of the wall is aiding in the perception of vertical. The goal of this type of haptic task in a real-life setting is typically not orientated towards estimating the direction of vertical. Nevertheless, during a static upright stance without any other visual cues, both visual and haptic estimates are estimated very accurately (Bringoux et al., 2009; Fraser, Makooie, & Harris, 2015; Mars, Popov, & Vercher, 2001). However, this is likely because these estimates are combining the cues used in the task with cues from the vestibular system which is constantly detecting force of gravity in the upright stance.

Another type of SV task that has been used, but to a much lesser extent, is tilting the entire body using a rotatable platform or chair and asking the participant to determine vertical through vestibular cues via their body orientation. These types of tasks, while costly, utilize a commonly used cue to determine the direction of vertical. Namely, this type of task directly attempts to tap into the functioning of the vestibular gravitational receptors, mainly the otolith organs. When the body moves, these ototlith organs can sense the direction of movement due to the shearing force that occurs along their receptors. Inside these otolith organs are hair cells that are mechanically activated by the movement of otoconia, pieces of calcium carbonate, across their surface. The nerves of these receptors do not adapt; thus, healthy individuals can always detect the otolith's signal of the direction of gravity, even when the body is in the same position over a long period of time.

To understand how these cues may differ, researchers have introduced contextual shifts and have observed how SV estimates are altered depending on their modality. One commonly used visual contextual shift is the shift in the environmental orientation of common surfaces that would indicate the direction of gravity, such as in the rod and frame task (RFT). Another contextual shift is the change in the body or head orientation, which effectively changes vestibular and haptic sensory cues. These contextual shifts will be the main tools used to probe how SV estimates are made from different modalities and will be discussed in detail in the coming chapters.

1.2 General methodology

Throughout the next chapters I will describe not only research from previous literature, but also our own investigations that have tested various aspects of sensory cues involved in SV estimation. In our investigations, we use primarily two types of psychophysical methodologies, the alignment and discrimination methods. While these two methods attempt to estimate the same underlying construct, the end estimates can be affected differently and can more or less represent the participants' true perceptual experiences. These differences will be discussed in detail in Chapter 2.

1.2.1 Alignment Task

The first is an alignment task, in which participants rotate an SV probe (e.g. a visually or haptically perceived rod or one's own body orientation) to their perceived SV. This task is performed multiple times. Averages and standard deviations of the repeated trials are recorded for each participant. The initial position of the probe will always be randomly selected from a range of orientations. This type of SV methodology has been used most often due to its ease of implementation and robust results. We include it in all of our investigations for two main reasons. Historically in the literature, this methodology has been used the most often, thus we include it to compare our results with the majority of the previous literature on SV estimates. Additionally, we use it as a preliminary assessment to set up the parameters in the discrimination task. However, as discussed later, the alignment task might not provide an accurate representation a participants' true SV.

1.2.2 Discrimination Task

The second methodology used is an orientation discrimination task using the method of constant stimuli. For this method, the probe is presented at a range of preset orientations in subsequent trials. On each trial, the participant indicates whether the probe is rotated clockwise or counterclockwise from vertical. Each preset orientation is presented a set number of times throughout the randomized trials. The proportion of 'clockwise' responses is calculated for each preset orientation. The resulting function of the proportions of clockwise responses to probe orientations will take on a psychometric function. We fit each subject's data using a cumulative gaussian function using the *psignifit* function in Matlab (Wichmann & Hill, 2001). The rod orientation estimated to occur at the 0.5 ‘clockwise’ response proportion is considered to be the participant’s SV estimate. The slope of this function determines the sensitivity to the SV estimate and is the equal to the inverse of the standard deviation of the SV estimate. Each participants’ data is individually inspected in comparison to the fitted gaussian to determine if the function adequately fit the data. Participants who responded randomly or uniformly (i.e. always responding ‘clockwise’) throughout the experiment were not used in data analyses as the cumulative gaussian function would be unable to accurately capture their psychometric function. We discuss, how many participants were excluded in each of the studies individually. Lastly, in all our reports and calculations, we assign vertical to 0° with counterclockwise rotations reported as negative values.

1.3 The present investigations

In an effort to investigate the ways in which visual, vestibular and proprioceptive cues influence SV estimates the remaining chapters will focus on each modality individually and then the last chapter before the general discussion will investigate the integration of these cues on SV estimates. Specifically, chapter 2 will focus on visual cues of SV and how those cues can be biased using contextual shifts such as in the RFT, in which a tilted frame surrounding a visual probe biases visual SV estimates towards the rotation of the frame. Experiment 1a will validate our adapted version of the RFT in two virtual reality environments. Experiment 1b will compare the traditional alignment method to the method of constant stimuli in an orientation discrimination task in the RFT. Experiments 2a and 2b will attempt to demonstrate the utility of using a virtual environment by manipulating environmental richness and texture to enhance depth cues in the RFT.

Chapter 3 will focus on the effects of vestibular cues of SV. Experiment 1 investigates visual SV biases when vestibular gravitational cues become irrelevant in the RFT. Experiment 2a and 2b uses electrical stimulation of the vestibular nerve to induce a sense of tilt towards one side of the body while participants perform the RFT. Experiment 3 utilizes the vestibular SV estimation method to explore the biases sensitivities without visual cues.

In chapter 4, I consider the possible confounding factors of proprioceptive cues on methods in attempting to isolate visual and vestibular vertical cues. Experiment 1 tests the effect of wearing a foam neck pillow of visual SV estimates to limit movements of the neck and to provide a reduced sense of neck proprioception. Experiment 2a and 2b will test global and local vibration to the neck can affect visual SV estimates. Lastly experiment 3 will test the use of foam on vestibular SV estimates.

In chapter 5, I test an optimal observer model using independently made visual and vestibular SV estimates using the methodologies outlined in the previous chapters. Chapter 6 will feature a general discussion of the present experiments and the implications they have on healthy subjects and patient populations. I will discuss possible implications of individual differences in SV estimates and estimation weighting schemas. Lastly, I will outline the future of the work as it pertains to situations in which multisensory integration is thought to cause maladaptive ailments, such as in motion sickness and vertigo.

Collectively, these experiments outline important both methodological and phenomenological considerations when studying subjective vertical and body orientation. The experiments outlined here only begin to delve into the potential various lines of work that can be brought to fruition in their respective areas.

2 CHAPTER 2: Visual influences on subjective vertical and body orientation

Humans primarily gather visual cues about verticality through vertical surfaces in the environment that are also subject to gravitational force. These lines are projected on the retina and the orientation at which they are situated in the environment is represented through the mapping of selectively activated photoreceptors. This orientation is preserved throughout the various pathways of the visual system and is integrated early with other gravitational information to determine one's spatial orientation. As mentioned, SV has primarily been studied using visual probes. While the contexts under which visual SV estimates can vary, the most basic experiments employ an alignment task by presenting a rotatable visual 3D rod or 2D line in the absence of any other visual cues. The participant's task is to rotate the rod or line to their perception of gravitational vertical. The appeal of these kinds of visual SV tests is that they are low cost and can help to quickly identify vestibular or visual dysfunction. They have been adapted to be performed on a computer, using projections on a wall, or using a bucket (Bagust, Rix, & Hurst, 2005; Brodsky, Cusick, Kenna, & Zhou, 2016; Chetana & Jayesh, 2015). These types of alignment method probes have found to be very reliable across time periods without feedback (Bauermeister et al., 1964). Healthy adults are on average within ± 2° of true vertical on these types of SV tests, with patients with vestibular disorders making greater deviations (Brodsky et al., 2016; Yang et al., 2014).

While this simple method of testing for the perception of vertical is helpful in clinical research for the identification of vestibular disorders, allowing for contextual interference can help us understand the types of cues that play into the determination of the direction of vertical in healthy individuals. Visual SV estimates have been shown to be influenced by the context in which the estimate has been given. The most robust effect of contextual influence is shown using the classic rod and frame task (RFT). The RFT, originally developed by Witkin & Asch (1948) presents a luminous rod at the center of a luminous frame, of which both can be independently positioned and rotated. The testing room is completely darkened, and the rod and the frame are situated about 5 feet from the participant. While the frame is kept in a stationary position, the participant's task is to verbally instruct an experimenter to continue to rotate the rod clockwise or counterclockwise until they believe that it is vertical. In the original conditions, the frame was either at a 28° clockwise or counterclockwise tilt or at 0°. When the frame is rotated at this orientation while the person remains upright, visual SV estimates are biased towards the tilt of the frame (Witkin & Asch, 1948a). While this apparatus was used in these first experiments by Witkin and his colleagues, it was difficult for other researchers to replicate the conditions needed to perform this test outside of laboratory settings. Oltman (1968) developed a portable RFT that could be used on a table top surface. Using this apparatus, the participant's field of view was limited to the inside of the apparatus using a headrest with an added shield. Oltman (1968) found that RFT verticality estimates using the portable version highly correlated with estimates made using the original apparatus at .89 for females and .90 for males. More recently, other researchers have adapted the original RFT into different forms, such as 2D computerized tests and 3D virtual reality (VR) environments, that yield similar results to the original tests (Bagust et al., 2005; Bringoux et al., 2009). In fact, it was found that a single line orientated in a particular direction presented around a second line is enough to bias the second line towards the orientation of the first (Vingerhoets, De Vrijer, Van Gisbergen, & Medendorp, 2009). With the adaptability of using a computerized version of the RFT, there are many research avenues to explore to understand the types of cues that can further influence the perception of subjective vertical. In this chapter, we explore the possibilities of adapting the RFT in virtual reality (VR) using a head-mounted display. The portability and flexibility that VR provides can be a valuable tool for sensory researchers. Using VR, we can manipulate features that would be difficult to quickly and precisely manipulate in real-like apparatuses. We further explore the difference between methodologies used to collect SV estimates within the VR setting that can lend to better designs that capture the percept of the individual.

2.1 Experiment 1a: Using Virtual Reality for Visual Subjective Vertical Estimation

Previous studies have found little differences in visual SV estimates between 3D representations of the RFT in VR compared with the physical RFT (Bringoux et al., 2009). Here we compare alignment estimates made using two virtual RFTs recreated in different programs to estimates made using other RFT setups as reported in previous studies. We used mainly two programs to present the RFT to participants, OpenSim and Unity3D. This experiment tests the effectiveness of a virtual RFT, performed using a head-mounted display in both OpenSim and Unity3D. Each program had its advantages and limitations in the type of estimates we were able to gather. Specifically, experiments in which we used OpenSim, only alignment estimates could feasibly be collected. Experiments in which we used Unity, we were able to collect both alignment and discrimination estimates when the experimental procedures allowed. There have only been a handful of studies that have utilized a discrimination method for the RFT. These studies however, while finding the same overall classic rod and frame effect, have not compared their discrimination task results to the traditional alignment task, which we do in Experiment 1b.

2.1.1 Method

2.1.1.1 Oculus DK1. The Oculus DK1 head-mounted display uses two screens, one projected to each eye with slightly different viewpoints to create a 3D perception of the environment. The Oculus DK1 has a field of view of 110°, a total resolution of 1280 × 800, and a refresh rate of 60 Hz. The screen is a 7-inch LCD monitor with 215 pixels per inch. End-to-end latency is between 50-60 ms. The Oculus has an internal gyroscope, accelerometer, and magnetometer to track the position and rotation of the participant's head while wearing the headset with a 2 ms tracking latency and 1000 Hz tracking frequency. Both OpenSim and Unity are equipped to project 3D environments in the Oculus for a fully immersive environment using the Oculus SDK version 0.3.2 with version 0.18 tracker firmware. The headset weighed less than 1 lb. The wires and adaptor were placed in a small backpack that the participant wore during the experiment in order to keep them out of the way and safe during the experiment. The weight of the adaptor and wires were also less than 1 lb. Given the alleged effects of wearing a backpack on perceptual tasks without an explanation, most likely due to demand characteristics, we told participants the reason for wearing the backpack (Durgin et al., 2009). The lenses of the Oculus were cleaned with alcohol lens wipes before and after each participant. Participants also wore a protective face mask between their face and the headset for sanitary purposes. The Oculus came with three sets of lenses to accommodate for moderately and very nearsighted individuals. Participants who wore glasses for nearsightedness were given the option to either wear their glasses in the VR or try the corrective Oculus lenses. The vast majority of people with glasses could wear their glasses in the VR comfortably. For those who opted to try out the corrective VR lenses, in Unity, we made sure that they were able to read the words at beginning of the experiment presented on the back wall of the frame. In OpenSim, we had a testing text board the same length as the frame in order to test for acuity with the corrective lenses. No participant was unable to read our test text in the environment before the experiment. While participants were in the VR headset, the main lights of the experimental room were turned off and only low light, ambient desk lights were left on for experimenters to interact with the computer. We ensured participants could not see outside of the virtual scene by adjusting the headset to fit snugly on the participants face.

***2.1.1.2 OpenSimulator*.** OpenSimulator (OpenSim) is an online open source platform and hosting service in which users can create virtual avatars and interactable environments that users can navigate in real-time. Outside of creating interactable objects and environments in which a participant can be placed, there is no way to script an experiment with specific timed trials. Procedures of an experiment in the OpenSim environment are reliant upon the experimenter keeping pace and transporting the participant to different trials. Thus, we used this environment to conduct only SV estimates made with alignment tasks. We created the RFT using built-in building blocks and duplicated the experimental setting for 9 frame orientations ($\pm$ 0, 8, 18, 28, 38). The frame was a uniform grayscale color. Natural lighting provided by the environment caused the ceiling to appear darker than the other walls. This was because one side of the frame was a one-way window so that the experimenter could observe the participant from the outside of the frame and provided natural light to come into the enclosed space. However, if the participant were to rotate their head upwards and stare directly at it, the wall would become indistinguishable from the other walls. The rod was made luminous by use a glow feature on top of the white color. This glow setting helped to smooth out pixilated edges of the rod. Additionally, we used the maximum anti-aliasing setting to further reduce the pixilation of the rod.

Participant avatars were transported into each frame using a world coordinate system. The participants were placed at the same position inside the virtual frame which was always the same virtual distance from the rod for each trial. Participants took on the first-person point of view of a 2-meter tall avatar when putting on the Oculus headset, see figure 2.1. The avatar was situated 20 virtual meters from a 3-meter tall rod that appeared at the back center of a 25-virtual meter long frame (see figure 2.2). The back wall measured 5 × 5 virtual meters. Headtracking was enabled for the Oculus headset to allow for a 3D sense of depth to the RFT. During trials, participants were instructed to keep their head straight.

We created an interactive control panel that was scripted to control the rotation of the rod inside the frame from outside the experimental environment (see figure 2.3). In order to both control the rotation of the rod and provide the participant with the experimental view of the RFT in the headset, both the experimenter and the participant saw through the eyes of separate virtual avatars using separate computer set-ups within the world. For the alignment task, participants verbally instructed the experimenter how to adjust the rotation of the rod to achieve verticality (see section 1.2 for general methods). In order to clarify the concept of true vertical in the context of the virtual world, we specified that true vertical meant "in line with the direction of gravity" and "parallel to your body axis". Using the control panel, the experimenter continued to rotate the rod in the specified direction until the participant told them to stop. Experimenters always started initial rotations using large increments (±0.45°) until participant told them to stop. After which, only smaller increments were used (0.25° – 0.1°). Participants were allowed to make as many adjustments as they liked until they believed that the rod was at true vertical. The final estimate was then reported, and the experimenter transported themselves to the next trial location to set up the random initial rod position. They then virtually transported the participants' avatar to the next trial using the coordinate system. During transportation between trials, participants were asked to close their eyes as the graphics of this movement and initial rendering of the environment can cause dizziness and motion sickness. For each of the nine frame orientations, participants made 2-4 alignment estimates per frame, time permitting. All trials were randomly ordered.

Figure 2.1: Participant's first-person point of view of traditional RFT with a luminated rod in OpenSim. Room is tilted -38° and rod is tilted 0°. Pixelization is not representative of actual view from inside headset.

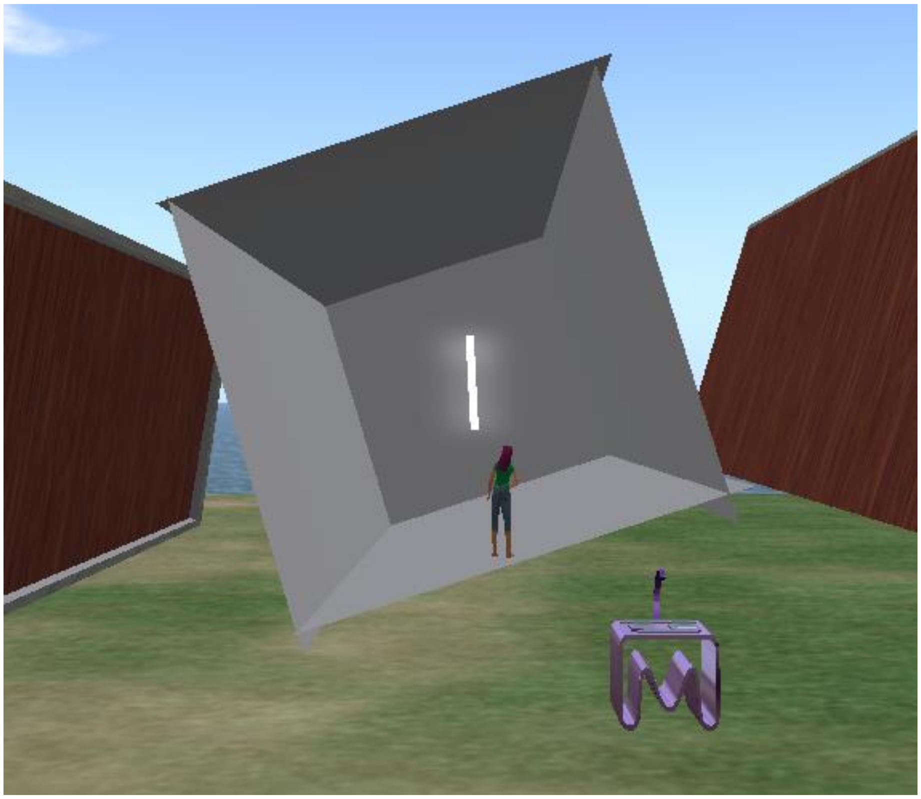


Figure 2.2: Outside point of view of a single RFT setup in OpenSim. Frame is tilted -18° and the rod is tilted 0°. Pixelization is not representative of actual view from inside headset.

Figure 2.3: Experimental control panel in OpenSim. Preset initial rod angles were located at the top. Arrow keys indicated large, medium, and small (from top to bottom) rod adjustment increments used during participant adjustment. "Report Rotation" button reported the degree of the rod rotation in an output that was paired with the angle of the frame.

***2.1.1.2 Unity*.** Unity is a cross-platform gaming engine that can be used to develop 3D and 2D simulations and video games. Unity allowed us more automated control over timing and methodological scripts as this platform is not in real-time but rather can be used to develop a canned experiment. Using Unity, we developed another version of the RFT using similar building blocks as we did in OpenSim to create the RFT. We originally used the same types of grayscale colors and luminated rod as we did in OpenSim but found that due to the innate physics built into Unity, the illumination of the rod created afterglow effects in the VR when presented with quick (< 500 ms) sequential trials in a discrimination task. This was not an issue in the OpenSim environment because there were separate environmental settings for each frame condition in which participants were virtually transported. Thus, in Unity, we opted for a low contrast, darkened rod and grayed walls. A hidden spot light was present behind the point of view of the participant to illuminate the inside of the frame. Because we had increased control over the procedural element of the experiment in Unity, we were able to conduct a discrimination task along with an alignment task. Due to its versatility, we used Unity for the majority of the experiments presented throughout these chapters. Nevertheless, we wished to compare visual SV alignment estimates from OpenSim with those made in Unity to establish the robustness of virtual RFT environments, even with slightly different parameters.

The alignment task in Unity was similar to the alignment task in OpenSim. Participants completed a series of 4 alignments estimates to vertical when the frame was tilted $\pm 18°$ and 0°. The presentation of the frames was randomly ordered. The initial rod orientation was randomly selected at the beginning of each trial between $\pm 25°$. Upon presentation of the rod and frame, participants used mouse buttons to rotate the rod in 0.2° increments (left mouse button for counterclockwise) until they believed that it was vertical. Participants could hold down a mouse button for a smooth, continuous rotation. Once complete, the participant verbally confirmed their belief that the rod was vertical, and the experimenter pressed enter to move the participant to the next trial. A blank gray screen was shown between trials for 1.5 seconds before the next trial was presented.

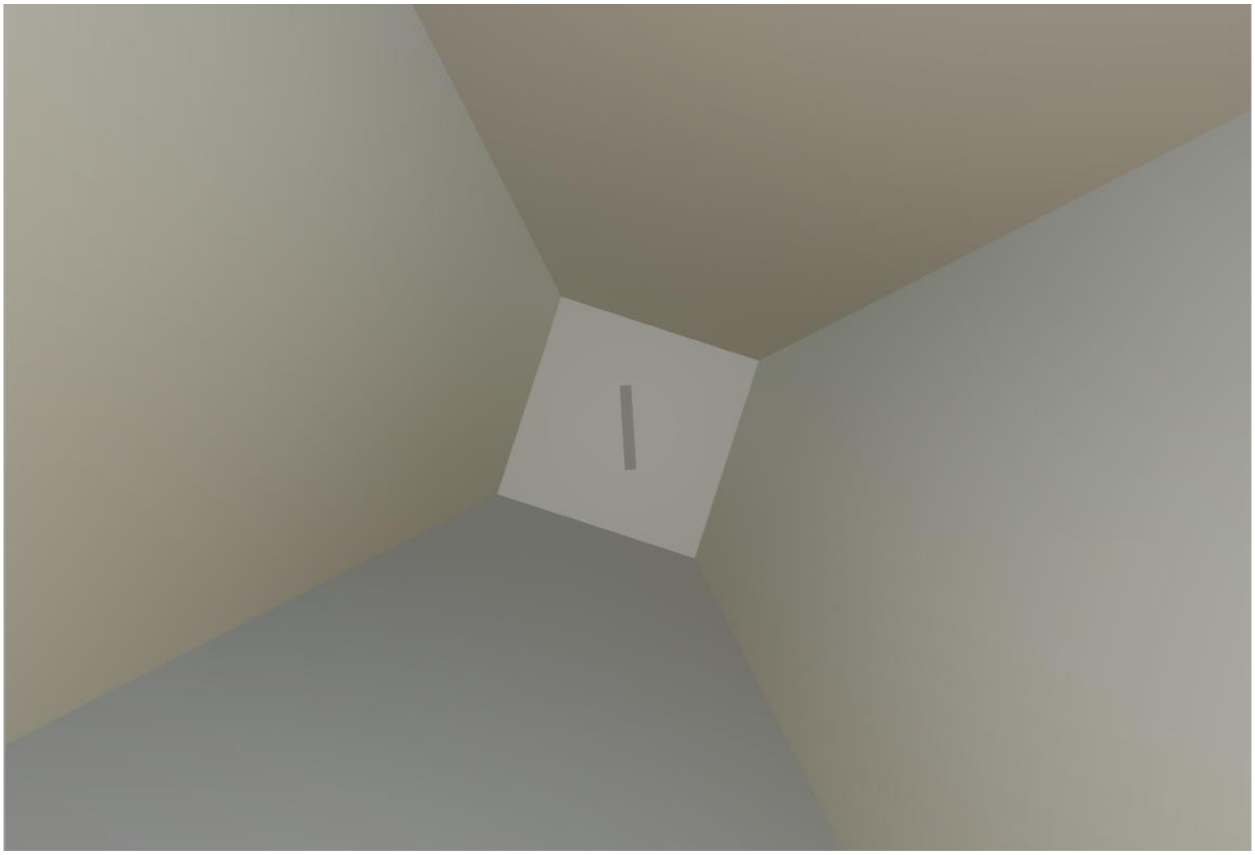


Figure 2.4: Participant view of RFT in Unity. The frame is tilted 18° and the rod is tilted 0°.

During all RFT experiments using OpenSim and Unity in upright stance conditions, participants stood with their feet together, legs straight, and their hands by their sides. All participants stood on 20 cm thick, high-density foam and wore a memory foam neck pillow in order to limit feet and neck proprioceptive cues, respectively. All participants were tested for visual acuity, eye dominance, and height before engaging in the RFT in the virtual environments. In Unity, when using the mouse to indicate their response, participants held the mouse in their right hand and rested it upon the right side of their leg.

2.1.2 Results

We randomly sampled 20 participants who completed the RFT in Unity to compare with the 19 participants who performed this task in OpenSim in frame tilts of $\pm 18°$ and 0°. We took 3 different random samples of 20 participants that made SVV estimates in Unity and compared them with those that used OpenSim and found similar results. Overall, using 2 (VR Platform) $\times$ 3 (Frame), we found no significant differences between RFT alignment estimates made in OpenSim compared to RFT alignment estimates made in Unity, see figure 2.5. We only found the expected main effect of frame in which visual SV estimates in the tilted frame conditions were biased towards the tilt of the frame, F (2, 74) = 66.61, p < .001, η_p^2 = .643. Using the same ANOVA on within-subject standard deviations, we found an effect of frame, in which the tilted frame produced greater variability between trials, F (2, 74) = 6.16, p = .003, η_p^2 = .143. We also observed a significant interaction effect of frame and VR platform in within-subject standard deviations, F (2, 74) = 3.17, p = .048, η_p^2 = .079. This interaction mainly suggested that at the positive frame tilt, participants had smaller standard deviations in OpenSim than participants using Unity, which was not expected, see figure 2.6.

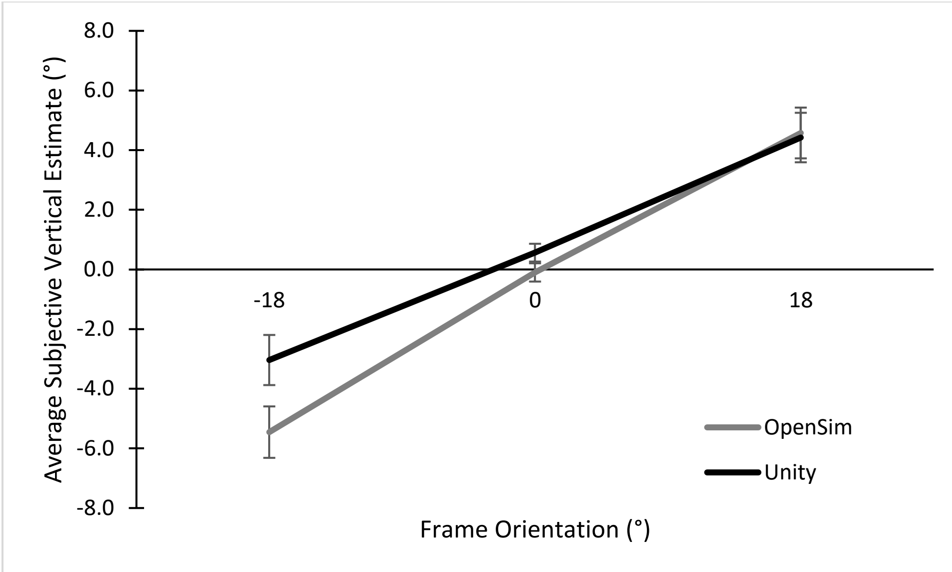


Figure 2.5: Average visual subjective vertical estimates made in OpenSim and Unity using the alignment method. Error bars represent standard errors about the mean.

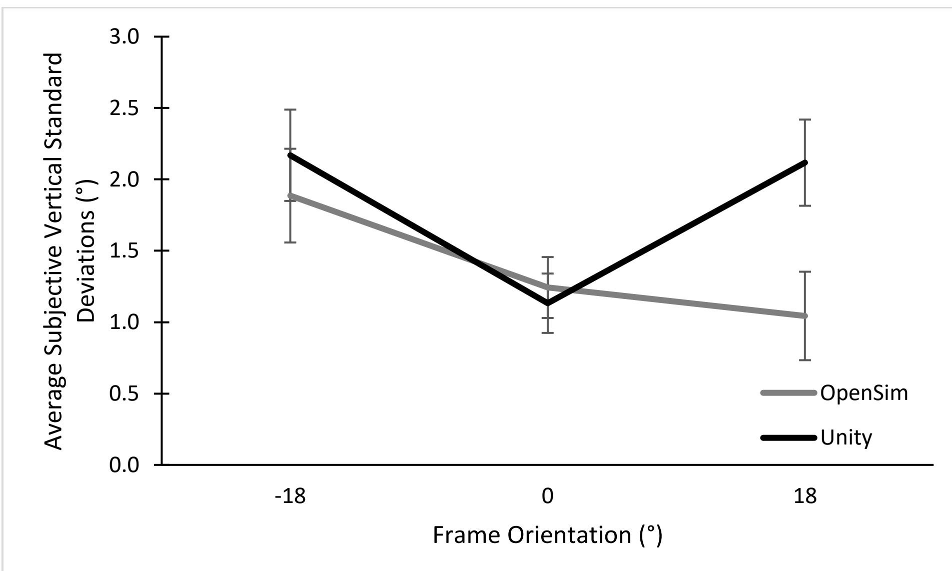


Figure 2.6: Average within-subject standard deviations of visual subjective vertical estimates made in OpenSim and Unity using the alignment method. Error bars represent standard errors about the mean.

2.1.3 Discussion

Although, there were no significant differences between virtual reality platforms in SV estimates, we found that OpenSim consistently yielded slightly larger absolute estimates overall when the frame was tilted. These small differences between the two platforms could be due to a number of factors that differed between the two protocols, such as the experimenter keeping control of the rotation of the rod or the illumination levels of the frame (Long, 1973). Further, there was a difference in within-subject standard deviations in OpenSim on the positively tilted frame. This could be the result of sampling error, as some participants were unable to make all four estimates in each of the frame conditions in OpenSim, thus it was not uncommon for a few participants to yield no variation in their estimates in OpenSim. As we will see in later experiments, within-subject standard deviations consistently take on a function in which the tilted frame conditions yield greater variability in SV estimates than the non-tilted frame condition.

Comparing these alignment results to previous research, suggested that our virtual RFT conditions yielded similar results to the physical RFT and other VR methods using the alignment method (Bringoux et al., 2009; Oltman, 1968). What seems to be important in these methods is that they all provide a sense of depth, whether ‘real’ or virtually created. Additionally, in these methods, the 3D frame takes up the majority of the peripheral field of view. In a separate pilot study, we adapted the RFT in Matlab to project a 2D version of the alignment and discrimination tasks. We found significantly smaller errors in the tilted frame conditions. The reduction of errors when using a 2D RFT was consistent with past research on 2D displays of the RFT in which on average errors in the tilted frame conditions did not exceed 2° (Docherty & Bagust, 2010; Razzak, 2013). These results suggest that our virtual 3D RFTs are valid measures to test for the influence of a 3D tilted frame SV measures.

2.2 Experiment 1b: Alignment vs Discrimination Methods

Due to its ease of implementation and production of reliable estimates, the alignment method has been used for decades. Additionally, due to the low overhead of the portable apparatus, the alignment method was feasible for any setting. However, now that the RFT has been adapted to digital formats, the ease in which we can utilize other, more informative methods has become a possibility. Recently, multisensory researchers interested in the psychometric function of the RFT effect began utilizing alternative methods, such as orientation discrimination tasks to better understand how people were estimating vertical under the tilted frame conditions (Alberts, de Brouwer, Selen, & Medendorp, 2016). Methods of alignment, although robust, may introduce higher cognitive factors involved in decision making. The longer the presentation time of the stimuli introduces biases that may not be solely contributed to perceptual phenomenon but rather response biases. These can manifest in both experimental demand characteristics in which the participant may overestimate their percept and bias more towards the tilt of a frame or in the case where participants may attempt to overcorrect for an obvious illusion towards the frame, resulting in underestimates compared to their actual perception. Both of these kinds of higher-order cognitive response biases are undesirable in perceptual research and introduce variability in group data. Perceptual discrimination tasks minimize these cognitive biases through the method of constant stimuli. In the method of constant stimuli in an orientation discrimination task, pre-selected rod orientations are presented on each trial and are only shown for a fraction of a second. The participant's task on each trial is to indicate whether the rod is oriented clockwise or counterclockwise to vertical. For each pre-selected rod orientation, the proportion of clockwise responses are calculated to indicate on average, the perceived direction for each orientation. The point in which the proportion of clockwise responses yields 50%, is the point of subjective vertical. Using the range of responses to the rod orientations, we can measure how sensitive a participant is to this SV estimate by looking at how drastically the proportion of clockwise responses change between rod orientation increments. The change in proportion of 'clockwise' responses will determine how sensitive they are to the detection of their own subjective vertical. The greater the uncertainty, the less change in responses from the 50% response rate. The perfectly sensitive and accurate observer would thus only respond ‘clockwise’ to clockwise rod orientations, respond ‘clockwise at a rate of 50% for 0° rod orientations, and never respond ‘clockwise’ to counterclockwise rod orientations.

Experiment 1b investigates how participants differ using the alignment and discrimination task methods in Unity. This is an important distinction to make due to the differences in decision-making processes for each type of task. Additionally, discrimination tasks have the added ability to detect the sensitivity of the estimate given. This additional estimate will ultimately be used to help determine how multisensory cues are combined to form an end estimate.

2.2.1 Method

Because there are such large individual differences between participants on the RFT, the method of constant stimuli would normally be a costly endeavor because the researcher would need to test all potential rod orientations in hopes of capturing each participant’s underlying psychometric function of their subjective vertical. In order to save time and resources, we first used an alignment task to help center the preset rod orientations for the discrimination task. Fifty-three participants completed both alignment and discrimination visual SV trials for each frame tilt condition ($\pm$18° and 0°) in Unity. The average SV estimates from 6 alignment trials for each frame tilt were used to determine the preset rod angles to which the participants responded in the discrimination task. For each of the tilted frame conditions separately, rod orientations were chosen to be $\pm$ 1°, 2°, 3°, and 4° away from the average SV estimate made during the alignment task. For the 0° frame condition, we chose rod orientations that were $\pm$ 0.5°, 1°, 2°, and 3° away from their average SV estimate made in the 0° tilt alignment condition. Each rod orientation/frame orientation pair was presented 8 times throughout the experiment, resulting in 192 total trials. The presentation of angles and frame orientations were all randomly presented. The rod and frame were presented for 250 ms before the screen returned to the background gray. Participants had 2 seconds to respond to each trial presentation with a right or left mouse click to indicate whether the rod was tilted clockwise or counterclockwise (respectively) to vertical. Even if the participant responded before the 2 second period was over, the screen continued to be a blank gray for the remaining time (see figure 2.7). We fitted a cumulative gaussian function to the data and determined the orientation in which the participant would have responded clockwise 50% of the time, their subjective vertical bias. We also measured the slope of this function to determine their sensitivity to their subjective vertical estimate. Shallow slopes indicated more uncertainty in their subjective vertical estimates and thus greater variability in their responses. Our main comparison looked at how biases and standard deviations from the discrimination task compared with SV estimates made using the alignment task.

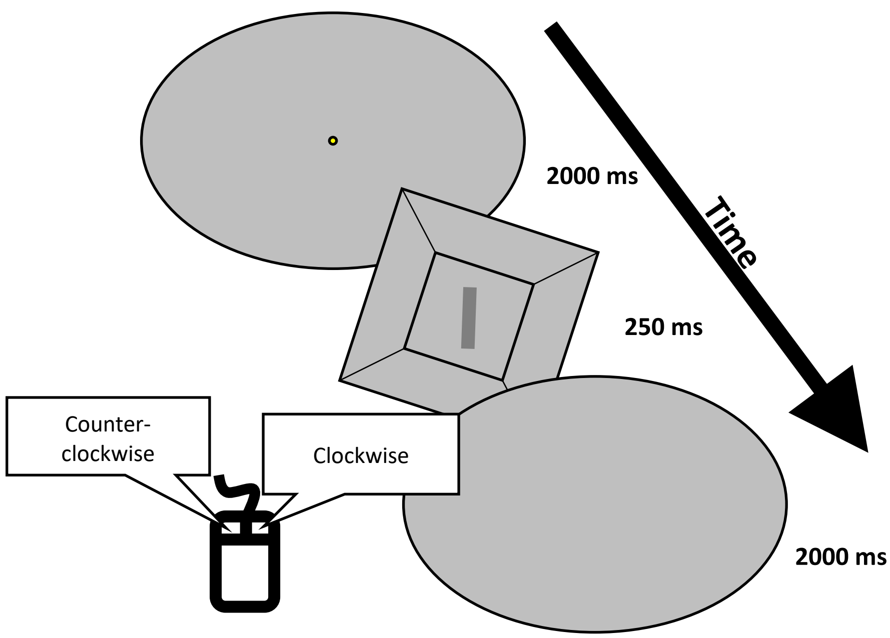


Figure 2.7: Schematic of a single orientation discrimination trial in the discrimination task.

2.2.2 Results

Two participants were excluded from analyses that contain the discrimination task because we were unable to fit a psychometric function their data. Their alignment scores did not significantly differ from the remaining 51 participants. Using a 2 (Method) × 3 (Frame) repeated-measures ANOVA, we found that there was an expected main effect of frame orientation, F (2, 100) = 89.66, p < .001, η_p^2 = .642. Most interesting to this investigation was that there was also an interaction effect of method and frame suggesting that in tilted frame conditions, there were greater visual SV biases when using the discrimination method compared with the alignment method, F (2, 100) = 12.32, p < .001, η_p^2 = .198, see figure 2.8.

We also compared within-subject standard deviations from the alignment and discrimination tasks using the same repeated-measures ANOVA. We found no differences between RFT methods and only found a main effect of frame in which tilted frames yielded greater within-subject variability, F (2, 100) = 54.09, p < .001, η_p^2 = .520, see figure 2.9.

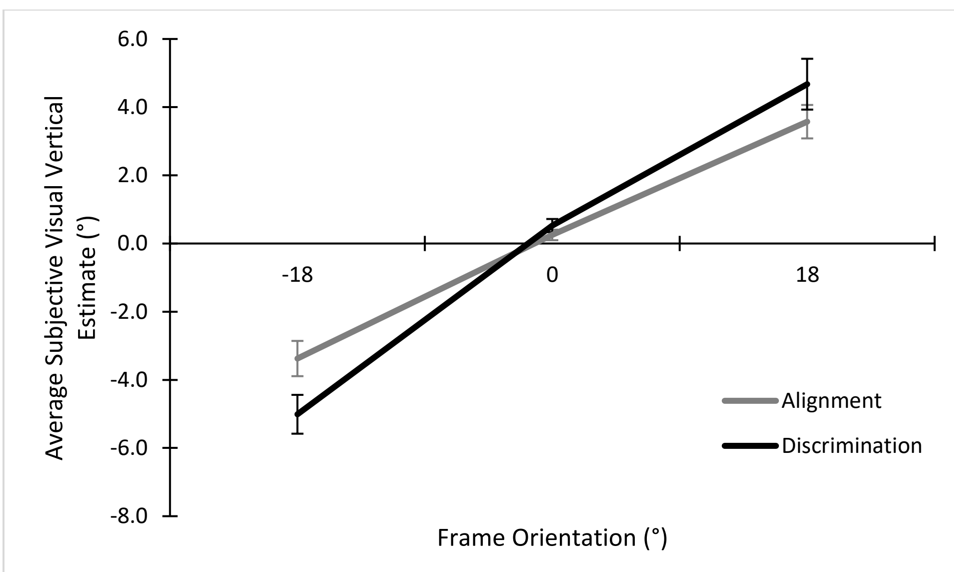


Figure 2.8: Average visual SV estimate using the alignment and the discrimination orientation tasks.

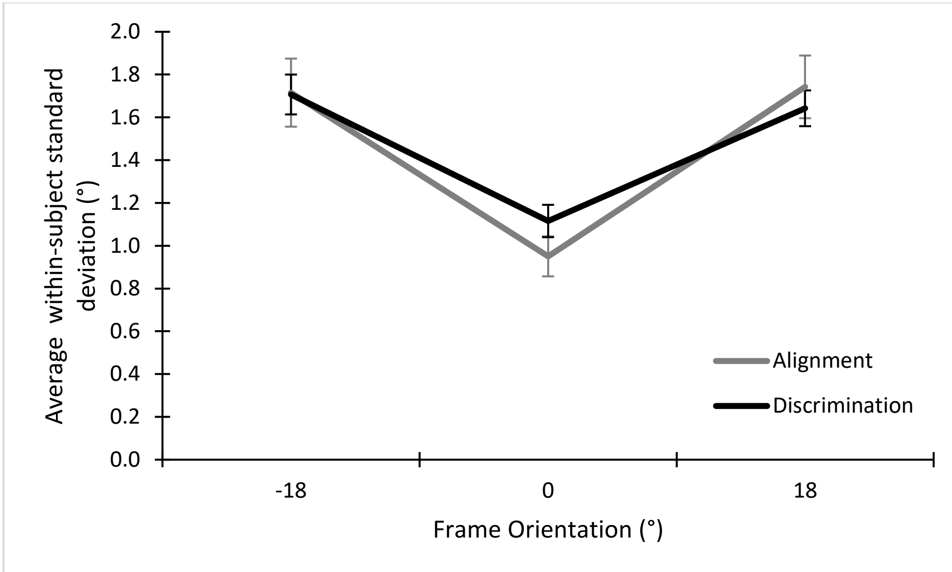


Figure 2.9: Average within-subject standard deviations of visual SV estimates in the alignment and discrimination tasks.

Additionally, we collapsed estimates made in the frame tilt conditions by multiplying the SV estimates made in the negative frame condition by -1 and averaging these estimates with the SV estimates made in the positive frame condition. We then used these averaged tilted frame estimates to observe the correlation between alignment and discrimination methods on the effect of the tilted frame. SV estimates from the alignment method and the discrimination method significantly correlated with one another, r (49) = .721, p < .001, see figure 2.10. No such correlation was found between averaged frame within-subject standard deviations in the alignment and discrimination tasks, r (49) = .110, p = .441. Further, we found that within-subject standard deviation in the alignment task significantly correlated with SV estimates within the alignment condition, r (51) = .659, p < .001, and the discrimination SV estimates, r (49) = .586, p < .001, suggesting that as biases increased so did the alignment standard deviations. However, we did not find that within-subject standard deviations in the discrimination task were correlated within the discrimination SV estimates, r (49) = .174, p = .222. Between subjects, there was overall less variability in within-subject standard deviations in the discrimination task (M = 1.72, SD = 0.54) then there was in the alignment task (M = 1.73, SD = 0.98), see error bars for standard errors in Figure 2.9.

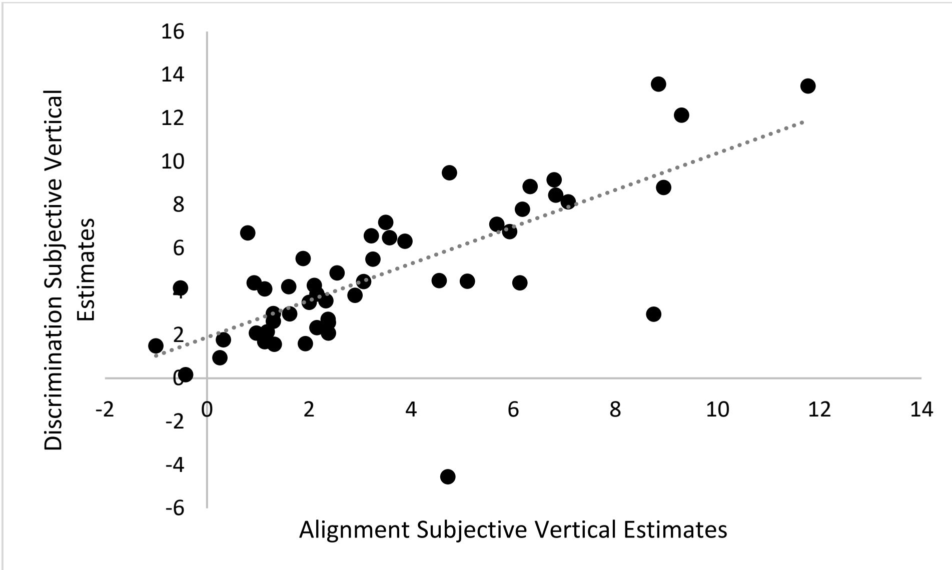


Figure 2.10: Scatterplot of subjective vertical estimates made in the alignment and discrimination tasks.

2.2.3 Discussion

These results suggest that there may be differences in how people cognitively make SV estimates based on the methodology used. As perceptual researchers the main goal of perceptual studies is to understand how people are taking in information through their perception. Unfortunately for perceptual research, behavioral experiments require responses from participants and the act of responding to stimuli necessarily have to involve higher-order cognitive areas in order for a response to be produced. We attempt to limit the amount of cognitive processing that is unrelated to the pure percept that we wish to measure but nonetheless it will always be present. This study may be one example in which given the opportunity, participants may knowingly or unknowingly alter their responses through post-perceptual cognitive processes. The opportunity for this to occur is greater in the alignment task in which participants are given more control over their final estimate. Attempting to compensate for the illusion that the frame creates can result in participants correcting for their perceptual tendencies and underestimate their SVV biases. Within a single alignment trial, participants have an unlimited number of comparison rod orientations to compare their final estimate to as they watch the rod rotate. In the discrimination task, participants are under a time constraint to determine the rotation of the presented rod, participants only have the last trial to compare their response. Overall, given these considerations, the method of constant stimuli used in this discrimination task, may be a better representation of participants' subjective perception of vertical with limited influences from higher-order decision making processes.

Interestingly, we did not find any differences in within-subject standard deviations between the two methods, suggesting that the consistency of each estimate is relatively the same for both tasks. However, there was also no correlation of within-subject variability between the two tasks, again suggesting that the strategy for responding may vary between these different tasks.

2.3 Experiment 2a: Texture cues in the Rod and Frame Task

Given that we were able to replicate the general effects produced by a tilted frame in our VR RFTs, we wished to use the advantages that using VR provides to test other visual cue effects in the RFT. There is evidence to suggest that increasing the richness of the visual cues inside the frame will result in overall greater biasing towards the frame tilt (Bringoux et al., 2009). As mentioned earlier, it seems to be that depth cues in the RFT are the main driving force behind the strength of the frame tilt effect as evidenced by the large differences between 2D and 3D RFTs. As such, we wished to further test this hypothesis by enhancing the depth cues through the use of a checkerboard texture gradient along the walls of the frame in the RFT. We expected that this would enhance the perception of depth of the RFT in the VR environment and thus increase SV estimates particularly in the tilted conditions.

2.3.1 Method

Forty-four participants performed the discrimination task in the RFT using a checkerboard texture on the walls. All had normal or corrected to normal vision. In this experiment, we wished to examine the effect of high contrast texture cues on the classic rod and frame effect. All experimental procedures were the same as outlined above for the discrimination task in Unity. The sole difference was that the walls of the frame in which the participant viewed were a low contrast (20%) gray checkerboard pattern (see figure 2.11). A gray screen still appeared between trials in the discrimination task. We compared participants' RFT estimates in the checkerboard condition to participants that estimated the RFT in the gray condition from Experiment 1b.

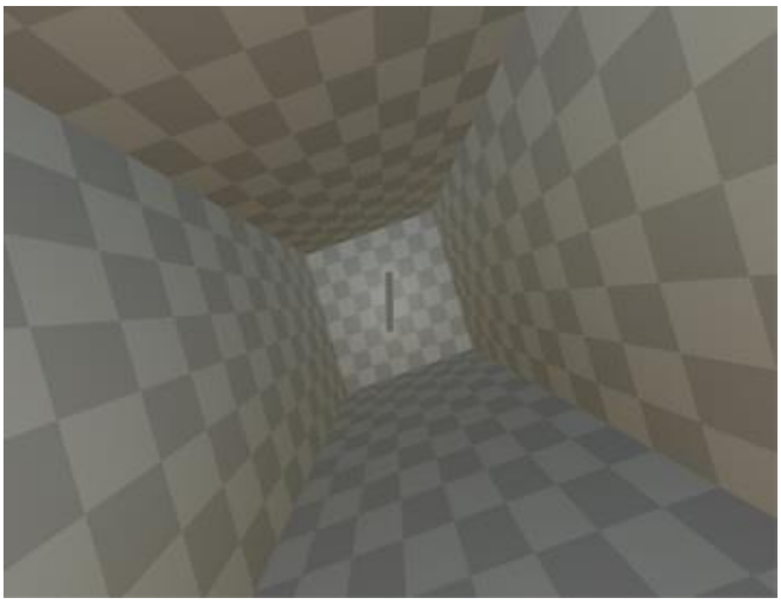


Figure 2.11: Rod and Frame Task in unity with checkerboard texture pattern. Frame is tilted -18° and the rod is tilted 0°.

2.3.2 Results

Four participants were excluded from analyses that contained the discrimination task because we were unable to fit a psychometric function their data. Using a 2 (Texture) × 3 (Frame) ANOVA on SVV biases, we found a main effect of frame, demonstrating the RFT effect, F (2,178) = 202.165, p < .001, η_p^2 = .690. We also found an interaction between texture and frame suggesting that in the tilted frame conditions, participants had significantly greater biases when making their estimates within the checkerboard texture compared to the gray texture, F (2,178) = 3.26, p = .041, η_p^2 = .035, see figure 2.12. Although, not significant, the average difference at the tilted frames, between the gray and checkerboard textures was 1°. Using alignment SV estimates, we only found an effect of frame. There were no differences nor an interaction involving texture.

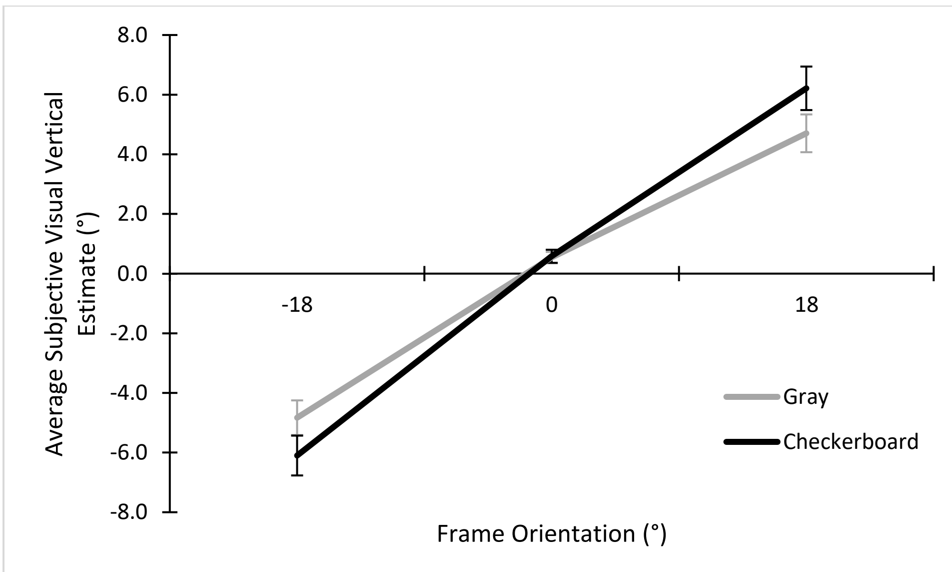


Figure 2.12: Average subjective vertical estimates in the RFT using frames with solid gray and checkerboard textures in the discrimination task.

Using the same ANOVA design, I compared the within-subject standard deviations between gray and checkerboard conditions. I found the typical significant effect of frame, F (2, 178) = 50.88, p < .001, η_p^2 = .359. There was also a significant main effect of texture condition such that participants in the checkerboard condition had greater variability than the participants in the gray condition, F (1, 89) = 7.65, p = .007, η_p^2 = .078, see figure 2.13. Using the alignment within-subject standard deviations we found a similar main effect of texture and frame. However, we also found a marginally significant interaction suggesting that only the tilted frame conditions had greater variance in the checkerboard condition compared to the gray condition, F (1,87) = 3.64, p = .06, see figure 2.14.

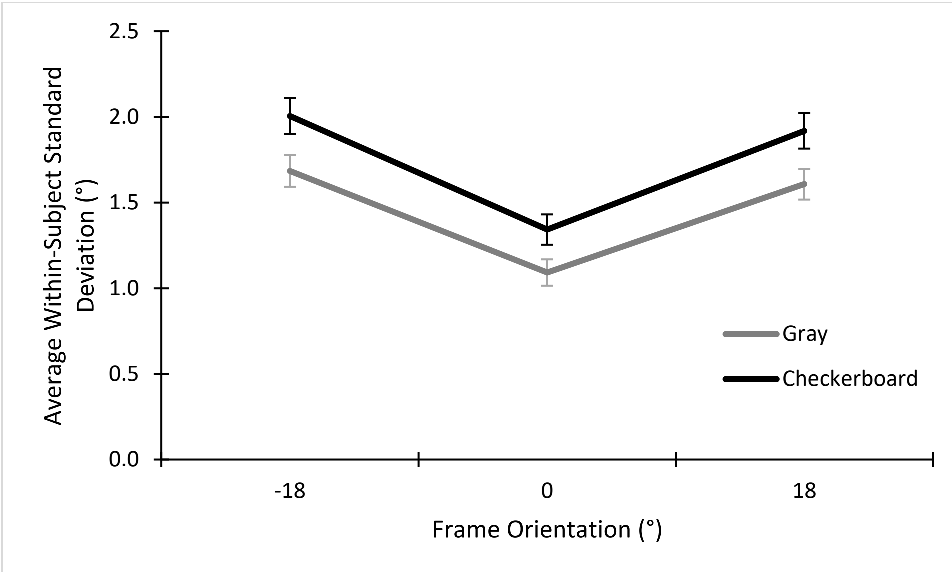


Figure 2.13: Average within-subject standard deviations of subjective vertical estimates in the RFT using solid gray and checkerboard textures in the discrimination task.

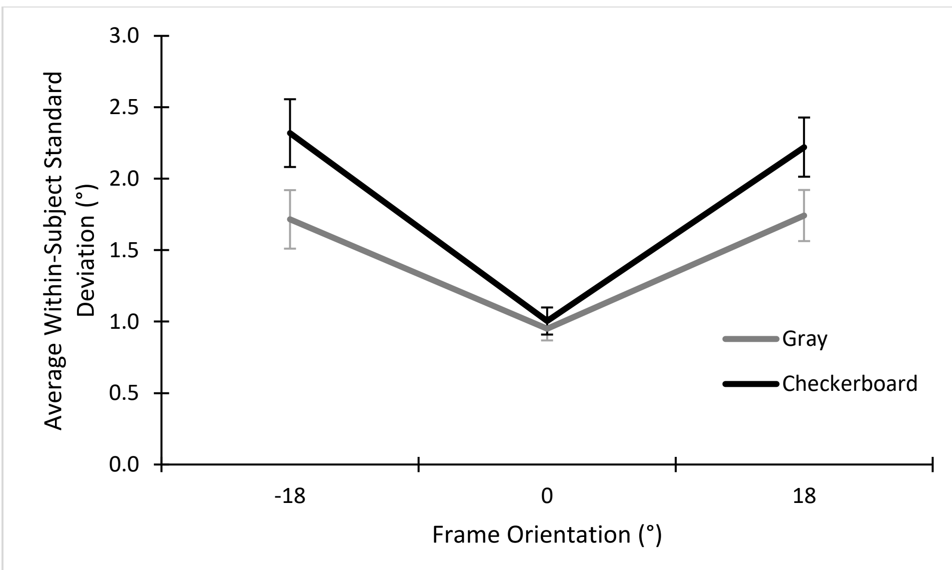


Figure 2.14: Average within-subject standard deviations of subjective vertical estimates in the RFT using solid gray and checkerboard textures in the alignment task.

2.3.3 Discussion

We found some support that participants have greater biases and larger within-subject standard deviations in the checkerboard condition compared to the gray frame condition.

However, this effect was small. Further, we found that within-subject standard deviations tend to increase in the checkerboard texture condition. These results suggest that our checkerboard condition may have been more difficult than the gray condition and in the discrimination task had a greater effect on tilted frame SV biases.

2.4 Experiment 2b: Additional Scene Cues in the Rod and Frame Task

We expanded upon Experiment 2a by further enhancing the cues in the RFT task by including objects within the frame in a natural scene. We also attempted to test a greater number of frame tilts to investigate whether there was a change in the classic RFT sinusoidal curve that occurs with increasing frame tilt. Specifically, in the RFT, it is well reported that the maximum effect of the frame on visual SV biases is found when the frame is tilted to about 18° (Bringoux et al., 2009; Oltman, 1968). At smaller frame orientations, the bias towards the frame tilt increases in strength up until the frame reaches a ±18° tilt, after which SV biases tend to plateau off and do not increase with greater frame tilt. We wished to test whether this effect persists in a natural scene setting that included objects as well as textures in the scene, all of which would enhance the depth cues seen in the frame through apparent size and texture gradient. Other researchers have employed a similar inquiries (Bringoux et al., 2009; L. Harris, Dyde, & Jenkin, 2007), but none have noted differences between enhanced visual cues and the classic RFT in pattern of responses up to 45° frame tilts. However, there was some support for a larger RFT effect in a naturalistic scene that included furniture, and textured walls (Harris, et al, 2007).

2.4.1 Method

We used OpenSim to present participants with the traditional gray room (see figure 2.1) as well as an office scene in which common office objects were presented within the frame. In addition, the walls of the frame contained a wood grain texture that ran parallel to the walls themselves, see figure 2.15. Eighteen participants made alignment estimates in both gray and office frame conditions. Each participant made 4 alignment estimates per 9 frame orientations (0°, ± 8°, 18°, 28°, 38°) in each of the frame conditions. The initial placement of the rod was randomly placed at either ± 15° or ± 25° from vertical. The average was used to determine their visual SV estimate. The procedures were the same as described above for the OpenSim program, see section 2.1.1.2.

Figure 2.15: Office scene in OpenSim from the point of view of the participant. Frame is tilted 18° and luminated rod is tilted 15°.

2.4.2 Results

First, using a 2 (RFT condition) × 9 (Frame Tilt) ANOVA, we found a main effect of frame, in which larger frames had greater SV biases, F (8,136) = 38.01, $p < .001$, $\eta_p^2 = .691$. We also found an interaction between frame and condition, F (8,136) = 7.72, $p < .001$, $\eta_p^2 = .312$. Looking at each condition individually, we found that the gray frame condition was best characterized by a cubic function across frame tilts, F (1, 18) = 15.68, $p = .001$, $\eta_p^2 = .466$, while the office frame condition was best characterized by a linear function across frame tilts, F (1,18) = 50.87, p < .001, η_p^2 = .728, see figure 2.16.

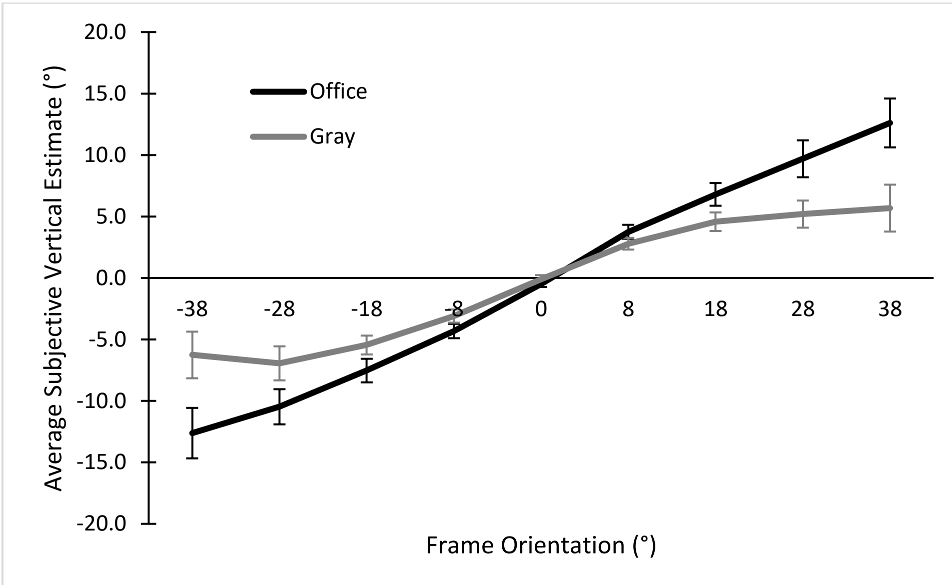


Figure 2.16: Average subjective vertical estimates at each degree of frame tilt in the gray and office RFT conditions.

We found no differences between the absolute magnitude of responses in negative and positively tilted frame and further collapsed estimates across symmetrical frame orientations. We collapsed across negative and positive frame angles by multiplying estimates given in the negative frame conditions by −1 and averaging them with the respective estimates made in the positive frame conditions. We then performed a 2 (RFT) × 5 (Frame Tilt) ANOVA and found a main effect of frame, F (4, 68) = 33.21, p < .001, η_p^2 = .661. We also found a main effect of RFT condition such that the office frame condition had greater biases overall than the gray frame condition, F (1, 17) = 9.73, p =.006, η_p^2 = .364. Lastly, we found a similar interaction effect between frame and condition, suggesting that larger frame tilts yielded larger biases, F (4, 68) = 7483, p < .001, η_p^2 = .306 (see figure 2.17).

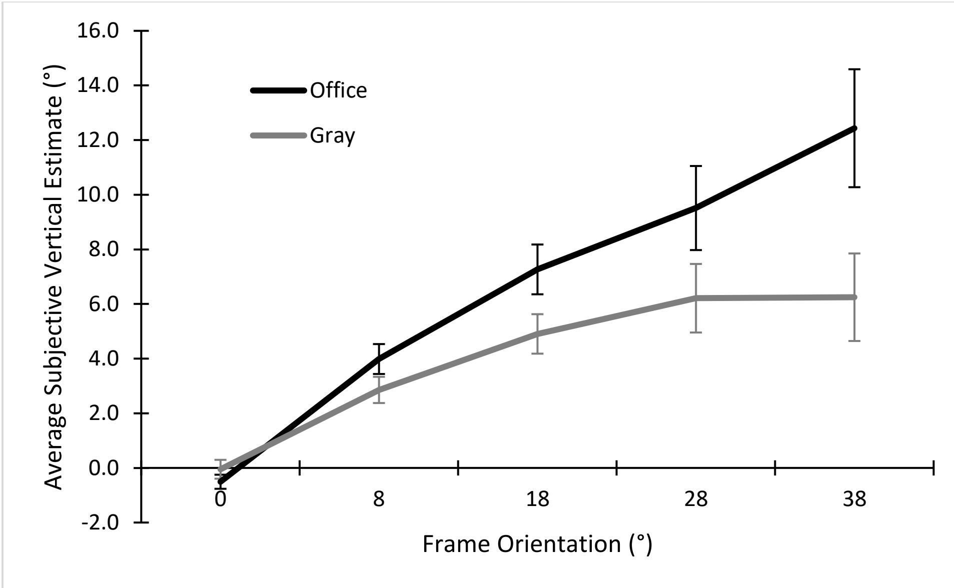


Figure 2.17: Average subjective vertical estimates, collapsed across symmetrical negative and positive frame tilts for varying degrees of frame tilt in gray and office RFT conditions.

We performed a similar 2 (RFT) × 9 (Frame) ANOVA using within-subject standard deviations and found similar results between gray and office RFT conditions and found only a main effect of frame in which more extreme tilts yielded greater variability of trial alignment estimates, F (8, 136) = 9.73, p =.006, η_p^2 = .364. Interestingly, the extreme positive tilts did not seem to yield standard deviations as large as the extreme negative tilts, however these differences were not significant, mirroring the earlier effect found in experiment 1b in OpenSim. Combined, the function of frame tilt on within-subject standard deviations took on a quadratic relationship, F (1, 17) = 14.99, p < .001, η_p^2 = .469, see figure 2.18.

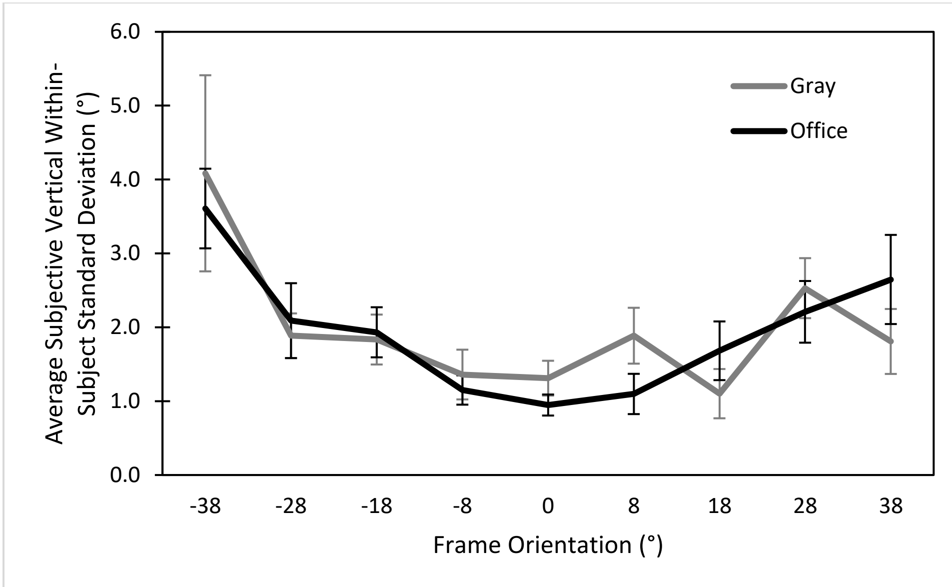


Figure 2.18: Average within-subject standard deviations of subjective vertical estimates across frame tilts for gray and office RFT conditions.

2.4.3 Discussion

This study is one of the few to examine how life-like objects and textures can contribute to the biased perception of SV when parallel with the tilt of the frame in the RFT. These results suggest that RFT biases can increase with tilted frames greater than 18° with increased cues that signal the depth, such as texture and object size. Additionally, the presence of the objects themselves tilted in the same direction as the frame could have also contributed to this increase in effect. These results are in line with a previous study that investigated the role of different aspects of a tilted room on perception of upright (Harris, Dyde, & Jenkin, 2007; Harris, Jenkin, Dyde, & Jenkin, 2011). Using a virtual environment, they simulated four virtual conditions: an empty room with textured walls, a room with textured walls and furniture, only the furniture, and only a wire frame. They rotated these scenes from 0°- 360° and found that the wire frame and the empty room yielded the most accurate results of perceptual upright, while the furniture alone condition yielded the greatest errors towards the orientation of the frame.

Also, as expected, we found greater variability at larger frame tilts. Interestingly, however, there were no differences between conditions on average standard deviations suggesting that the conditions presented similar reliabilities in their visual cues about tilt. More research is needed in this area to determine the individual visual cues that can play a part in the biasing of SV estimates in RFT, such as texture gradient, color, contrast, apparent object size, frequency and location of objects, etc. Additionally, these methods can be used to differentiate between the contribution of local object tilt on the perception of vertical compared with global frame effects by changing the consistency of each within the same scene. This area will be a future line of research.

2.5 General Discussion

In this chapter we explored the use of VR and a VR headset in the investigation of visual biases on subjective vertical. We found that our recreation of the RFT in virtual environments are comparable to other investigations of the 3D RFT. Additionally, we explored a newer methodology of testing RFT effects using the discrimination task and found that while biases obtained using the discrimination task in tilted frame conditions were in general larger than those found using the classic alignment task, that they followed the same expected trend seen in the RFT. Further, given the limitations of the alignment task, discrimination tasks may actually better reflect SV estimates made in the RFT. Lastly, in experiments 2a and 2b, we explored some of the manipulations that one could make when testing the RFT effects using a VR setup. Specifically, we could effortlessly change the texture of the walls in the frame to test for effects of texture gradient on RFT as well as build an entire office scene with multiple depth cues to test the RFT effect in an ecological setting. The utility of a VR environment will be very useful in further investigations of the RFT and the visual cues that may affect the magnitude of the effect.

In the next chapter, we will discuss vestibular contributions to SV and their interactions with visual tilt cues in the RFT.

3 CHAPTER 3: Vestibular influences on subjective vertical and body orientation

Vestibular cues about vertical arise from mainly two sources; rotational and linear acceleration of the observer's head. The semi-circular canals can sense head rotations within each of the three dimensions via a fluid filled chamber that innervates embedded hair cells at the ampulae in the vestibular apparatus attached to the cochlea in the inner ear. When tilting one's head clockwise around the line of sight while looking straight ahead, manual transduction occurs and there is an increased firing rate from the person's right posterior semi-circular canal while there is inhibition of firing rate in the left posterior semi-circular canal. The otoliths, small calcium carbonate particles move with the head within the otolith organs, manually displacing the hair cells embedded in the otolithic membrane and otoconia and activating hair cells that decode the direction of gravity in relation to otolith position. Afferents coming from the semi-circular canals and the otoliths are joined with a bundle of cochlear afferents to make up the vestibulocochlear nerve. The vestibular afferents then travel to the vestibular nucleus located in the brainstem, the first place in which they are processed by the brain. Impressively, integration of vestibular cues with visual and proprioceptive inputs occurs at the level of the vestibular nuclei in the brainstem. Given the time sensitive nature of these inputs, quick integration is extremely important. In the case of stabilization of eye gaze via the vestibule-ocular reflex (VOR), this integration happens using a three-neuron arc ensuring extremely fast responses. After the head rotation innervates the semicircle canals sending information to the vestibular nuclei, neurons from the vestibular nuclei project to extraocular motoneurons in the abducens nuclei to make compensatory eyes movements in the opposite direction of head movements within less than 10 milliseconds of initial head rotation. The short latency to integrate other sensory information with the vestibular system gives us the perception of smooth and seamless conscious awareness during head rotations. However, the VOR does not fully compensate for the head rotation and in fact the eyes only rotate by about 10% of the degree that the head was tilted. While not fully compensating for the head tilt, there does not seem to be biases due to the VOR alone. For example, when asked to tilt their head and align a visual line with their head's axis, participants tend to perform very well, suggesting that VOR does not produce any biases because it does not fully compensate for the head tilt (Mittelstaedt, 1983).

In one of the first investigations of body tilt on visual SV, Aubert (1861) found that when an observer's body is physically roll-tilted at large angles (> 30°) visual SV is biased towards the tilt of the body (A-effect). However, when tilted at smaller angles, visual SV is found to error in direction opposite of the body (E-effect). He attributes E-effect errors mainly to internal noise of the vestibular system. He suggests that due to imperfections of the distributions of hair cells in the otolith organs, humans must compensate for the internal imprecision at smaller tilt angles. Further, he suggests that the A-effect may be due to a tendency to bias towards the body's longitudinal axis. Other researchers have suggested that this might not be the case. Specifically, when decoupling the head and body, there tends to be a strong SV bias towards the tilt of the head rather than the body (Clemens, De Vrijer, Selen, Van Gisbergen, & Medendorp, 2011; Fraser et al., 2015). Others have suggested that instead of a natural bias towards the body axis, there is a bias towards the vestibular signal given the body's most natural position, which is usually the upright position (De Vrijer, Medendorp, & Van Gisbergen, 2008; MacNeilage, Banks, Berger, & Bulthoff, 2007; Vingerhoets et al., 2009).

We attempt to understand the effects of the vestibular system on visual SV and the interactions it may have with visual tilt cues in the RFT. Thus, in experiment 1 in this chapter we test the effect of lying supine while performing the RFT task using an egocentric vertical. We then, in experiment 2a and 2b, attempt to isolate the vestibular afferent signals using galvanic vestibular stimulation to investigate vestibular tilt cues without accompanying head tilts on visual SV. Lastly, in experiment 3 we introduce the vestibular SV method in which we use whole body rotation while standing to measure SV.

3.1 Experiment 1: Supine vs Upright

One intuitive way to eliminate the presence of gravitational vestibular cues of vertical is to eliminate the gravitational force that is providing the cue. One of the advantages of using a VR head mounted display is that the wearer can take on a virtual spatial awareness that does not mirror that of reality. Given a virtual visual scene in the ego-centric upright, regardless if the participant is standing upright or lying down, they can take on the viewpoint that the headset provides in the virtual environment, particularly in a first-person point of view (Pfeiffer, Grivaz, Herbelin, Serino, & Blanke, 2016). Visual gravitational cues, regardless of vestibular gravitational cues have been shown to have a strong influence on the adoption of the first person perspective in VR (Pfeiffer et al., 2013, 2016). However, movement in the VR without movement in real life can become a problem and can disrupt this adoption of virtual spatial awareness and cause motion sickness. We can utilize this adoption of virtual spatial awareness to test for SV in cases in which vestibular gravitational cues do not align with the perception of virtual SV. In this study, participants are situated in the supine position to perform the RFT within the head-mounted display. Thus, the RFT continues to be along the plane of the participant's bodily axis as in the standing position, but gravitational cues are now perpendicular to the plane of the RFT. Studies have looked at subjective vertical in the supine position but have focused on allocentric gravitational vertical in the real world (Lejeune et al., 2004; Luyat, Ohlmann, & Barraud, 1997). Thus, while lying down they attempt to estimate a direction perpendicular to their body orientation. The semi-circle canals have the ability to detect both rotational and linear velocity. This allows it to estimate the direction of gravity in any direction. Thus, when the head is tilted or placed in a supine position, the brain can still use gravitational vestibular information while making an allocentric vertical estimate. However, for an egocentric SV estimate, the vestibular gravitational cues are not as helpful in determining body orientation in the supine position. However, some have used a physical apparatus to test perception of body orientation, or egocentric SV, in a supine condition, without a tilted contextual frame (Guerraz, Luyat, Poquin, & Ohlmann, 2000; Templeton, 1973; Wade, 1970). However, there have been mixed findings among researchers as to the effect of the supine position on the egocentric SV. For example, Templeton (1973) reported greater errors in visual SV when participant lay in a supine position compared to the upright position while presented a tilted frame. Thus, the effect of the tilt of the frame increased in the supine condition compared to upright. However, without the visual frame or head tilt, there did not seem to be any differences in visual SV. Wade (1970) had similar findings. He found no differences in visual SV without tilting the head. Further, Guerraz et al. (2000) found no differences in supine compared to upright when the head was not tilted using a haptic SV estimate. It is currently unclear how the supine position affects SV estimates and how a tilted contextual frame in the RFT interacts with the new body position.

In order to test the effect of the frame in the absence of vestibular cues, we used the perception of vertical that coincides with the person's egocentric longitudinal axis. When a participant is lying on their back looking up towards the ceiling, while viewing the RFT scene in the VR headset, the participant can no longer use gravity as a cue as the direction of gravity is no longer in line with the task plane. Thus, in this position there are no gravitational cues aiding on the task plane to help in determining the orientation of the rod. Using an estimate that was on the same egocentric plane as the first estimate in the upright stance, could help to isolate the visual cues in the RFT. We expected to find results similar to that of Templeton (1973) using the VR headset. This would help to determine the role of vision in the bias produced by the tilted frame. Further, a comparison between estimates made in the supine position and those made in the upright condition would allow us to assess the role of vestibular gravitational cues in the perception of body orientation.

3.1.1 Method

Participants made alignment and discrimination visual SV estimates in both supine and upright positions. We compare the bias and sensitivity produced by the tilted frame in both positions. A total of 107 participants completed discrimination tasks for both upright and supine conditions. A subset (n = 48) of them, in addition, completed alignment and orientation discrimination tasks for both upright and supine conditions. This subset of participants completed all upright tasks in a specially designed tilt-table. The tilt table used for this upright condition was modified from an inversion table. It was designed such that the participant stood on a foam-lined platform with their shoulders touching two side panels, also lined with foam. Experimenters could manually rotate in either direction up to 35°. For this current experiment, the tilt table remained in the upright position while participants performed the upright conditions. See figures 3.2 and 3.3 for front and back views of tilt table. The remainder of participants (n = 59) completed only an upright alignment task and both supine and upright orientation discrimination tasks while free standing on a 20 cm high-density foam mattress. There may be important vestibular differences between the platform in which participant stand. Standing on the mattress introduces instability due to the decrease in proprioceptive cues from the feet. This increased postural sway could influence how participants weigh vestibular cues. In contrast, when participants stand on the tilt table, they are secured via the two side panels limiting postural sway. We explore the potential effects of proprioceptive cues present in the tilt table condition in the next chapter, however they are relevant to the differences in SV estimates made in this current experiment.

For both sets of participants, upright alignment and discrimination conditions followed the same procedures as described in the previous chapter in the VR headset using Unity. For the alignment tasks, participants made 6 alignments per frame orientation (0, $\pm 18°$). For the discrimination tasks, they completed 8 trials per 8 rod orientations per frame orientation for a total of 192 trials. The increments used in the discrimination task were the same as the increments away from the alignment SV estimate used in the previous chapters. The supine condition procedures were the same as the upright conditions. Participants lay supine on the mattress with their arms by their sides, and their right hand holding the mouse on the surface of the mattress (see figure 3.1). Participant viewed the RFT along the same plane as their body's orientation and were asked to align the rod or make judgements about the rod's orientation with respect to the virtual vertical or their own body's orientation.

Figure 3.1: Top-down view of participant in supine condition.

Figure 3.2: Front view of participant standing in the tilt table at 0°.

Figure 3.3: Back view of participant standing in tilt table at 0°. Digital angle gauge in center recorded the lateral tilt of the participant.

3.1.2 Results

We first compared the upright conditions when standing on the tilt table in contrast to standing on the mattress. In a 2 (Upright Standing Platform) × 3 (Frame) ANOVA using the discrimination task estimates, we found no differences between the estimates while standing on the tilt table vs standing on the mattress, F (1, 105) = 1.27, p = .262, nor an interaction, F (2, 210) = 0.23, p = .793. We only found the expected effect of frame that demonstrates the classic rod and frame effect, F (2, 210) = 283.98, p < .001, η_p^2 = .730. Using upright alignment estimates in a 2 × 3 ANOVA, we found similar effects of standing platform and frame, see figure 3.4.

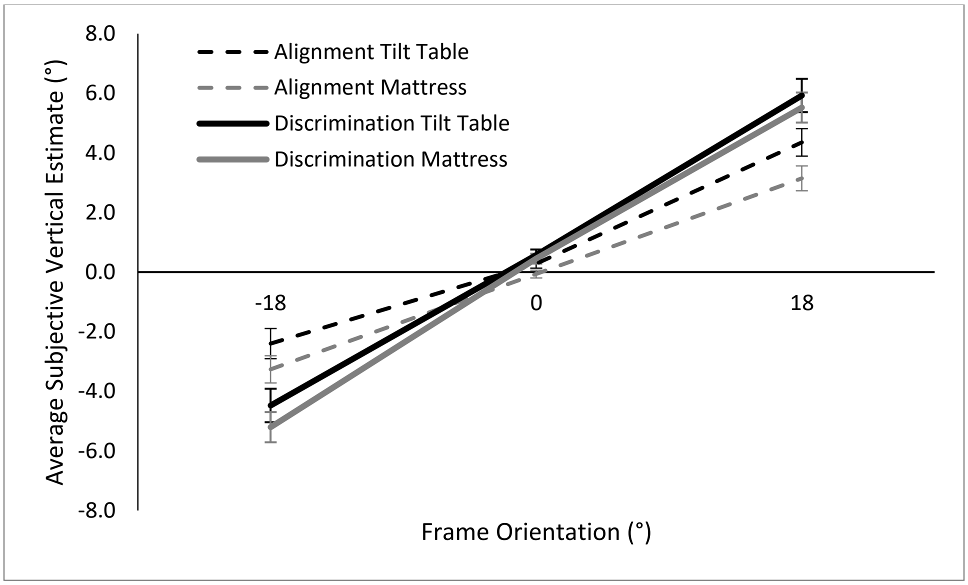


Figure 3.4: Average visual subjective vertical estimates for alignment and discrimination tasks on the tilt table and mattress for each of the three frame tilt conditions.

Using another 2 × 3 ANOVA using discrimination within-subject standard deviations, we found the expected frame effect, F (2, 210) = 111.031, p < .001, η_p^2 = .514 in which tilted frames had greater variability. We also found an interaction suggesting greater variability from the no tilt frame condition while standing on the mattress compared to standing on the tilt table, F (2, 210) = 3.34, p = .037, η_p^2 = .031, see figure 3.5. Using the alignment within-subject standard deviations, we found a similar effect of frame, however there was no interaction and only a marginally significant main effect of standing platform, F (1, 105) = 3.18, p = .078, η_p^2 = .029.

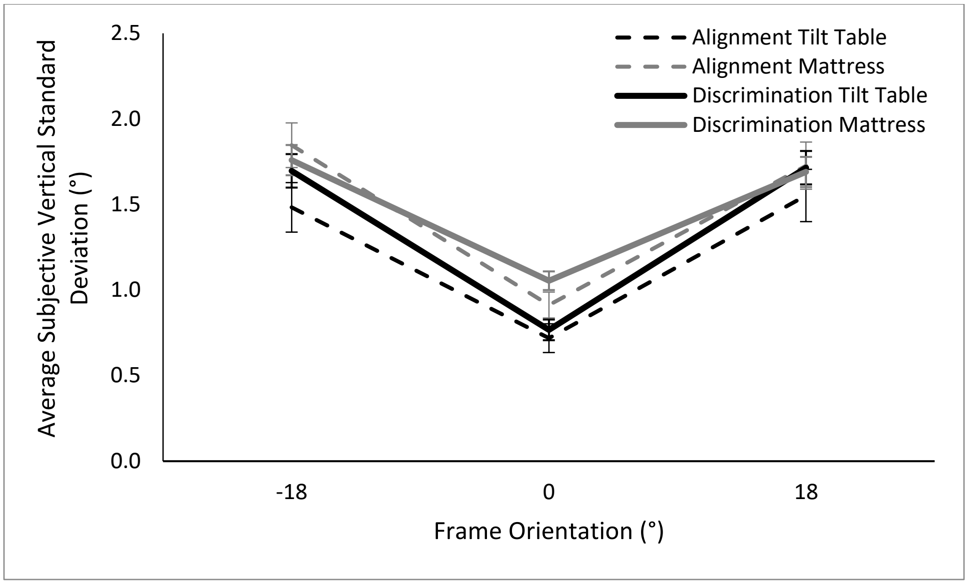


Figure 3.5: Average within-subject standard deviation for alignment and discrimination tasks on the tilt table and mattress for each of the three frame tilt conditions.

Next, we compared visual SV estimates and within-subject standard deviations for supine and upright conditions. Using a 2 (Position) × 3 (Frame) ANOVA on the visual SV estimates using the discrimination method, we found the expected main effect of frame, F (2, 212) = 285.60, p < .001, η_p^2 = .729, as well as an interaction between position and frame, F (2, 212) = 8.54, p < .001, η_p^2 = .075, see figure 3.6. The interaction suggested that participants had greater biases when the frame was tilted in the upright condition compared to the supine condition. Using t-tests, we found this to be the case for both the negative frame tilt, t (106) = 2.29, p = .024, and for the positive frame tilt, t (106) = 2.48, p =.015.

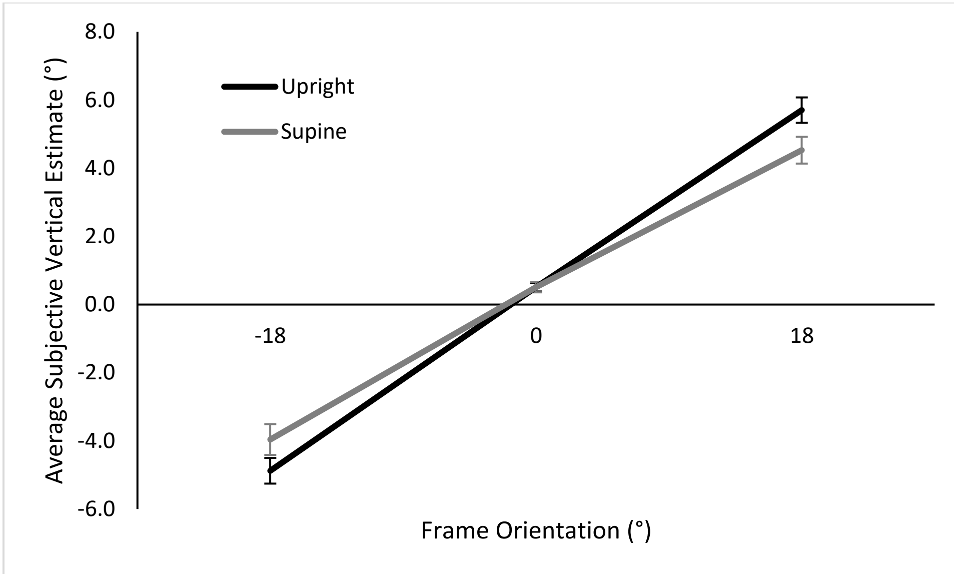


Figure 3.6: Average visual subjective vertical estimates for upright and supine conditions using discrimination method (n = 107). Error bars represent standard errors about the mean.

Using a 2 (Position) × 3 (Frame) ANOVA on the visual SV estimates using the alignment method, we found the expected main effect of frame, F (2, 94) = 69.31, p < .001, η_p^2 = .596, as well as a main effect of position, F (1, 47) = 7.72, p = .008, η_p^2 = .141, see figure 3.7. The interaction was not significant, F (2, 94) = 2.24, p = .113, η_p^2 = .045. The main effect of position suggests that during the upright alignment estimates, participants tended to have an overall bias towards the counterclockwise direction compared to the supine condition, however this meant that their SV estimates were slightly more accurate in the supine condition in the positively tilted condition and the no tilt condition, see figure 3.7. We performed 3 paired samples t-tests to compare each frame tilt condition between supine and upright in the alignment SV estimates. After correcting for multiple comparisons (corrected α = .016), we found that there was only a significant difference between supine and upright in the positive tilt condition, t (47) = 2.73, p = .009. However, it is noteworthy that the no tilt condition came close to significance, t (47) = 2.03, p = .048.

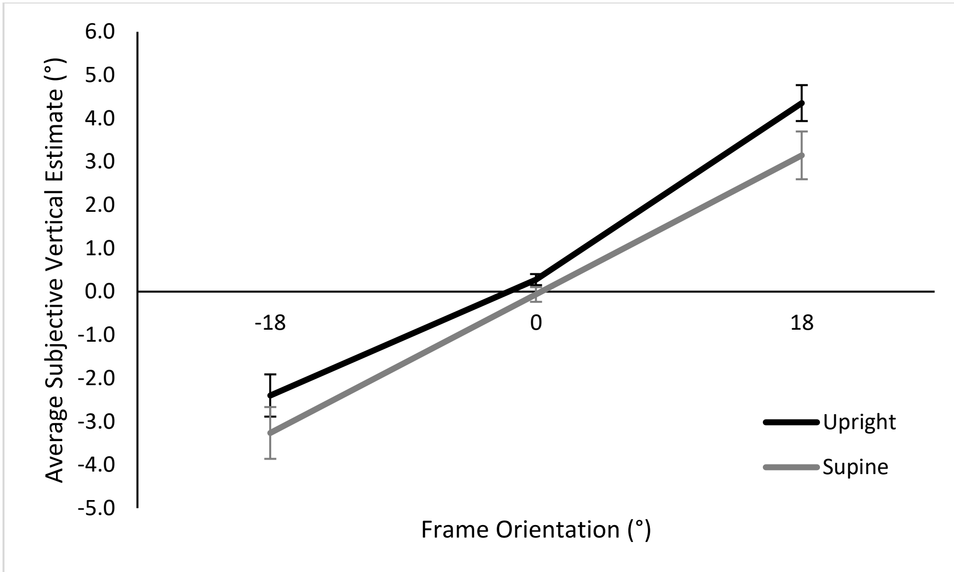


Figure 3.7: Average visual subjective vertical estimates for upright and supine conditions using the alignment method (n = 48). Error bars represent standard errors about the mean.

Using a 2 (Position) × 3 (Frame) ANOVA on the visual SV within-subject standard deviations using the discrimination method, we found the expected main effect of frame, F (2, 232) = 149.60, p < .001, η_p^2 = .585, in which the non-tilted frame condition had lower standard deviations than the tilted frame conditions. We did not find differences between body position, see figure 3.8.

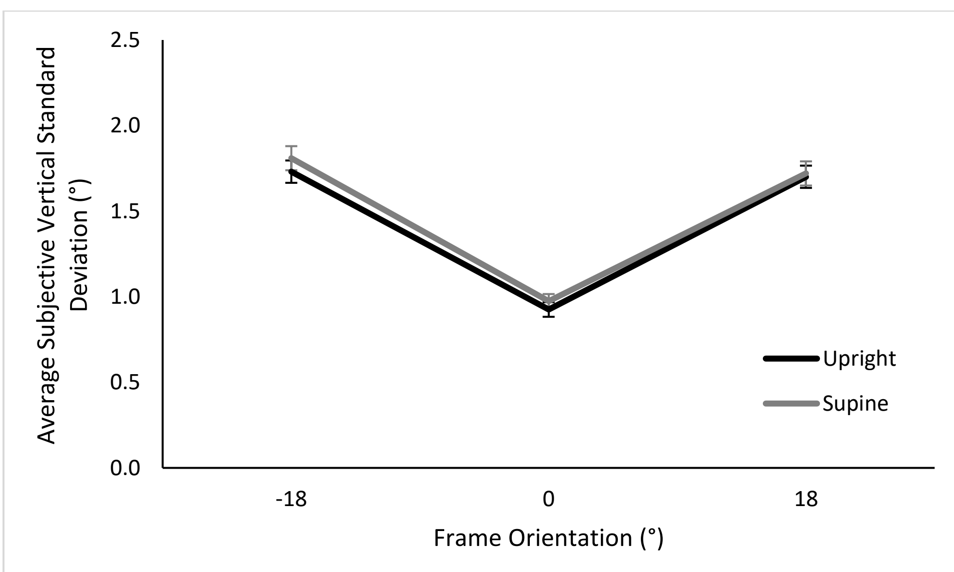


Figure 3.8: Average within-subject standard deviation for upright and supine conditions using the discrimination method (n = 107). Error bars represent standard errors about the mean.

Using a 2 (Position) × 3 (Frame) ANOVA on the visual SV within-subject standard deviations using the alignment method, we found the expected main effect of frame, F (2, 94) = 25.08, p < .001, η_p^2 = .35, in which the non-tilted frame condition had smaller standard deviations than the tilted frame conditions. We also found a significant effect of position, F (1, 47) = 6.35, p =.015, η_p^2 = .119, suggesting that overall the supine condition yielded larger within-subject standard deviations than the upright condition, see figure 3.9.

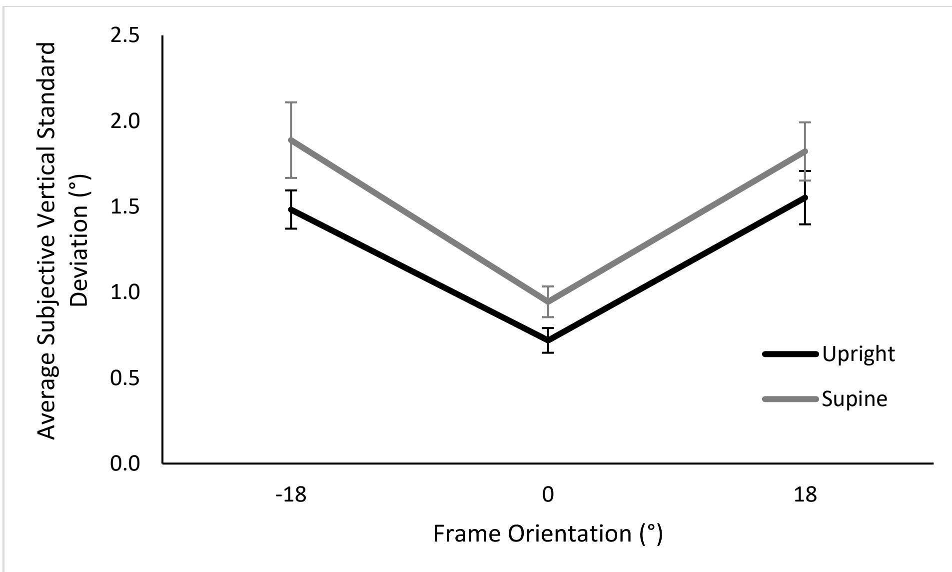


Figure 3.9: Average within subject standard deviation for upright and supine conditions using the alignment method (n = 48). Error bars represent standard errors about the mean.

3.1.3 Discussion

Overall, we found some support that in the supine condition, visual SV estimates are made differently. In contrast to Templeton (1973), we found that estimates made in supine were more accurate than estimates made in the upright position, particularly in the tilted frame conditions. In the alignment condition, this extended to the no tilt condition as well. These results more coincide with findings of better performance in allocentric SV estimates in supine positions. Given the Mittelstaedt (1983) assumption concerning a bias towards the idiotropic vector in visual SV estimates, participants in our sample could have had obtained a stronger bias towards the body axis in the supine condition because of the lack of postural instability. In both of our upright conditions, participants were asked to stand on a foam platform. While in the next chapter, we find that there is no effect of foam on the tilt table in vestibular SV estimates, it is well documented that while free standing, foam can increase postural instability. This increase in postural sway, could affect how visual SV estimates are made. Lying in supine provides the participant with a view of the rod and frame unaffected by postural sway. Future studies should investigate the role of postural sway and stance on visual SV estimates. At the same time, we found some support that overall participant sensitivity is decreased (i.e. variability is increased) in supine conditions, at least for the alignment conditions. These results fall in line with the hypothesis that gravitational cues are reduced in the supine condition. Thus, although estimates are more or less accurate in supine conditions, the absence of an informative cue could increase the variability of the estimates. However, we cannot rule out the possibility that this finding in the alignment condition was due to the type of task itself and the limitations that come along with that task. The fact that we found no differences in discrimination within-subject variability may suggest that gravitational cues may not have had much of an influence on subjective vertical over the visual tilt of the frame. More research in this area is needed and will be pursued in the future.

3.2 Experiment 2a: Effects of Galvanic Vestibular Stimulation on Subjective Vertical

While many studies have focused on all the different angles in which the head and body can be tilted away from vertical in order to test the contribution of the vestibular and proprioceptive systems on visual SV, a recent method has been developed to directly manipulate the afferent pathways of the vestibular system. The vestibular system has been traditionally difficult to isolate and test in human participants. It is well known that the vestibular system is intimately entangled in perceptual and motor functioning. Within the past decade, galvanic vestibular stimulation (GVS) has become an increasingly popular method used to isolate vestibular signals. GVS involves applying a low intensity current between the two mastoid processes behind the ears to affect vestibular afferents. Specifically, participants undergoing GVS experience a transient tilt sensation towards the anodal electrode. The flow of the current works intrinsically on the push-pull coordination of the vestibular system, activating afferents from the otolith organs and the semicircular canals (Kim & Curthoys, 2004). This stimulation results in the interpretation of a head tilt towards the cathodal electrode causing postural reflexes towards the anodal direction consistent with otolith reflexes (Dilda, Morris, Yungher, MacDougall, & Moore, 2014).

Research has shown that GVS intensity corresponds to biases in subjective body orientation and to a lesser extent SV estimates (Mars et al., 2001; Mars, Vercher, & Popov, 2005; Wardman, Taylor, & Fitzpatrick, 2003). These investigations have involved a steady state direct current at intensities up to 3.5 mA. After reaching the steady state, participants make alignment SV estimates in the absence of other visual cues to determine the effect of GVS on visual SV. These studies have only found small effects on SV estimates in these GVS conditions and some have found that the same effect regardless of the GVS intensity used. However, SV estimates in these studies were still larger than the magnitude of the VOR, suggesting that the body's axis bias induced by the GVS is mainly responsible for the bias in SV estimates beyond the effect that may have been produced by the VOR. In our own investigations of steady state GVS during free standing, we found no differences in visual SV estimates with or without GVS stimulation up to 4 mA. Indeed, the bias in subjective body orientation during GVS is much more exaggerated than visual SV biases while seated (Mars et al., 2005). This bias in subjective body orientation could be a catalyst in the small biases in the SV. However, we wondered why these biases in SV remained small.

During our investigations, the period of the greatest postural instability anecdotally seemed to be during the GVS ramp-up and ramp-down periods to the desired intensity. We hypothesized that during this period of fluctuation towards the desired intensity does not allow the participant to adjust to the current steady state and if the small SV biases in during steady state were the result of early adaptation to the stimulation. We additionally wanted to test the interaction effects of the tilted visual frame in the RFT with the effects of GVS on visual SV. Given the strong frame effects that we have previously found, we hypothesized that GVS induced reflexes that were opposite of the frame tilt may lessen the effect of the frame, while GVS induced reflexes in the same direction of the frame tilt would enhance the SV bias towards the vestibular and visual induced tilts.

3.2.1 Method

Forty-six undergraduate volunteers participated in the current study. All participants were recruited from the UCLA Human Participant Pool and all methods were approved by the UCLA Medical Institutional Review Board. Seven participants dropped out sometime during the experiment. Out of these seven dropout participants, six participants reported nausea and/or dizziness during stimulation. One participant fainted during the procedures of the study, unrelated to the effects of the GVS. Thus, the analyses consist of 39 participants. All participants had normal or corrected-to-normal vision. Participants performed a series of 54 (18 per frame) alignment estimates using the RFT in Unity. The tilts of the frame were the same as previous expeirments ($\pm$18° and 0°). During all RFT procedures participants stood on a foam mattress that was 20 cm thick with their feet together and their hands by their sides with their right hand holding the mouse against their upper thigh. Using mouse buttons, participants rotated the central rod to an orientation that they perceived as vertical within a 4 second timeframe. For any given trial, the orientation of the virtual frame appeared to be either tilted (±18°) or upright (0°).

3.2.1.1 Galvanic Vestibular Stimulation. We used an ActivaDose II iontophoresis device to deliver bipolar galvanic vestibular stimulation (GVS). This device has a non-adjustable ramp-up rate of 8 seconds per 1 mA of intensity and can deliver a max of 4mA (in 0.1mA increments). We used two, 5 x 7 cm, saline soaked sponges placed on either side of the head, over the mastoid processes, held securely with a silicon casing and a thick headband or swim cap (Figure 3.10). We used a range of 1-4 mA to test the effects of GVS on subjective vertical.

Figure 3.10: Placement of GVS electrodes. Not pictured is the neck pillow participants wore while making visual SV alignment estimates.

Figure 3.11: Participant standing on the mattress and ready for GVS RFT trials.

***3.2.1.2 GVS trials*.** The ramp-up time for each 0.5 mA increment took approximately 4 seconds. Beginning at 1 mA of stimulation until they reached a max of 4 m, during each 0.5 mA ramp-up period, participants completed 1 SV estimate, resulting in a total of 6 SV estimates per ramp-up block. During each block, participants made 2 estimates per frame orientation. To ensure that each frame had been represented during each of the 6 ramp-up time periods (for a total of 3 SV estimates per ramp-up increment), 9 permutations of these ramp-up blocks were presented, resulting in 54 total trials across all blocks. Thus, all permutations of the 6 trials were represented in the 9 blocks. The 9 permutated blocks were randomized for each participant. This order scheme allowed us to test whether intensity of ramp-up periods resulted in differential estimates, such would be suggested by Weber's law. If the participant completed the SV estimate before the 4 second ramp-up duration completed, the experimenter waited for the ramp-up period to finish before moving on to the next SV estimate and ramp-up period. Before running through SV trials using GVS, the participant was first stimulated to give them a sense of the range of stimulation that they would feel. Breaks were given between sets of trials.

3.2.1.3 Non-GVS trials. Participants completed a total of 18 SV estimates without GVS stimulation (6 trials per frame orientation). GVS equipment was secured to the participant's head as described above, however, no stimulation was given. All trials were randomized. Participants were instructed to make their estimates within the same 4-second time frame as in the GVS trials.

3.2.1.4 Analyses. In addition to raw average SV estimates obtained from the alignment trials, we calculated the effect of GVS by subtracting the mean SV estimate when the participant was not undergoing GVS from when the participant was either undergoing left anodal GVS or right anodal GVS. A zero-difference score that meant there was no difference between no GVS and a GVS condition, a positive-difference score that meant that participants had a clockwise bias in the GVS condition compared to the non-GVS condition and a negative-difference score that meant that the participant had a counterclockwise bias in the GVS condition compared to the non-GVS condition.

3.2.2 Results

Using a 3 (GVS condition) × 3 (Frame Orientation), we found a main effect of GVS condition, F (2, 76) = 8.86, $p < .001$, $\eta_p^2 = .189$. This main effect followed a linear trend, such that the right anodal GVS condition yielded overall more positive visual SV estimates than the non-GVS condition and the left anodal GVS condition overall yielded overall more negative visual SV estimates than the non-GVS condition. In addition to finding a main effect of frame, F (2, 76) = 97.62, $p < .001$, $\eta_p^2 = .720$, we also found an interaction between GVS condition and frame, F (4, 152) = 2.46, p = .048, η_p^2 = .061. This interaction suggests that when the GVS induced vestibular tilt towards the side of the anodal electrode was in the opposite direction as the frame, there were no differences between the non-GVS condition and the GVS condition. However, when the GVS anodal electrode stimulation induced a tilt towards the same direction of the frame, there was an increase in bias towards that side, see figure 3.12.

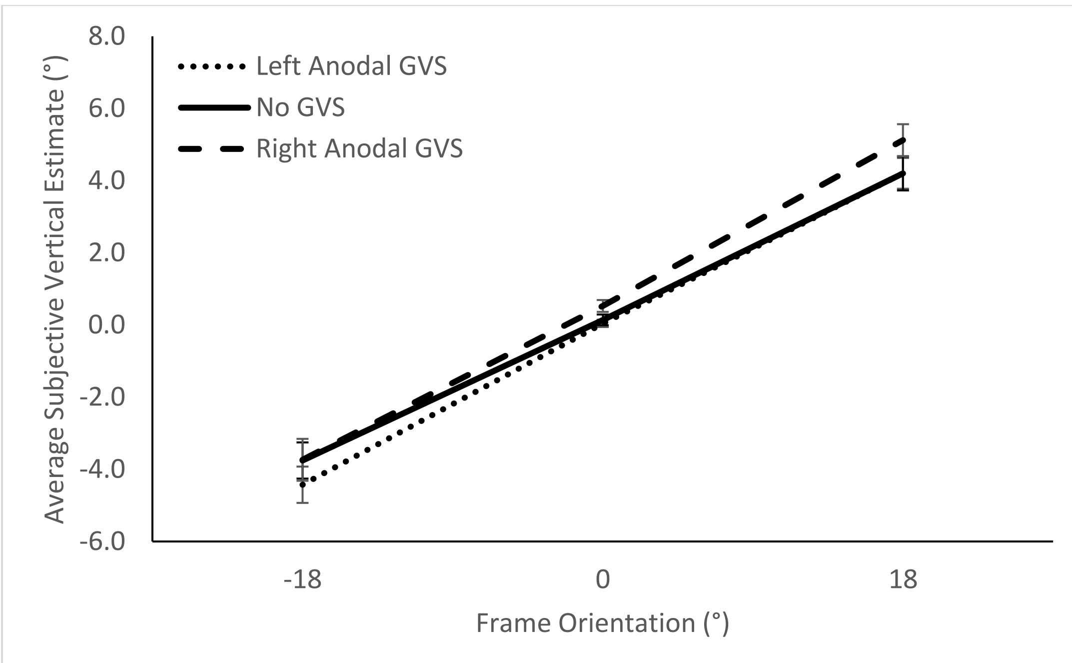


Figure 3.12: Average subjective vertical estimates for all GVS conditions across frame tilts. Error bars represent standard errors about the mean.

Using a 3 (GVS condition) × 3 (Frame) ANOVA on within-subject standard deviations of SV estimates we only found a main effect of frame that suggested larger standard deviations in tilted frame conditions, F (2, 76) = 41.88, p < .001, η_p^2 = .524. There were no differences between GVS conditions, see figure 3.13.

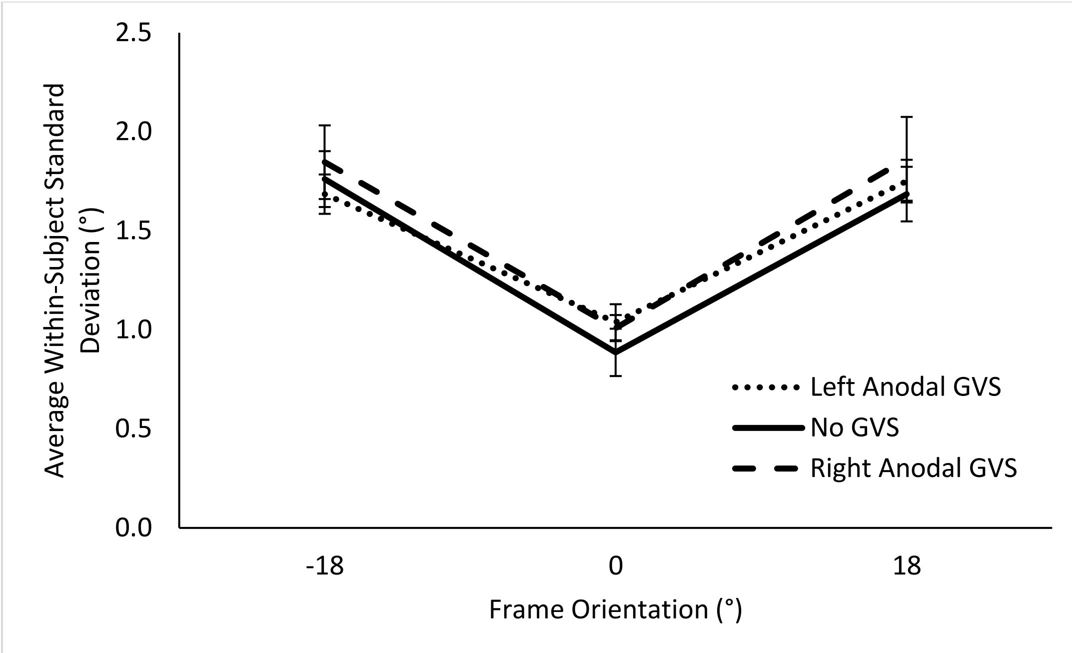


Figure 3.13: Average within-subject standard deviation of subjective vertical estimates for all GVS conditions. Error bars represent standard errors about the mean.

To unpack this effect further we used the differences between GVS and non-GVS conditions to reanalyze the data. Using a 2 (GVS effect) × 3 (Frame Orientation) ANOVA, we found a main effect of GVS, F (1, 41) = 13.35, p = .001, η_p^2 = .26, such that when the GVS anode was stimulating the left vestibule overall bias was negative, while when the GVS anode was stimulating the right vestibule overall bias was positive (Figure 3.14). We also found a main effect of frame orientation, F (2, 76) = 3.43, p = .037, η_p^2 = .08, demonstrating the classic RFT biasing effects, such that participants show a bias in the same direction of the frame tilt. There was no interactional effect.

We found no differences based on the magnitude of the stimulation. That is, SV estimates made between 1mA–1.5mA were similar to estimates made between 3.5mA – 4mA in the same condition.

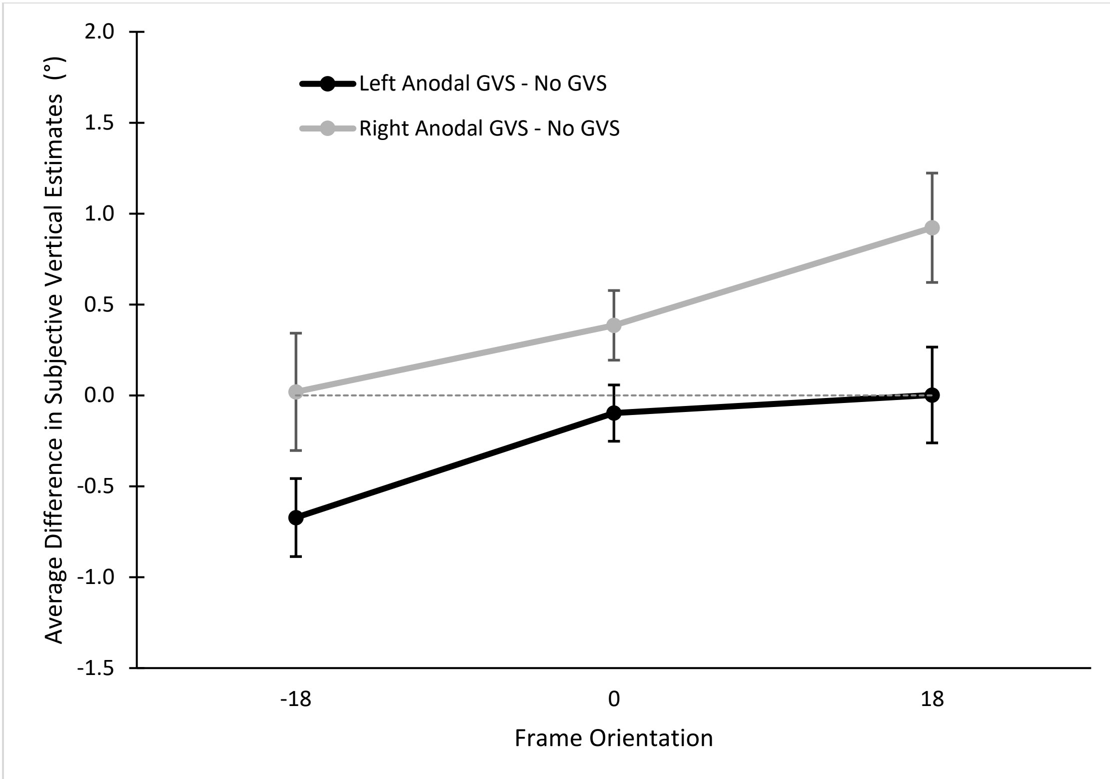


Figure 3.14: Average subjective vertical bias difference between galvanic vestibular stimulation (GVS) conditions and non-GVS conditions for each frame orientation. Error bars represent standard errors about the mean. Dotted line indicates a 0° difference in visual SV estimates between GVS and non-GVS conditions.

3.2.3 Discussion

When the anodal GVS was presented on the same side as the visual tilt of the frame, the two influences combined and biased the individual more towards that side beyond that of just the visual frame as we hypothesized. However, when the frame was tilted in the opposite direction as the anodal GVS, we saw no difference than when there was no GVS present, suggesting that the visual cue of the frame overrode the effect of GVS. Interestingly, we found no differences in within-subject variability suggesting that estimates made with and without GVS were similar in reliability. The magnitude of these SV biases corresponds to the small effects other researchers have found. However, due to the limitations of the direct current device, we could not test other ramp-up speeds. We should expect that the faster the ramp-up speed, the greater feeling of transient tilt and thus greater biases in SV estimates towards the feeling of tilt. Experiment 2b remedies this by using another direct current device with flexible ramp-up speeds.

3.3 Experiment 2b: Varying GVS ramp-up speeds and Subjective Vertical

As a follow-up to experiment 3, we pilot tested a group of participants with varying ramp-up speeds. If it is the case that the ramp-up speed correlates with the amount of vestibular tilt sensation, we should expect that faster ramp up speeds should produce greater subjective vertical biases towards the side of the anodal electrode, while slower ramp-up speeds should produce smaller visual SV biases. In this study, we used another direct current stimulation device, the NeuroConn, that allows for adjustable ramp-up speeds. In one condition, the NeuroConn was programmed to ramp-up at a speed of 4 sec/mA, twice the speed used in Experiment 3a. In the second condition, we used a ramp-up speed of 16 sec/mA, half the speed used in Experiment 3a.

3.3.1 Method

Thirteen right-eye dominant participants volunteered for this study. All procedures were approved by the UCLA Medical IRB before any data were collected. Since we found no effects based on the level of intensity in the previous experiment, we used a maximum intensity of 3 mA in both GVS conditions in order to keep participant dropout low. For the 4 sec/mA ramp-up speed to 3mA, participants had 12 seconds to complete 3 visual SV alignment trials (one per frame tilt). They were kept at a steady intensity for 45 seconds before the ramp-down period. Participants completed this procedure for 6 blocks. For the 16 sec/mA ramp-up speed to 3 mA, participants had 48 seconds to complete 9 visual SV alignment trials (3 per frame tilt). They were kept again at steady state for 45 seconds before the ramp-down period. Participants completed this procedure for 2 blocks. Participants were given breaks of no stimulation between blocks. The anode electrode was always placed over the participants' left mastoid process. Thus, we expected to see SV biases towards the counterclockwise direction during the ramp-up period. All participants made 18 visual SV estimates for all 3 conditions (non-GVS, 4 sec/mA, and 16 sec/mA). The non-GVS condition was always performed first while the order of the GVS conditions alternated between participants.

3.3.2 Results

Using a 3 (GVS ramp-up speed) × 3 (Frame) ANOVA on SV estimates, we found a main effect of GVS, F (2, 24) = 3.91, p = .034, η_p^2 = .246, as well as the expected main effect of frame, F (2, 24) = 35.71, p < .001, η_p^2 = .749, see figure 3.15. To unpack the main effect of GVS further, we analyzed the two ramp-up speeds separately and compared them to the non-GVS condition. Using a 2 (GVS) × 3 (Frame) ANOVA comparing the 4 sec/mA condition to non-GVS condition we found the same main effect of GVS, F (1, 12) = 12.65, p = .004, η_p^2 = .513, and no interaction. However, comparing the 16 sec/mA condition to the non-GVS condition, we did not find the same main effect of GVS, F (1, 12) = 1.25, p = .285.

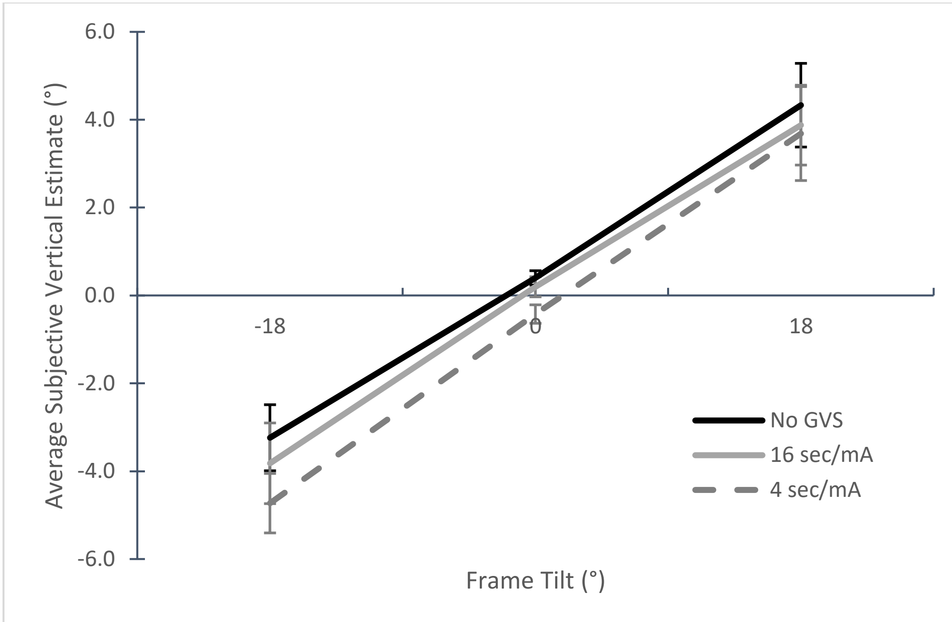


Figure 3.15: Average visual subjective vertical during no galvanic vestibular stimulation and ramp-up rates of 16 sec/mA and 4 sec/mA. Error bars represent standard errors about the mean.

Using a 3 (GVS ramp-up speed) × 3 (Frame) ANOVA on SV within-subject standard deviations, we found a marginally significant main effect of GVS, F (2, 24) = 3.37, p = .051, η_p^2 = .219, suggesting that as the GVS ramp-speed increased the within-subject variability of SV estimates also increased. We also found the expected main effect of frame, F (2, 24) = 29.63, p < .001, η_p^2 = .712, see figure 3.16. To unpack the main effect of GVS, we analyzed the two ramp-up speeds separately and compared them to the non-GVS condition. Using a 2 (GVS) × 3 (Frame) ANOVA comparing the 4 sec/mA condition to non-GVS condition we found the same main effect of GVS, F (1, 12) = 5.95, p = .031, η_p^2 = .331, and no interaction. However, comparing the 16 sec/mA condition to the non-GVS condition, we did not find the same main effect of GVS, F (1, 12) = 2.81, p = .120.

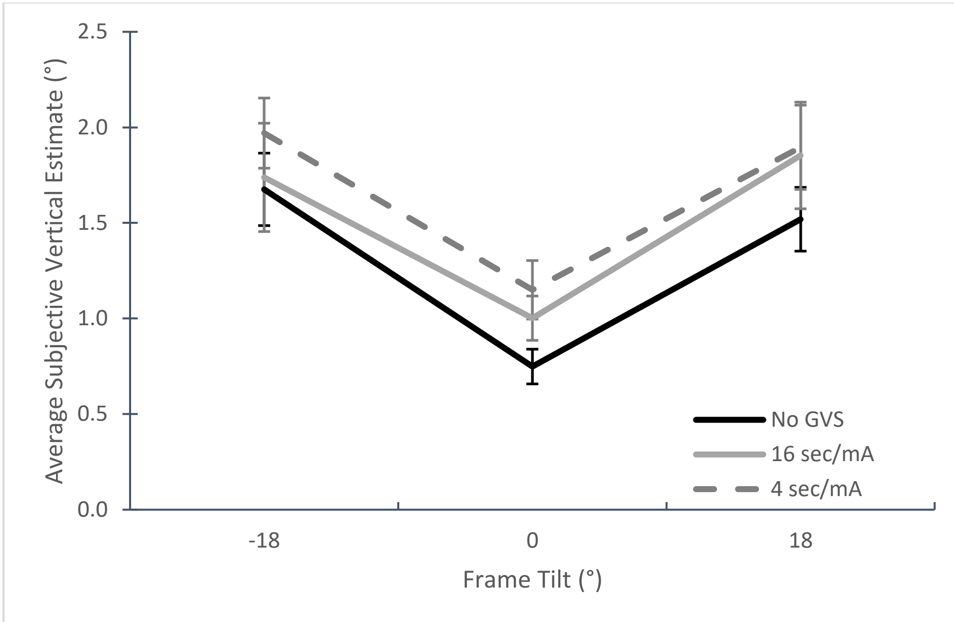


Figure 3.16: Average within-subject standard deviations of subjective vertical estimates during no galvanic vestibular stimulation and ramp-up rates of 16 sec/mA and 4 sec/mA. Error bars represent standard errors about the mean.

As in the previous experiment, we also calculated difference scores in which the SV estimates made in the non-GVS condition were subtracted from estimates made in the GVS conditions to obtain the effect of the GVS in the given condition. Using a 2 (GVS) × 3 (Frame) ANOVA we found no significant effects. This is most likely due to the large between subject variability as we only obtained 13 subjects in this experiment. In the figure 3.17, we can see that the trends towards the predicted hypotheses are present, such that estimates made during the 16 sec/mA ramp-up period were less biased by the GVS tilt cues. In contrast, the 4 sec/mA ramp-up rate biased estimates toward the anodal side of the body. More data is needed to determine if this trend is a true effect. We also compared these results to those found in the previous GVS experiment in figure 3.18. Although half the speed as the previous experiment, the 16 sec/mA condition yielded similar results to the 8 sec/mA condition. This may suggest that there is a speed threshold in which GVS begins to affect visual SV estimates. Again, more data is needed to determine the true underlying effect of ramp-up speed.

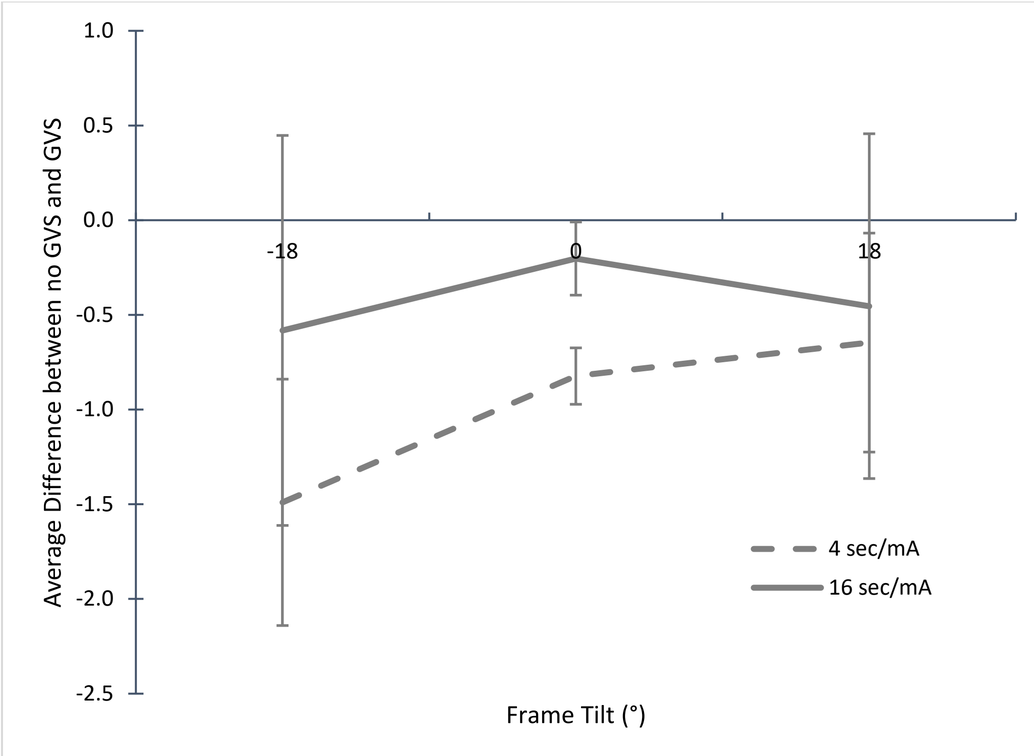


Figure 3.17: Average differences in subjective vertical estimates from the non-GVS condition for both 4 sec/mA and 16 sec/mA ramp-up speeds. Error bars represent standard errors about the mean.

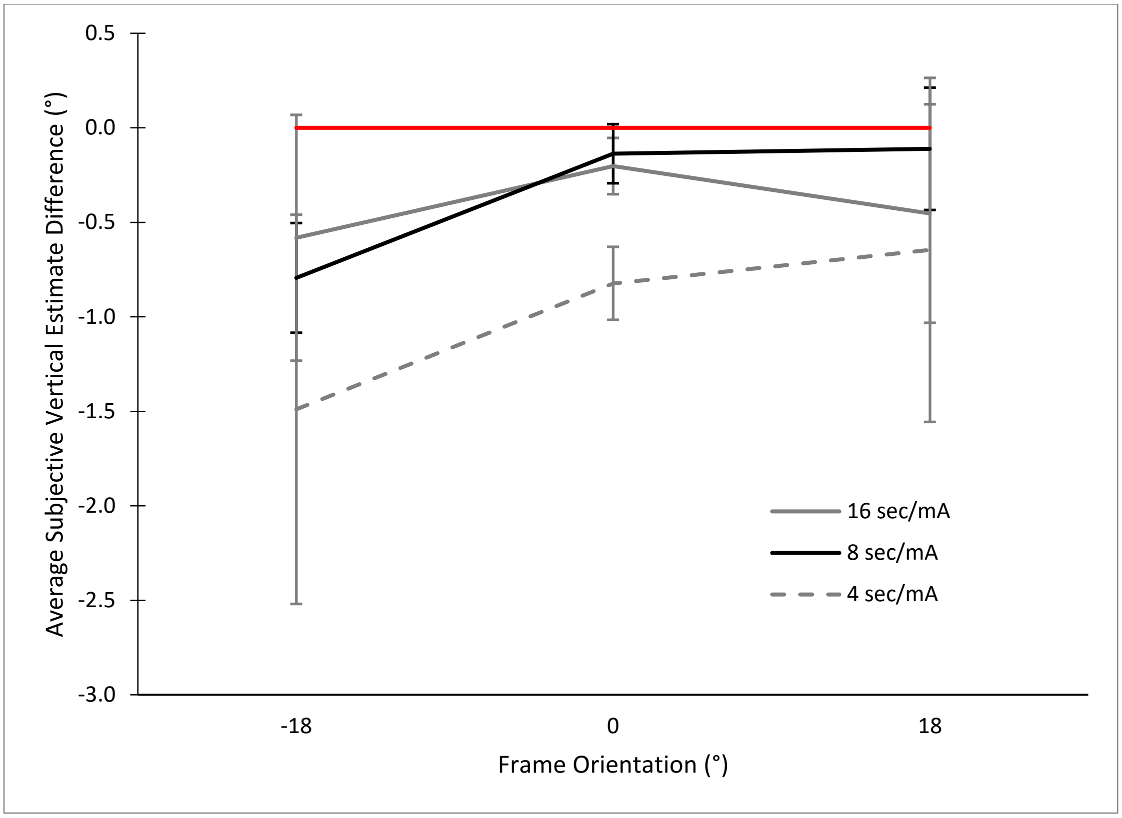


Figure 3.18: Comparison of Experiments 2a and 2b. Average differences in subjective vertical estimates from non-GVS conditions for all ramp up speeds in experiments 2a and 2b. Red line is serves as a reference of no difference between the non-GVS condition and the GVS conditions. Error bars represent standard errors about the mean.

3.3.3 Discussion

These preliminary results suggest that GVS ramp-up speed may have an effect on SV estimates, such that faster ramp-up speeds yield larger biases in the RFT. Interestingly we found that at slower ramp-up speeds, the bias was only prevalent when presented along with tilted frames in the same direction as the vestibular tilt sensation (towards the anodal electrode). This coincides with our findings in experiment 2a. However, at the fastest ramp-up speed, 4 sec/mA, SV biases towards the vestibular tilt sensation affected all visual SV estimates regardless of visual frame tilt. The role of the vestibular tilt bias remains unclear in the tilted frame conditions. It seems that if the tilt sensation is not strong enough or does not coincide with the visual tilt of the frame, it has little to no effect. This may suggest that neck proprioceptive cues may a larger part in the visual SV biases that occur during a head tilt compared to otolith signals. These results also may suggest that the visual tilt biases may have an overall stronger influence on visual SV. This may be different when using a probe other than vision to test for SV biases. This experiment serves as a pilot experiment into the effects of varying ramp-up speed of GVS on SV estimates. The function of ramp-up speed and visual SV estimates remains a future research goal.

3.4 Experiment 3: Vestibular Subjective Vertical Estimates

Experiment 1 investigated the influence of the presence of gravitational vestibular cues on the visual estimates of subjective vertical. We found that when participants made egocentric vertical estimates while participant lay in supine, the sensitivity of their visual SV estimates decreased suggesting that these estimates were made in the absence of all available cues that were present in the upright condition. Additionally, participants had smaller biases towards a tilted frame when in the supine condition, suggesting that the role of postural sway on SV may be reduced. However, in order to understand how the body uses vestibular tilt cues, it is imperative that we test how sensitive the body is to gravitational tilt cues. While many people have studied subjective body tilt using a visual probe (Mast & Jarchow, 1996; Van Beuzekom, Medendorp, & Van Gisbergen, 2001), few have looked into this using a vestibular-type of probe. In one such investigation, Clemens et al. (2011) asked participants sitting in a rotatable chair to decide whether they were clockwise or counterclockwise to some reference angle (including vertical) in a discrimination task. They found that participants were more accurate at this subjective body orientation task than they were at visual SV estimates, but with greater variability. In the next experiment, we use an alignment and discrimination task to determine how well participants can detect the direction of gravity based on their current body orientation while standing using a tilt table, without visual cues. We expected to find that participants would be able to estimates SV fairly accurately as per past research and pilot experiments. This was the first step to using a different form of SV estimate so that we may investigate the integration of visual and vestibular cues on SV estimates.

3.4.1 Method

Seventy-two participants volunteered to be a part of this study. Participants stood on the tilt table platform in the same stance as they stood on it for Experiment 1 above (see figures 3.2 and 3.3). They wore the VR headset; however, the headset was not turned on and only showed a black screen. Lights were turned off during all experimental trials. During the alignment phase, participants were slowly rotated (~ 0.2° per second) laterally to an extreme rotation of $\pm$5°. Experimenters asked the participant to confirm the direction in which they were tilted. If the participant was could not distinguish between the rotation of their body orientation, the experimenter continued to rotate the participant until they were certain of the orientation of their body. The experimenter then slowly rotated the participant back in the opposite direction, towards vertical at the same speed. The participant was instructed to verbally indicate when they believed their body was in the vertical position. Participants were allowed to make as many adjustments as they wished. They performed this alignment task in 4 trials, 2 trials per initial rotation direction ($\pm$). Two experimenters were always assigned to run a single participant through this experiment. Particularly, one experimenter maintained the steady rotation of the participant, while the other participant recorded the degree of rotation from a digital angle gauge. The digital angle gauge was set up to align with the participants longitudinal body axis and reported rotational degrees in 0.1° increments. The experimenter who manipulated the rotation of the experiment could never see the digital angle gauge due to their position on the side of the tilt table apparatus. The two experimenters communicated which the direction of rotation for the set up for each trial through hand signals as to not inform the participant of the next trial.

After completing the alignment task, average estimates of vestibular SV were used as a guide to determine which angles to present for the discrimination task, much like in the visual SV conditions. From our pilot testing, we found that vestibular SV estimates to have greater sensitivity than visual SV estimates (unlike other studies), therefore we used smaller increments around participants' SV estimates from alignment compared to those used in the visual SV discrimination task. We used $\pm$ 0.3°, 0.5° and 0.8° increments and each increment was presented in 4 trials, resulting in 24 trials. All trials were randomly ordered. At the start of each trial, the experimenter rotated the participant to an extreme orientation and then rotated back towards the select trial orientation angle. The direction of this extreme orientation was preselected such that 2 trials for each increment used a negative extreme value and the other 2 trials for each increment used an initial positive extreme value. This extreme value was always $\pm$2° from the trial orientation. For example, if a given trial to be discriminated by the participant was -0.6°, then the participant would first be taken to either 1.4° or -2.6° at the start of the trial. They would then be slowly rotated to -0.6° and asked to determine if their body was then tilted clockwise or counterclockwise from vertical. The use of the extreme angles at the beginning of each trial was to prevent the participant from using their response from their last trial as a cue to determine the current orientation. The use of these initial rotations also kept the participant from using the movement towards an orientation as a cue. Experimenters emphasized this point to the participants, specifically that the direction of the dynamic rotational movement from the initial orientation is independent from the end body orientation to be discriminated. Using this discrimination data, we fitted a psychometric function using a cumulative gaussian function to determine bias and sensitivity for each participant.

3.4.2 Results and Discussion

Three participants' data did not fit a psychometric function due to their response bias. These three data points were not included in the discrimination dataset. Averages and standard deviations for the alignment and the discrimination task can be seen in figures 3.19 and 3.20. All participants' vestibular SV estimates in both the alignment and the discrimination task fell within $\pm 2°$ of true vertical. Individual fitted psychometric functions can be seen in figure 3.21. Comparing these results to results in the no-tilt condition in the visual RFT, SV biases are comparable while sensitivities in the vestibular SV are much smaller than visual SV, suggesting that vestibular cues absent of visual cues may be more reliable compared to the virtual visual cues in upright or supine conditions.

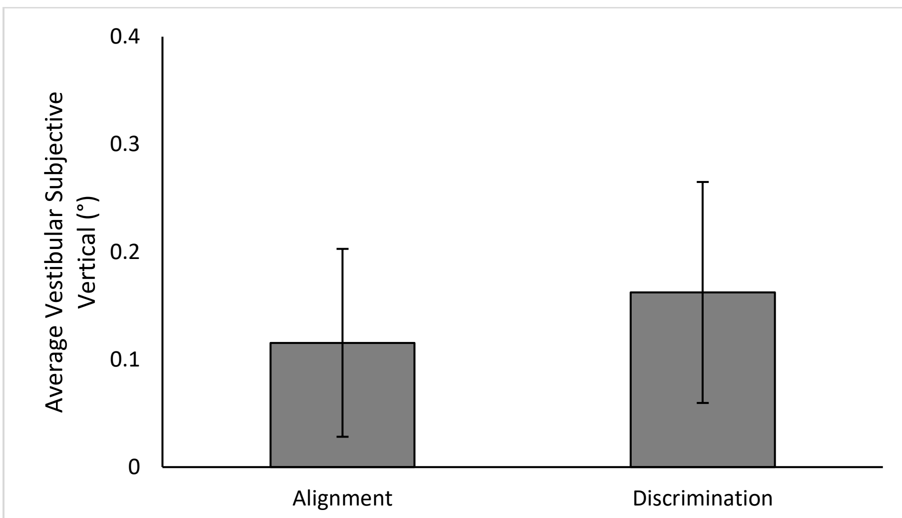


Figure 3.19: Average vestibular subjective vertical estimates in the alignment and discrimination task. Error bars represent standard errors about the mean.

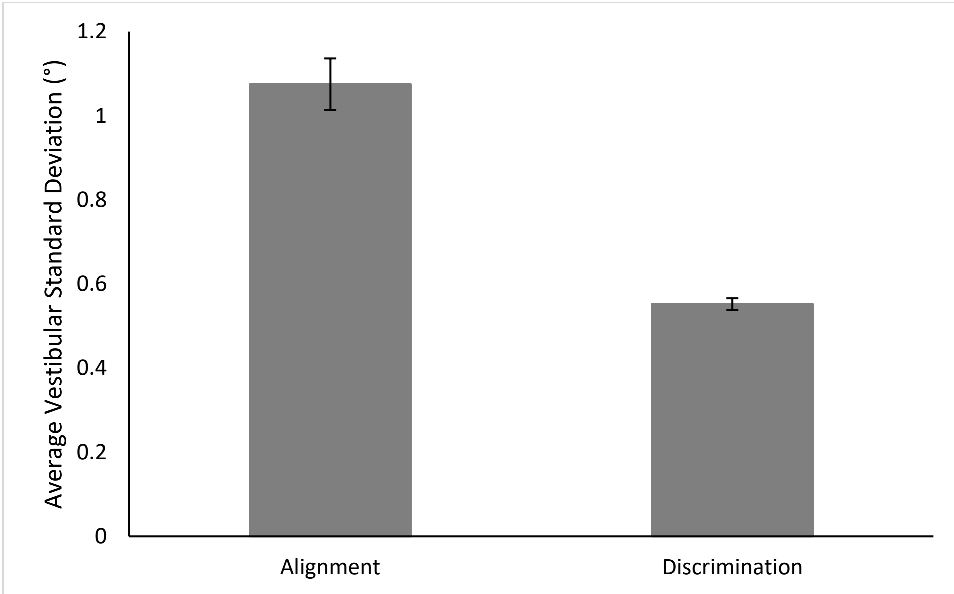


Figure 3.20: Average within-subject standard deviations in the vestibular subjective vertical alignment and discrimination tasks. Error bars represent standard errors about the mean.

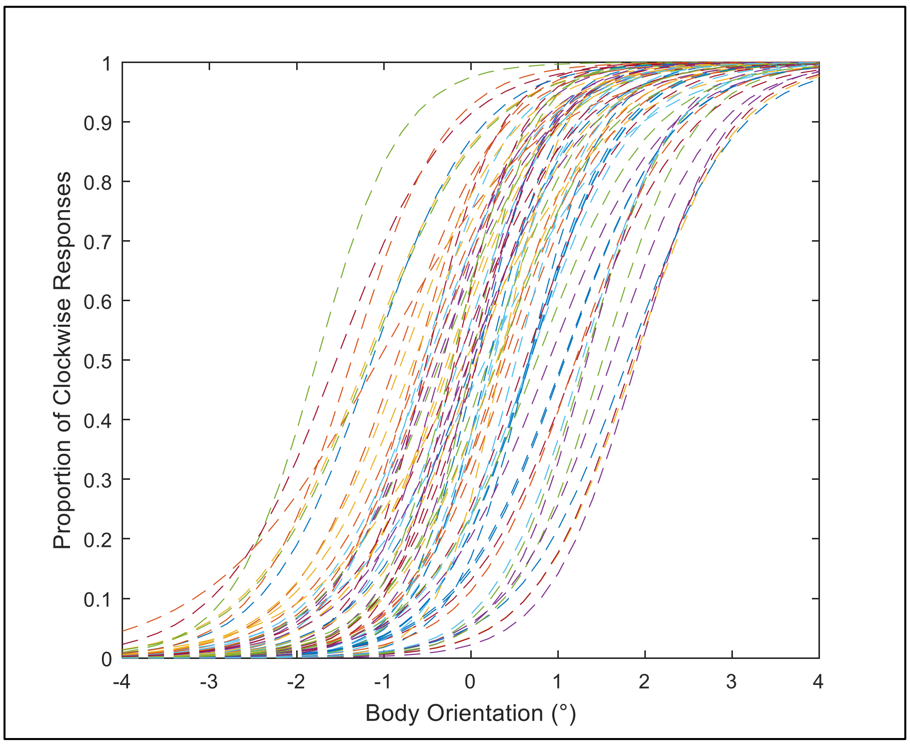


Figure 3.21: Fitted individual psychometric functions for all participants in the vestibular subjective vertical discrimination task.

3.5 General Discussion

In this chapter, we investigated some of the effects of vestibular cues on visual SV. Specifically, in the absence of vestibular cues in a supine position, SV biases towards the tilt of the frame in the RFT were reduced suggesting that the postural instability that may come with the upright condition could lead to a greater reliance on visual cues in the upright conditions. While in the supine, although there is a lack of gravitational cues that can aid in the estimation of body orientation, participants may utilize the idiotropic vector influencing the SV estimates more towards the body orientation. Further, there was some evidence that supine estimates may be more variable within subjects, however we only found this result using alignment estimates which could be a result of the estimation method rather than a true difference in sensitivities.

In experiments 2a and 2b, we investigated the effects of GVS ramp-up speeds on visual SV estimates. In the absence of actual head tilts, we used GVS to directly manipulate the vestibular feeling of tilt and how those manipulations interacted with visual frame biases produced by the RFT. We consistently found that when the vestibular and visual tilt biases aligned, there was an additive effect towards the tilt biases. When there was no visual frame tilt there were small biases towards the vestibular tilt bias. Lastly, when the visual tilt bias of the frame was incongruent with the vestibular GVS bias we saw no effect of GVS on SV biases towards the frame. If participants were using an idiotropic vector that was influenced by the vestibular GVS bias, then we would have expected that the visual SV bias in the direction of the frame would be reduced when the GVS bias was elicited in the opposite direction. Only in the faster conditions did we see a slight decrease in visual SV bias towards the frame in this condition. However, this study will need to be expanded upon to include more subjects.

Lastly, we introduced our methodology of studying vestibular SV. Up until this point we have focused on visual probes of SV. However, in order to test for optimal performance using a Bayesian model, we would need to be able to collect SV estimates in each modality separately. Past research has mainly used seated conditions in order to test for body orientation. Our tilt table allows us to study body orientation in a more or less ecological way through passive standing, while still keeping the participant secure. These estimates were found to be more accurate than visual SV estimates with average estimates between $0.1° - 0.2°$ error from vertical. Further, these estimates also had smaller within-subject standard deviations, suggesting that they are more reliable than visual SV estimates. In the next chapter, we deal with potentially confounding factors of proprioception while making these estimates.

4 CHAPTER 4: Controlling for proprioceptive cues

So far, we have focused mainly on the influences of visual and vestibular cues on SV estimates. However, as mentioned in the introduction, there is a third set of cues, proprioceptive and haptic cues, that are many times lumped in with vestibular cues. Proprioceptive cues come from joint and muscle activations and tell the brain how the body and its limbs are positioned at any given time. Other haptic cues can come from pressure and touch receptors on the skin to relay information about a given surface. These cues alone can give an indirect sense of the direction of gravity based upon environmental features.

Studies that have investigated haptic cues in the perception of gravity have mainly been focused on the perception of slant. That is, how well a person can detect the slope of a surface through touching it with their hand or feet. People are surprisingly good at these kinds of estimates using only a small portion of their body to feel the slant. These studies consequently indirectly test how well participants can determine the slant compared to a horizontally orientated surface, or a vertically orientated surface. Here in order to eliminate the potential use of the ground floor as a haptic cue of SV, in our studies we have asked participants to stand on a piece of high density 20 cm thick foam while making visual and vestibular estimates.

Another set of proprioceptive cues that can help to determine the direction of vertical come from the orientation of the head through the activation of neck stretch receptors and muscles. Information about where the head is in space relative to the body orientation can be informative if the body and head assume an upright prior. Many studies have investigated the role of changes in head orientation in comparison to body orientation on the perception of vertical (Clemens et al., 2011; Fraser et al., 2015; Fraser, Makooie, & Harris, 2014; Mars et al., 2005; Mittelstaedt, 1997; Wade, 1968). While when the whole body is roll-tilted in a particular direction, visual SV estimates are biased towards the tilt of the body (Aubert, 1861). However, when the head alone is tilted while the body remains upright, this effect increases (Fraser et al., 2015; Wade, 1968; Wetzig & von Baumgarten, 1992). This difference in effect suggest that the role of proprioceptive neck cues may be important to the estimates of visual SV. However, they may not be as important in other types of SV estimates, specifically, in vestibular and haptic SV estimates (Clemens et al., 2011; Fraser et al., 2015). Clemens et al. (2011) suggests that neck proprioceptive cues may act as indirect cues to both head centric estimates like visual SV and body-centric estimates like vestibular SV. The visual SV differences seen between whole body tilt and isolated head tilt suggest that the additional proprioceptive cues in the head tilt condition result in the larger biases.

In the following studies, we have examined how our own manipulations that have attempted to minimize the effects of proprioceptive cues affected both visual and vestibular subjective vertical estimates. In experiment 1, we investigate the use of a foam neck pillow on visual SV by comparing foam and no foam conditions while performing the RFT in an upright position. In experiment 2, we investigate the use of global vibration to the feet and neck in order to further reduce proprioceptive influence by increasing noise. In experiment 3, we selectively vibrate each side of the neck independently to test the effects on visual SV in the RFT. We then move to test the role of proprioceptive cues on vestibular SV estimates by comparing conditions in which participant stood on foam compared to when participants stood on a solid platform.

4.1 Experiment 1: Using a Neck Pillow During Visual Subjective Vertical Estimates

In all of the experiments thus far, we have asked participants to wear a memory foam neck pillow while performing visual and vestibular SV tasks. This decision was motivated by desire to reduce proprioceptive cues in the neck that would aid in estimating subjective vertical.

Specifically, a neck pillow would limit the movement of the participants head and provide a uniform amount of pressure around the neck. This experiment tests whether the neck pillow affected visual SV estimates by comparing SV estimates of people that were tested in upright conditions with the neck pillow to a sample of participants that were tested without the neck pillow. If neck proprioception cues are important in the estimation of visual SV, we should expect that those who performed the task without the neck pillow to have smaller errors in the frame condition than those with the neck pillow.

4.1.1 Method

Seventeen participants performed the alignment and discrimination RFT tasks in Unity without the neck pillow. We could not capture the psychometric function of one participant in the neck pillow condition using the discrimination task, thus she was left out of this analysis, but still included in the alignment analyses. We compared these participants to 20 participants who ran the same procedures with the neck pillow. Both sets of participants ran other conditions unrelated to testing for the effects of the neck pillow in the upright condition. The neck pillow used was made of memory foam and featured a thick Velcro strap in the front to strap around the front of the participants' neck. Participants were asked to first place a sanitary garment loosely around their neck, then place the neck pillow over the sanitary garment, and then use the Velcro strap to tighten it to a comfortable tension around their neck. Participants stood on the tilt table while it was in the upright position. Participants in both the neck pillow and no neck pillow conditions ran through both alignment and discrimination tasks.

4.1.2 Results

We first conducted a 2 (Neck pillow) × 2 (SV Method) × 3 (Frame) ANOVA in which we found no significant effects of the neck pillow. We found the main effect of frame, F (2, 68)

= 104.29, $p < .001$, $\eta_p^2 = .754$ and an interaction between method and frame, F (2, 68) = 43.36, $p < .001$, $\eta_p^2 = .560$, suggesting the previously found effect that alignment estimates were less bias in tilted frame conditions. All other results were not significant. Within each of the methods individually, we performed a 2 (Neck pillow) × 3 (Frame) ANOVA. In addition to the expected frame effect, we found a significant interaction effect within alignment conditions, F (2, 70) = 3.99, $p = .023$, $\eta_p^2 = .102$, suggesting that the no neck pillow yielded less biased SV estimates in the tilted frame conditions, see figure 4.1. Using the discrimination conditions, we did not find an effect of neck pillow and only the expected effect of frame, see figure 4.2.

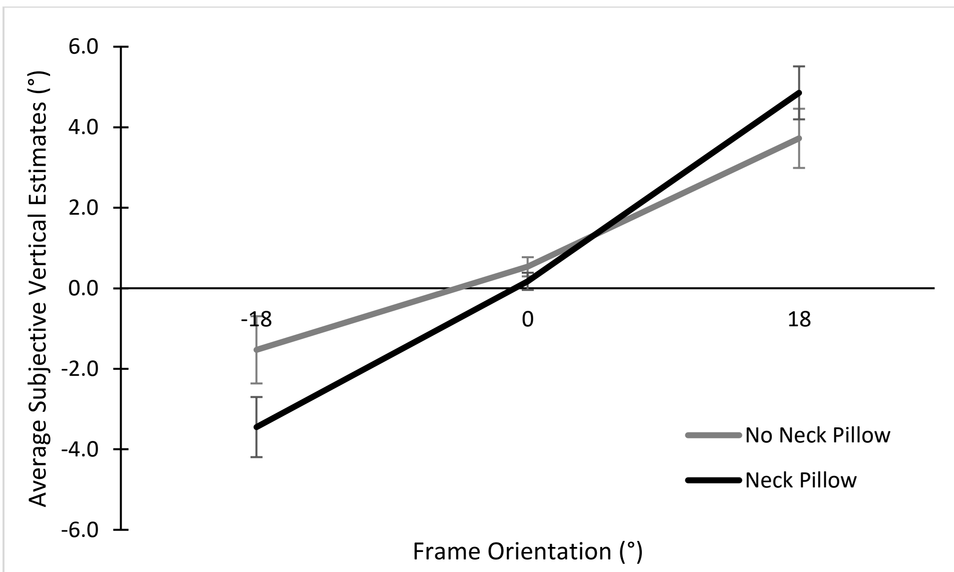


Figure 4.1: Average subjective vertical estimates made in the alignment task for groups wearing a neck pillow compared to wearing no neck pillow while standing upright. Error bars represent standard errors about the mean.

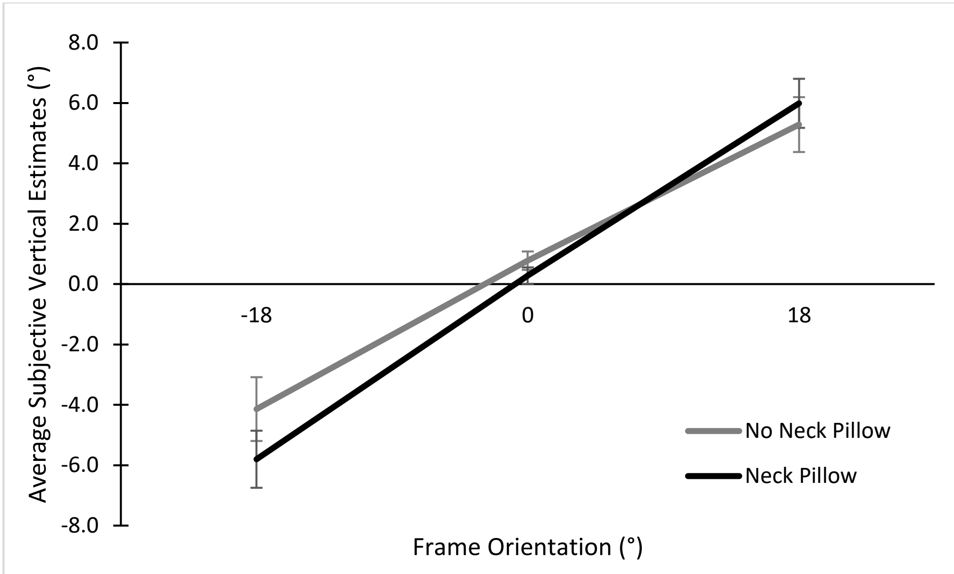


Figure 4.2: Average subjective vertical estimates made in the discrimination task for groups wearing a neck pillow compared to wearing no neck pillow while standing upright. Error bars represent standard errors about the mean.

Using the same 2 (Neck pillow) × 2 (SV Method) × 3 (Frame) ANOVA using within-subject standard deviations, we found the effect of frame, F (2, 68) = 42.99, p < .001, η_p^2 = .558, as well as marginal interactions between frame and neck pillow, F (2, 68) = 2.45, p = .094, η_p^2 = .067. We investigated this further with the separate analyses within each method. In both the alignment and discrimination tasks, we only found the expected frame effect. We found no effects of neck pillow, see figures 4.3 and 4.4.

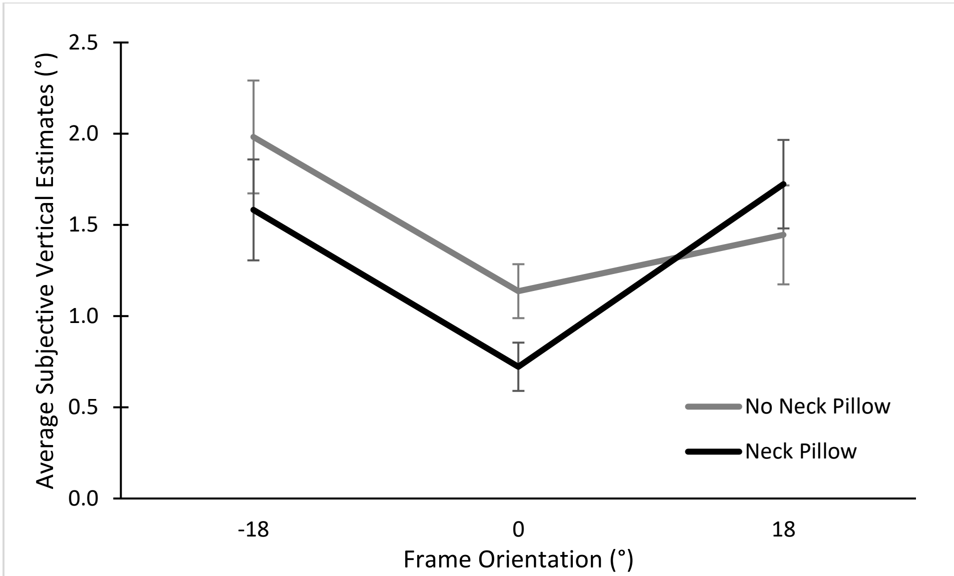


Figure 4.3: Average within-subject standard deviations for subjective vertical estimates made in the alignment task for groups wearing a neck pillow compared to wearing no neck pillow while standing upright. Error bars represent standard errors about the mean.

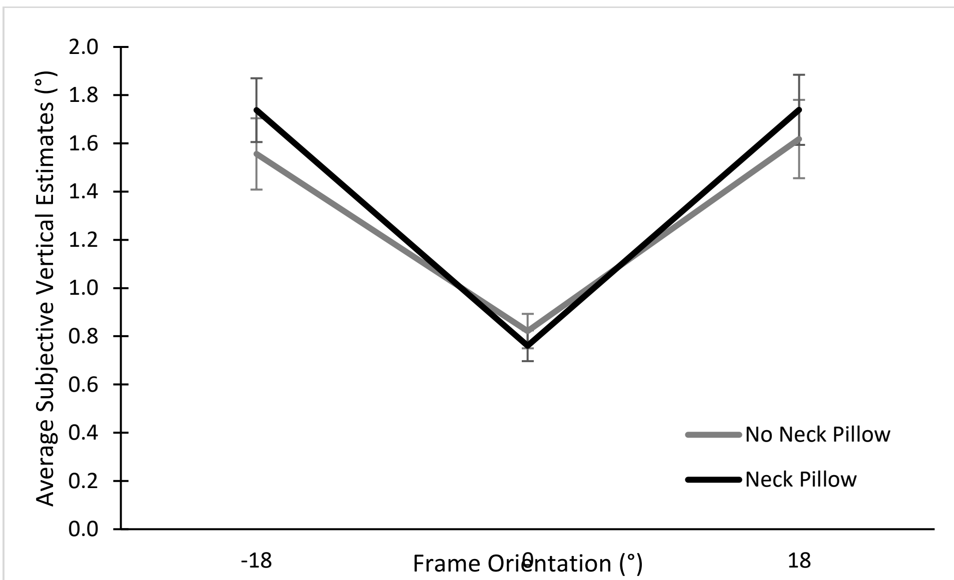


Figure 4.4: Average within-subject standard deviations for subjective vertical estimates made in the discrimination task for groups wearing a neck pillow compared to wearing no neck pillow while standing upright. Error bars represent standard errors about the mean.

4.1.3 Discussion

We found support for the hypothesis that the neck pillow limited proprioceptive neck information. The finding that SV estimates were more accurate without the neck pillow compared to with the neck pillow suggests that increased neck proprioception in the no neck pillow condition may aid in determining the head-centric visual SV estimate. This is in line with Clemens et al (2011) model in which neck proprioception provides and indirect contribution to both head and body orientation estimates. Thus, from these findings we assume that in our other investigations of visual SV, we at least partially suppressed neck proprioceptive cues. Next we ran a series of experiments that tested the effects of vibration on the body and neck.

4.2 Experiment 2a: Local Vibration on visual SV

Another way to simulate neck movement without producing head movement is through the use of vibration. Some studies have attempted to stimulate neck proprioception through selective vibration of neck muscles (Betts, Barone, Karlberg, MacDougall, & Curthoys, 2000; McKenna, Peng, & Zee, 2004). It is believed that the vibration of the neck muscles can simulate the lengthening of the muscles spindles to induce a perception of neck rotation or movement. McKenna, Peng, & Zee (2004) vibrated the left or right neck as well as the left and right mastoid processes (directly over the location of the vestibular nerve) while the head was tilted or upright during visual SV estimates. When the head remained upright, they found little change in visual SV estimates with the added vibration of the different areas of the neck. Most estimates remained around 0°. However, when the head was tilted, the vibration of the neck resulted in visual SV estimates that were biased towards the opposite side of the head tilt greater than the biases induced by the head tilt alone. They suggest that when the neck is tilted the muscle spindles are more sensitive to vibration because they are closer to their maximum stretch. Thus, when stimulating the muscle spindle while they are already stretched may cause a greater perception of stretch. Unfortunately, these studies used high frequency vibration (100 Hz) that can stimulation both muscle spindles as well as vestibular afferents, such as in GVS.

We first examined the influence of vibration on one side of the neck on subjective vertical estimates using an alignment task. We expected to find similar results as previous studies, such that the asymmetric vibration would have little to no effect on visual SV biases in the upright position. If asymmetric vibration did have an effect, the effect should show that the vibration would cause a bias in the opposite direction of the vibrated side. This is because if the vibration simulated the lengthening of the muscle spindles it would indicate a head tilt in the opposite direction. SV estimates then should be biased towards the simulated head tilt. Additionally, if vibration induced a proprioceptive response, we may expect within-subject standard deviations be larger during vibration conditions.

4.2.1 Method

Twenty-three participants participated in the study. In order to administer vibration to the neck, we used a set of 7 vibrating pods (http://www.innomax.com/index2.php?crn=248). We placed two vibrating pods inside the memory foam pillow that could be independently switched on to selectively vibrate one side of the neck. All participants performed an alignment task 3 times, once while each side of the neck was vibrated separately, and once with no vibration. Participants wore the same neck pillow secured with a Velcro strap for all conditions. In the no vibration condition, the vibrating pods continued to be attached to match the increased weight in the other conditions but were left turned off. Conditions were randomly ordered for each participant. While one side of the neck was being vibrated, participants made alignment 18 SVV estimates, 6 estimates for each frame condition ($\pm 18°$ and 0°). Participants also performed a discrimination task in an upright condition as well as in a supine condition without any vibration after all alignment tasks were completed.

4.2.2 Results

Using a 3 (Vibration) × 3 (Frame) ANOVA, we found the expected effect of frame, F (2, 44) = 63.19, p < .001, η_p^2 = .742 and a significant interaction between vibration and frame, F (4, 44) = 3.81, p < .001, η_p^2 = .148. Specifically, when participants' necks were vibrated on the right side, SV estimates were less extreme when viewing the counterclockwise tilted (-18°) frame than when compared to when the left side of the neck was vibrated, *t* (22) = 3.28, *p* = .003, when there was no vibration, *t* (22) = 3.37, *p* = .003. No other conditions were significantly different from one another, see figure 4.5.

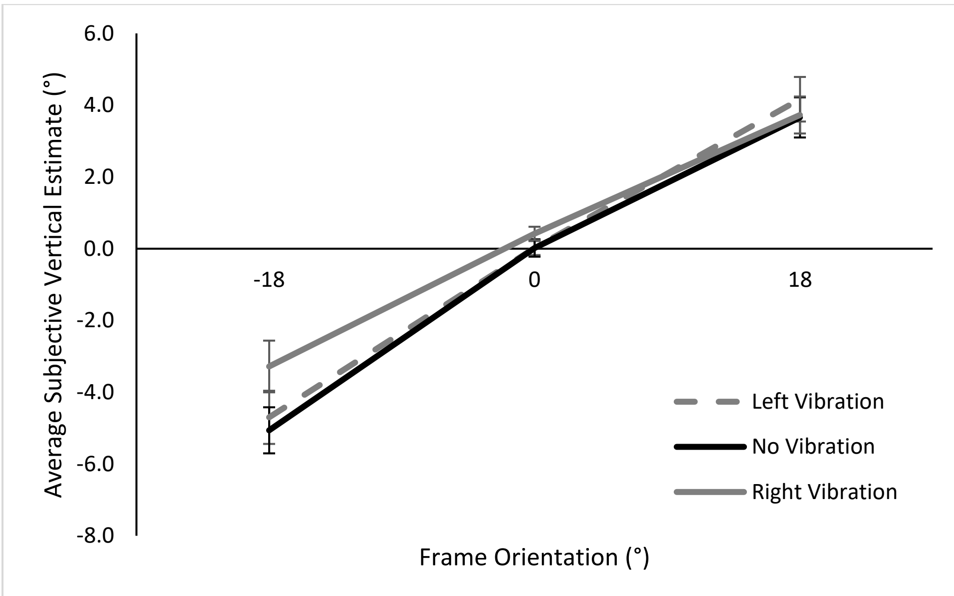


Figure 4.5: Average subjective vertical estimates made with and without vibration to either the left or right side of the neck separately. Error bars represent standard errors about the mean.

Using within-subject standard deviations, we performed the same ANOVA analyses. We only found the expected effect of frame, *F* (2, 44) = 21.52, *p* < .001, η_p^2 = .494. We found a small interaction effect, but it was not significant, *F* (4, 44) = 1.94, *p* = .111, η_p^2 = .081, see figure 4.6.

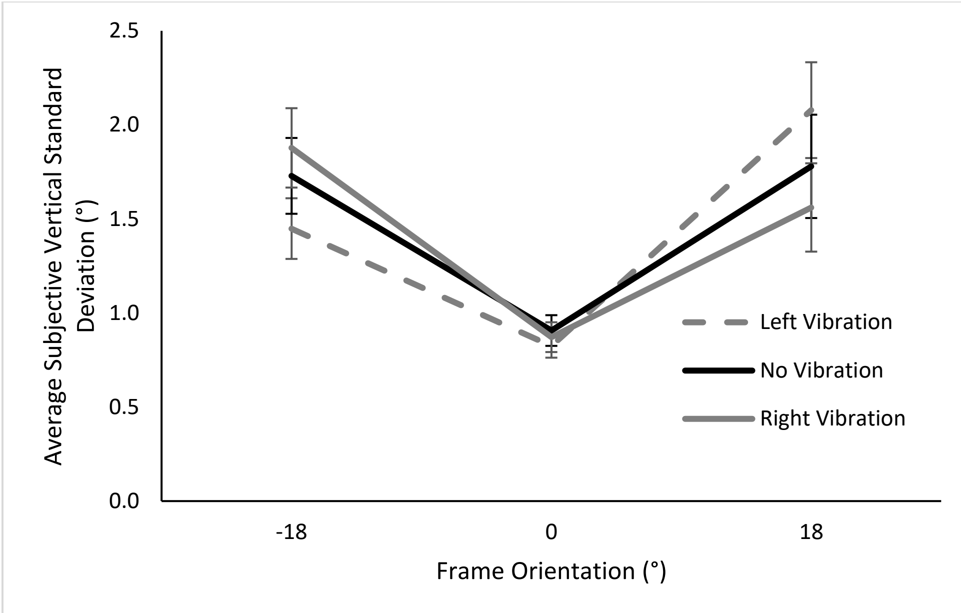


Figure 4.6: Average within-subject standard deviation of subjective vertical estimates made with and without selective vibration of the left or right side of the neck separately. Error bars represent standard errors about the mean.

Similar to the GVS experiment, we also calculated difference scores in which we subtracted SV estimates made during vibration from estimates without vibration to give us the effect of vibration on SV. Using these scores in a 2 (Vibration) × 3 (Frame) ANOVA, we found similar results. First, we did not find a main effect of frame, suggesting that the vibration conditions had similar effects across frame conditions overall. However, we did find an interaction between frame and vibration, again suggesting that during right vibration, the SV was biased towards the right in the left tilted frame condition (see figure 4.7).

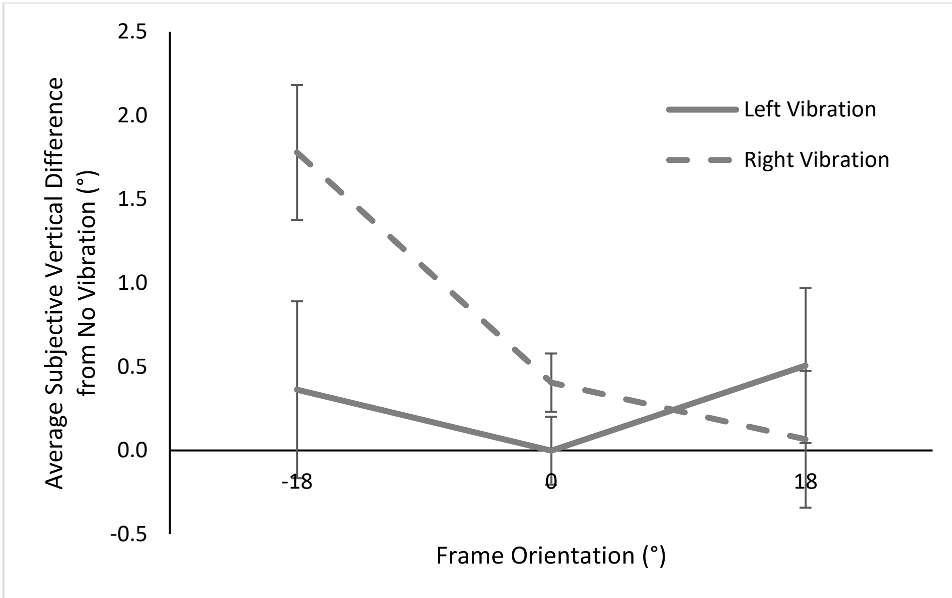


Figure 4.7: Average differences between subjective vertical estimates made without vibration and those made with vibration on the right or left side of the neck separately. Error bars represent standard errors about the mean.

4.2.3 Discussion

We found only limited support that local vibration on one side of the neck changes SV estimates. Additionally, the small effect that we did find was not in the predicted direction. The lack of significant results coincides with previous research that has not found this effect in upright individuals. These researchers suggest that the neck must already be tilted in order to find a larger effect of vibration (McKenna et al., 2004). Next, we tested the effect of global vibration of the neck and body on visual SV estimates, to investigate the use of vibration to create noise within the proprioceptive system.

4.3 Experiment 2b: Global Vibration on visual SV

Another approach to using vibration is to use it to introduce noise by simultaneously vibrating the entirety of the neck. Fraser et al. (2015) investigated the effect of providing global vibration to both sides of the neck simultaneously in order to introduce noise in the neck proprioceptive system. They found that there was a strong E-effect (opposite of the body tilt) in haptically-made SV estimates when the entire body was tilted 45° beyond the effect found without vibration, suggesting that they had disrupted the indirect contribution of neck proprioception on haptic SV estimates. However, they found no differences in visual SV estimates using vibration during body tilt. Interestingly, they found a similar effect in haptic SV estimates when introducing GVS noise bilaterally to the vestibular nerve during head tilt only, again suggesting that these two effects could be due to the disruption information about the head's position in space indirectly through neck proprioception.

4.3.1 Method

In this experiment we use the same neck pillow used in the previous experiment. We used two sets of the same 7 vibrating pods we used in the previous experiment. We placed two vibrating pods from one set inside the pocket of the neck pillow and situated them on either side of the neck. In addition to the neck vibration, we also used the second set to vibrate the bottom of their feet by placing three vibrating pods underneath the mattress pad where the participant stood. The vibration frequency measured 50 Hz. Eleven participants performed an orientation discrimination task once while their necks were being vibrated on both sides simultaneously as well as their feet and once without any vibration. We counterbalanced the order of the conditions between participants. We also tested these same participants in the supine position, once while their entire backside was vibrated using all 7 vibrating pods from a single set embedded into the mattress pad, and once without any vibration.

4.3.2 Results and Discussion

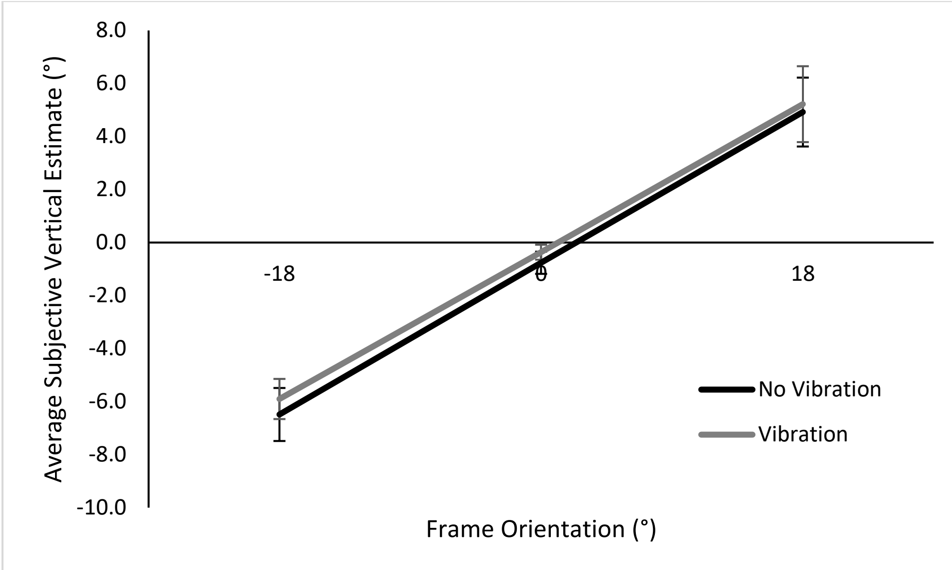


Figure 4.8: Average subjective vertical estimates made with and without vibration to both sides of the neck and to the bottoms of the feet. Error bars represent standard errors about the mean.

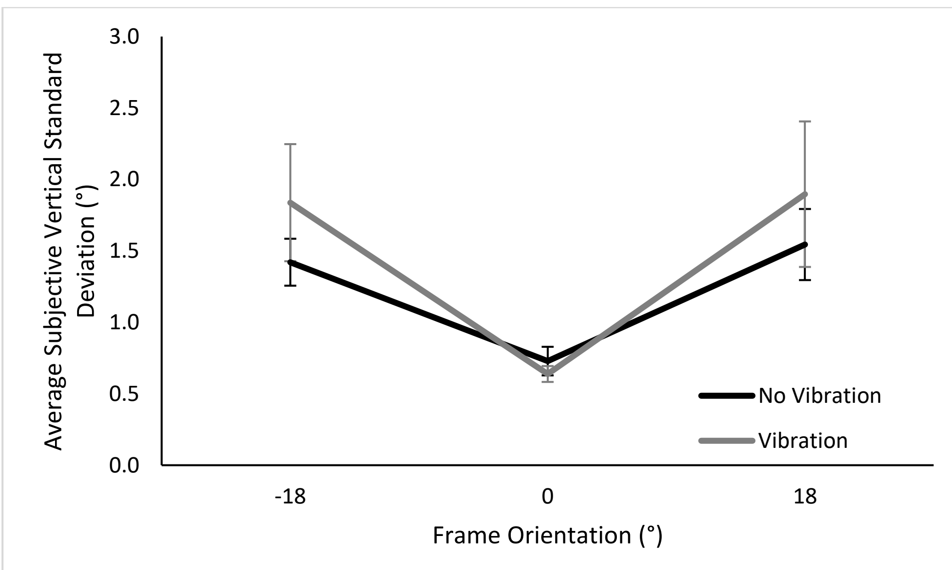


Figure 4.9: Average within-subject standard deviation of subjective vertical estimates made with and without vibration to the neck and feet. Error bars represent standard errors about the mean.

Using a 2 (Vibration) x 3 (Frame) ANOVAs, we did not find any differences in using global vibration in either type of SV estimates or within-subject standard deviations in either supine or upright, see figures 4.8 and 4.9 for upright conditions. These results suggested that global vibration to the entire body may not be useful in creating noise in the proprioceptive neck cues. Specifically, we expected to see that the within-subject variability uniformly increased as a result of vibration. Perhaps, this study was underpowered to detect such the effect. However, such a small effect would not be useful in eliminating or significantly reducing proprioceptive cues. In future studies, we plan to investigate the effects of vibration on vestibular SV estimates, as it is hypothesized that because these types of estimates rely more on the body's longitudinal axis, the effect of vibration may be larger.

4.4 Experiment 3: Foam vs No Foam on Vestibular Estimation

During our investigations of vestibular SV using the tilt table, we anecdotally became aware of the possible subtle differences in weight shifts that may occur during rotation. Using the foam platform, some participants felt as though they were able to detect these weight shifts more intensely then if they were to simply stand on the wooden platform. Given that we were interested in a pure vestibular estimate rather than one that may have been influenced by weight shift felt in the legs and feet, we tested the whether the foam provided additional cues compared to the solid platform. However, given that most individuals had vestibular SV estimates that centered around 0°, we believed that these weight shifts would be negligible with or without the foam platform

4.4.1 Method

Using the tilt table procedures described in the previous chapter, we tested 7 people using foam that lined the inside and bottom platform of the tilt table and without (see figure 3.2 and 3.3). The same participants participated in both conditions on separate days about a week apart. The foam rested against both sides of participants arms as they were secured in the tilt table apparatus as well as underneath their feet. In the condition without foam, the sides of the apparatus were made with hardened vinyl panels and underneath their feet was a wooden platform. Seven participants first engaged in an adjustment phase as described in the previous chapter before performing the discrimination task based upon their estimates in the alignment phase. We compared average SV biases and within-subject SV standard deviations.

4.4.2 Results and Discussion

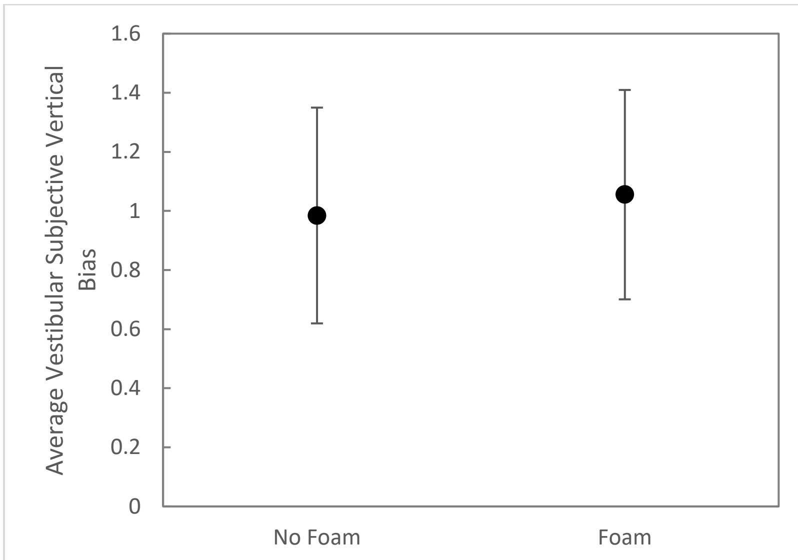


Figure 4.10: Average vestibular subjective vertical biases for foam and no foam conditions. Error bars represent averaged within-subject standard deviations.

Using a 2 (Foam) x 3 (Frame) ANOVAs, we did not find any differences in using foam in either vestibular SV estimates or their within-subject standard deviations, see figure 4.10. Additionally, we found a significant correlation between foam and no foam within-subject standard deviations, suggesting that participants were consistent in their SV estimate errors, r (5) = .780, p = .038, see figure 4.11.

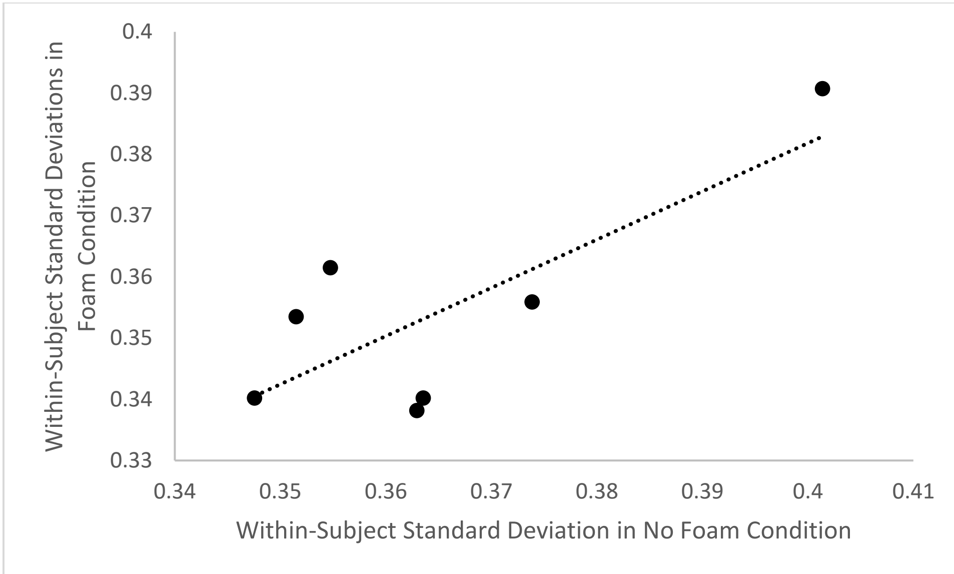


Figure 4.11: Scatterplot of within-subject standard deviations in foam and no-foam conditions.

Overall, we found no support for the foam linings influencing vestibular SV estimates or standard deviations. If the foam exaggerated weight shift changes due to the rotation of the tilt table, we should have expected that estimates would have been less accurate in the no foam conditions, suggesting that the weight shifts in either conditions are negligible or similar in influencing vestibular SV estimates.

4.5 General Discussion

In this chapter, we delved into some of the most probable proprioceptive influences on our estimates of SV. We found little support for the influence of proprioceptive information mainly because our investigations involved the head aligned with the body orientation. Specifically, we only found an effect of using a neck pillow on visual SV estimates, suggesting that the visual SV estimates reported throughout this manuscript have a reduced influence of neck proprioceptive cues. We did not find differences in visual SV estimates using vibration to either reduce or enhance neck proprioceptive cues nor did we find differences in vestibular SV estimates when using foam lining the tilt table. We wish to use conditions that are unaffected by proprioceptive cues to ultimately test optimal integration of vestibular SV and visual SV. This will be the topic of the next chapter.

5 CHAPTER 5: Optimal integration in the estimation of vertical

Incorporating valid and reliable sensory information is essential to successful movement through an environment. These sensory cues must be quickly and constantly updated to relay the current position of the body as one moves through an environment. Many times, cues from different sources communicate redundant information about the state of the environment. One of the most essential aspects to navigation is the ability to perceive one's body orientation within the environmental context. Cues about body orientation are effortlessly perceived through various sensory systems and integrated to produce an end estimate. The perceivable results from the integration of these cues will depend how each type of cue is weighted and factored into the final percept. While sensory systems use similar and sometimes overlapping information, they each can obtain information about body orientation independent from one another that can be used a basis for their final estimate.

Self-orientation is determined by visual, vestibular, and proprioceptive cues that provide the observer with overlapping egocentric and allocentric information about the position of the body under environmental gravity. Subjective vertical (SV), or the estimate of the direction of true vertical, has been widely studied under many different contexts. Estimates of SV have primarily been conducted using visual stimuli but are usually a consequence of the combination of the same three sensory modalities. Although, SV explicitly measures environmental vertical, an allocentric type of estimate to a human observer, it also implicitly estimates one's body orientation within the environmental context. Specific types of sensory cues from each modality can influence the perception of subjective vertical and self-orientation.

Visual cues about self-orientation and subjective vertical arise from environmental features that are subject to the same laws of gravity as is the body. Vertical lines and edges are ubiquitous in everyday environments and serve as stable visual cues that inform the observer of the direction of gravity. Studies have shown that visual vertical cues are greatly relied upon when making estimates of vertical and when these cues are biased or distorted, estimates of vertical are significantly influenced (Shimamura & Prinzmetal, 1999; H. A. Witkin & Asch, 1948; H.A. Witkin & Asch, 1948). However, this may be biased due to the fact that the majority of experiments use a visual probe in order to test for SV. Further, distorted visual cues or the absence of visual cues have been shown to interact with vestibular processing of body orientation (Black, Wall, Rockette, & Kitch, 1982; Guerraz & Bronstein, 2008; Nishiike et al., 2013; Stoffregen, Smart, Stofregen, & Smart, 1998). For example, it is well known that the visual presentation of a tilted room, rotating dots, or darkened scene significantly increases standing postural sway.

Vestibular cues about self-orientation arise from mainly two sources; rotational and linear acceleration of the observer's head. The vestibular sensory organs are made up of the semi-circular canals which sense head rotations in 3D space, and the otolith organs which can sense linear acceleration due to self-motion as well as the constant force of gravity. These cues together allow the observer to detect all types of movement within space and the position of the head relative to the body. Vestibular cues have also been shown to influence the processing of visual cues. For example, in one of the first investigations of visual and vestibular integration on visual SV, Aubert (1861) found that when an observer's body is physically roll-tilted greater than 30°, visual SV is visually biased towards the tilt of the body (A-effect). However, when tilted at smaller degrees, visual SV is found to be slightly biased towards the direction opposite of the body (E-effect). Mittelstaedt (1983) suggests that these A-effects occur mainly because there is a bias towards an idiotropic vector, along the body's longitudinal axis. This idiotropic vector was later characterized as a prior in the Bayseian framework in visual vestibular integration (MacNeilage, Banks, Berger, & Bülthoff, 2007). This idiotropic bias cannot however account for the smaller E-effects found at small body tilts. Recent investigations of visual SV have found that this type of idiotropic vector would create more accurate estimates than what has been observed when there is a discrepancy between head and body positions in space than observed. Specifically, when the head is rotated while the body is upright, there are larger visual SV biases towards the head than when the body is rotated while the head remains upright. This result suggests that the idiotropic vector is either only used for particular types of SV estimates or is head-centric rather than body-centric in nature. Thus, recent studies have assumed a uniform prior for body orientation, rather than one that assumes an upright position (Clemens et al., 2011; Fraser et al., 2015). Another possible source for these effects come from ocular torsion, in which the eyes rotate slightly in the opposite direction when the head is tilted. However, when asking participants to adjust a visual probe to the head orientation, rather than subjective vertical there are only small errors, suggesting that ocular torsion may not play a large role in SV estimates (Mittelstaedt, 1983).

Lastly, proprioceptive sensory cues can also provide important information about body and head position with respect to gravity. These cues come from muscle contractions moving with or against gravity from their neutral positions as well as from points of contact with support surfaces, such as feet on a solid, flat ground, or a hand touching a surface. One of the most salient cues from determining the direction of gravity and body orientation come from the turning and tilting of the neck. Contractions of neck muscles give away the position of the head in space and can be compared to the body’s orientation based on the degree of tilt. These cues provide information about the position of the head relative to the body, but also relay information about the direction of the pull of gravity as muscles coordinate to move with or against gravity to keep the head in a stationary position. These cues highly overlap with vestibular tilt cues as the vestibular apparatus is confined within the head. Thus, it can be difficult to separate vestibular and proprioceptive neck cues as they are naturally simultaneously activated when one moves their head.

Another rich source of proprioceptive information comes from the ankle muscles that can help to determine the degree of slope on which the person is standing. Along with tactile perception from the bottom surface of the feet, the observer can make estimates about the direction of gravity using positional cues from ankle muscles. Multiple studies have shown that standing on high density foam greatly destabilizes the observer due to the greater variance in ankle muscle activations and reduced tactile cues from the feet (Chiang & Wu, 1997; Patel, Fransson, Lush, & Gomez, 2008; Paulus, Straube, & Brandt, 1984). In fact, standing on foam has become a popular way to improve one's balance due to the reduction of haptic and proprioceptive cues.

There have been few studies that have investigated optimal integration models of visual, vestibular, and proprioceptive cues in subjective vertical and body orientation. Most notably, Clemens et al. (2011) proposed an internal model of integration based on the incoming sensory cues about the positions of the head and body in space. They used an inverse probabilistic approach in which they estimated noise parameters of sensory cues by assuming optimality and backwards engineering how sensory systems may be integrating single modality cues. They tested visual SV, as well as subjective body tilt while participants sat in a rotatable chair. Their visual SV task involved participants sitting upright or tilted to one of eight tilt angles between $\pm 120°$, while performing discrimination tasks about a luminous reference line with respect to gravitational vertical. In the subjective body tilt task, participants performed a discrimination task about their body orientation in reference to a particular tilt angle, 0°, ±45°, and ±90°, using the rotatable chair in darkness. Their model suggests that these two tasks are performed differently due to the presence of two underlying estimates of gravity, one produced through sensory information from the body separate from one produced through sensory information from the head, a key element to empirically studying optimal integration. They found that this model could account for visual SV and body tilt estimates using a Bayesian approach. They posit that to perform the visual SV task, participants directly accessed otolith cues and indirectly access body sensors through the mediation of the neck proprioceptive cues, which combined cues from the body and the neck. These two sources of cues provide weighted estimates that then combine with information about the eye's position in the head (degree of ocular torsion), the information about the visual line on the retina, as well as a prior that suggests the head is usually upright to produce a final visual SV estimate. Further, to perform the subjective body tilt task, participants directly reference body sensory cues while indirectly accessing positional head information through the meditation of the neck proprioceptive cues, subtracting out the neck cues from the head in space cues. These direct and indirect cues combine to produce a subjective body tilt estimate.

Fraser, Makooie, & Harris (2015) found further support for this model using a forward Bayesian cue combination experiment. They tested both visual and haptic SV separately in single cue conditions as well as in a combined-cue condition. The haptic SV estimation method was conducted by indicating the direction of vertical via physically feeling a hand-held rod with the hand without vision. They also used the classic visual SV estimation method using a luminous rod to make orientation judgments. Head and body tilt manipulations had different effects on haptic SV estimates compared to visual SV estimates. When the head was tilted while the body remained upright, the A-effect persisted in visual SV estimates, but was lessened compared to when the entire body was tilted. Similarly, when the body was tilted 45°, but the head remained vertical, the A-effect was lessened to an even greater extent, suggesting that visual SV estimates may be head-centric. In contrast, using haptic SV estimates they found the opposite. Specifically, when only the head was tilted, participants had on average no haptic SV biases from vertical. However, when the body was tilted strong A-effects were observed, suggesting that haptic SV estimates may be more body-centric. These results together suggest that haptically-made estimates might be more influenced by body orientation than head orientation, while visual estimates are more influenced by head orientation than body orientation. While the mode of estimation, using a hand-held rod to haptically estimate SV, is arguably not a commonly used estimation cue of vertical in everyday life, this and other studies that have investigated SV estimates made in modalities other than vision suggests that each modality that has access to information about vertical may be tapping into independent representations (Bauermeister et al., 1964; Bronstein, 1999; Lejeune et al., 2004).

Fraser et al. (2015) also investigated whether haptic and visual estimates combine optimally per the model proposed by Clemens et al. (2011) using a Bayesian approach. Specifically, they asked participants to make visual-only and haptic-only SV judgments using the same methods described above in an orientation discrimination task while the whole body was tilted 45° (head in line with body). They found that these single-cue estimates combined to produce optimal estimates comparable to participants' SV estimate made in a combined condition in which participants made haptic SV estimates while they could both see and feel the rod. However, they found that variances produced in the combined condition were greater than the variances predicted by the model. They posited that this could be due to the influence of the indirect pathways in the two estimates mediated by neck proprioception proposed by Clemens et al. (2011) potentially causing the estimates to be non-independent. They then replicated the experiment using neck vibration to reduce the influence of these indirect pathways. Using vibration, they found that their combined condition now reflected the optimal integration based on the single cue conditions. Clemens et al. (2011) and Fraser et al. (2015) both utilize two separate estimates of vertical in order to determine optimal integration and have found important differences in the modality of estimation suggesting that SV can be independently assessed through different modalities.

The current study seeks to expand on these studies by also using a Bayesian approach to multisensory integration of visual and vestibular cues on the egocentric perception of subjective vertical and self-orientation. The Bayesian approach proposes that independent sensory cues can be linearly combined, such that independent cue estimates are weighted by their reliability (or the inverse of their standard deviations to produce an optimal estimate when the cues are presented together (Ernst, 2006; Ernst & Banks, 2002). The standard deviation of the estimate in which cues are presented together thus should be smaller than estimates made from each modality independently. In order to test such a model, an estimate of the percept must be obtained from each modality independently, without the influence of the other. We can then compare this optimal result to an empirical condition in which all cues are represented to determine whether human observers integrated the cues optimally.

The current study uses isolated cue conditions that only use the modality as the source of estimation. We test visual subjective vertical in a discrimination task by placing participants in a supine position, such that gravitational receptors do not aid in the SV task. We also separately test for vestibular SV in a discrimination task around vertical using whole body tilts. We then compare a predicted optimal estimate based on these single-cue conditions to a combined condition in which participants perform the same vestibular SV task, with the addition of a visual cue. These results have implications on the how vestibular and visual cues optimally combine to produce an estimate of subjective vertical.

5.1 Method

Fifty-three participants participated in the current experiment. All participants had normal or corrected-to-normal vision. Participants performed orientation discrimination tasks in three conditions: a visual-only, a vestibular-only, and a combined visual-vestibular condition as described below. Four participants were removed from the analyses because we were unable to fit their data to psychometric functions.

The visual-only condition was performed while the participant was lying supine on a mattress. The remaining two conditions were performed while the participant stood on the tilt table that could rotate up to ± 30°. The entire study took two hours to perform. Participants were given 5-minute breaks in between each task. Participants also engaged in an upright visual SV condition that was not a part of the analyses here.

5.1.1 Visual only condition

To display our visual stimuli, we used the Oculus DK1 virtual reality headset to display visual stimuli rendered in Unity. Head tracking was enabled so that if participants moved their head, the image on the screen would coincide with their point of view. During all tasks, however, participants were asked to minimize all head movements and to continue looking straight ahead during trials. All tasks were performed in low lighting conditions to reduce any outside light that may be seen from the outsides of the VR headset.

We presented participants with a virtual rod-and-frame task in which a rod was presented in the back center of a 3D frame. Throughout the task, the participants were presented with the rod under the context of 3 different orientated frames (0°, ± 18°). In an alignment task, participants aligned the rod to an orientation that appeared to be in line with their body orientation (vertical within the virtual environment) to produce an estimate of subjective vertical (SV). Participants made four SV estimates for each of the three tilted frames. All 12 trials were randomly presented.

We used the average of these estimates from the alignment task from each room separately to determine the orientation angles that were presented during a discrimination task in which participants indicated whether the central rod was tilted clockwise or counterclockwise. For the 0° frame, the angles chosen for the discrimination task were ± 0.25°, 0.5°, 0.75°, 1.0°, and 1.5° around the average SV estimate made during the alignment task, for a total of 10 presented orientations. For the tilted frames, the angles were ± 1.0°, 2.0°, 3.0°, and 4.0° around the average SV estimate made during the alignment task and for a total of 8 presented rod orientations per frame tilt. Each angle was randomly presented during the task 8 times, resulting in a total of 208 trials across the entire task. All trials were randomly presented. During each discrimination trial, the rod and frame were presented for 250 ms. The rod was either tilted clockwise or counterclockwise from vertical at a predetermined angle, followed by a gray blank screen for 2 seconds during which participants were instructed to indicate the direction in which they perceived the tilt of the rod via mouse click. The computer mouse remained stationary on the mattress while participants used their right hand to manipulate the mouse buttons. Only trials using the non-tilted frame were used for analyses.

In order to remove vestibular influence on the task, participants performed this task while lying supine on a high-density 20 cm foam mattress, looking up towards the ceiling. While the vestibular system was no doubt active in this position, the pull of gravity was in an orthogonal direction as the rod presented in the task, thus the perception of gravity via the vestibular system could not aid in the decision of orientation of the rod in this task. The choice to use a high-density foam was guided by studies that have shown reduced proprioceptive input and feedback at points of contact (Hansson, Beckman, & Håkansson, 2010; Hirata et al., 2013; Patel et al., 2008).

5.1.3 Vestibular-only condition

In order to test the subjective vertical using only vestibular cues, the tilt table was used to tilt the whole body while participants responded to the tilt of their body orientation. To reduce any influence from proprioception, the platform on which the participants stood, and the two side panels of the tilt table were lined with 20 cm thick foam. Nevertheless, in a pilot study, we found no differences between using or not using foam on subjective vertical estimates. Throughout this condition, participants wore the Oculus headset which displayed a black screen.

Once participants were standing on the platform with their arms by their sides, an adjustable side panel was moved until the participant was snuggly secured on the tilt table. Participants also wore a memory foam neck pillow in order to reduce neck movement and proprioceptive cues. A power tool was used to grip a steel threaded rod that controlled the rotation of the tilt table. The rotation of the individual was done manually by rotating the power tool around the steel rod's axis. Two researchers coordinated using hand signals to silently rotate the participant. The first researcher sat behind the participant and recorded the results from a digital angle gauge and signaled to the second researcher the direction of rotation during each trial. The second researcher manually rotated the participant at a steady pace of about 0.3°/second and could not see the current angle at which the participant was tilted at any point during the experiment.

In the vestibular alignment task, participants were rotated to ± 4° while standing on the tilt table. At this magnitude of body tilt, nearly all participants knew the direction in which they were tilted, when asked by the researcher. If the participant was incorrect in identifying the direction of this tilt, the researcher continued to tilt the participant in the same direction until they were confident the direction in which their body was tilted. Once at this angle, participants were slowly moved back toward 0° tilt and were instructed to verbally indicate when they believed that their body was aligned with true vertical. Once they were satisfied that they stood vertically, the orientation was recorded in 0.1° increments using a digital angle gauge that was aligned with the middle of their core body axis. Four estimates of vertical were obtained in this manner (two starting in each direction, either clockwise or counterclockwise).

We used the average of these estimates from this alignment task to determine the angles of orientation for the discrimination task to obtain a full psychometric function of each participant's vestibular SV. Body tilt angles for the discrimination task were ± 0.3°, 0.5°, and 0.8° around the average SV estimate made in the vestibular alignment task. There were 4 trials per each discrimination angle, producing a total of 24 trials. Participants stood on the tilt table and were asked to indicate the direction in which they perceived their body to be tilted (clockwise or counterclockwise) while tilted at each angle. At the beginning of each trial, participants were taken to either ± 2° from the target angle for that trial (with random and counterbalanced design) and then was rotated slowly back to the target trial angle at which the participant was tested at. The participant was instructed not to use the direction of the motion during rotation but rather the static body orientation at the target trial angle. Participants were blindfolded in the same manner as in the vestibular alignment task.

5.1.2 Visual-vestibular condition

We created a combined visual-vestibular condition in which both visual and vestibular cues were present to compare with the predicted optimal observer SV estimates. This condition was similar to the vestibular-only condition, except the Oculus headset displayed the upright rod and frame, in which, in the upright body position, both the rod and frame were aligned with the participants' body orientation. The headtracking feature was still active, such that vertical within the virtual environment was always defined as the gravitational vertical.

When rotating the participant in the tilt table, it was possible that participants were reflexively maintaining their head in an upright position, regardless of the tilt of their body. Despite instructions to keep their head aligned with their body, and the use of the neck pillow, this reflexive movement may generate inaccurate measurements in our study and thus activate the indirect pathways involving neck proprioception.

For a subset of participants (n = 31), we recorded the rotational movement of the headset's cyclopean eye during the visual-vestibular and vestibular-only conditions using the headset's built-in gyroscope. Specifically, we measured the headset rotation at the beginning of each adjustment trial (while participants were tilted at ± 4°), and at the beginning of each discrimination trial (while participants were tilted at the trial angle). This allowed us to determine (1) how much participants moved their head during trials, (2) whether or not head movement was systematic across participants, and 3) whether or not head tilt influenced SV estimates in either the vestibular-only or the visual-vestibular conditions.

5.2 Analyses

5.2.1 Optimal Observer Model

In this study, we compared our empirical results from the combined visual-vestibular condition to a predicted optimal estimate based upon the isolated cue conditions using a Bayesian optimal observer model. Bayesian inference suggests that we can combine independent visual and vestibular cues optimally using the likelihood functions of each cue individually:

$$P(SV|visual, vest) \propto P(SV|visual)P(SV|vest)$$

Based on the Maximum Likelihood Estimation, the likelihood estimates are weighted based upon the relative reliabilities of each cue, which is calculated using the inverse of the variance across estimates of subjective vertical in both modalities (Ernst, 2006). For example, the weight of the visual cue is calculated as follows:

$$w_{visual} = \frac{\frac{1}{\sigma_{visual}^2}}{\left(\frac{1}{\sigma_{visual}^2} + \frac{1}{\sigma_{vest}^2}\right)}$$

Thus, the predicted optimal SV estimates and sensitivities are calculated from:

$$SV_{combined} = w_{visual} SV_{visual} + w_{vest} SV_{vest}$$

$$\frac{1}{\sigma_{combined}^2} = \frac{1}{\sigma_{visual}^2} + \frac{1}{\sigma_{vest}^2}$$

After obtaining the predicted bias and sensitivity using this model, we compared our results to the empirical SV estimates and sensitivities obtained from the combined visual-vestibular condition.

5.2.2 Empirical Analyses

We also compared the isolated cue conditions with the combined conditions, in order to estimate the effects that each type of cue had on SV estimates. We further examined the effect of head rotation during the vestibular-only and visual-vestibular conditions using correlations.

5.3 Results

The Bayesian cue combination model analyses found that participants' biases were not significantly different from optimal predictions, t (48) = 0.71, p = .484. Predicted estimates and actual estimates also had a significant positive correlation, r (48) = .51, p < .001, see figure 5.1. However, participant's sensitivity estimates in the combined condition were significantly lower than optimal sensitivity estimates based on isolated cue conditions, t (48) = 6.68, p < .001. Predicted sensitivity did not correlate with actual sensitivity in the combined condition, r (48) = .18, p = .220, see figure 5.2. Importantly, we did not find a significant correlation between SV estimates in the visual and vestibular only conditions, suggesting that they were indeed independent, r (48) = -.225, p = .120, see figure 5.3. See figure 5.4 for individual fitted psychometric curves for all participants in the single cue conditions and figure 5.5 for individual fitted curves in the combined condition and the predicted optimal estimates.

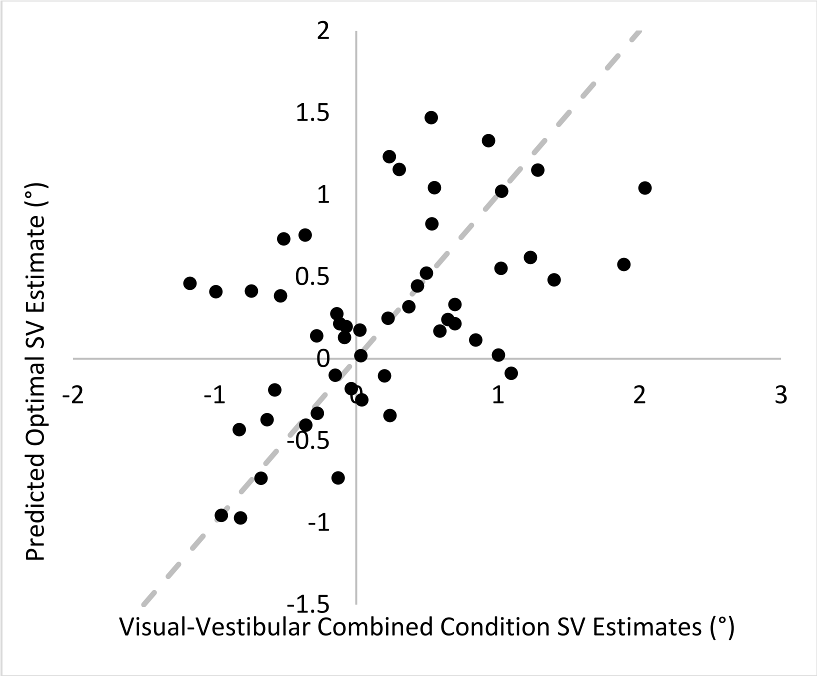


Figure 5.1: Scatterplot of predicted optimal SV estimate bias and actual SV estimate bias from the combined condition. Dashed gray line indicates what would be a perfect correspondence between optimal and actual performance.

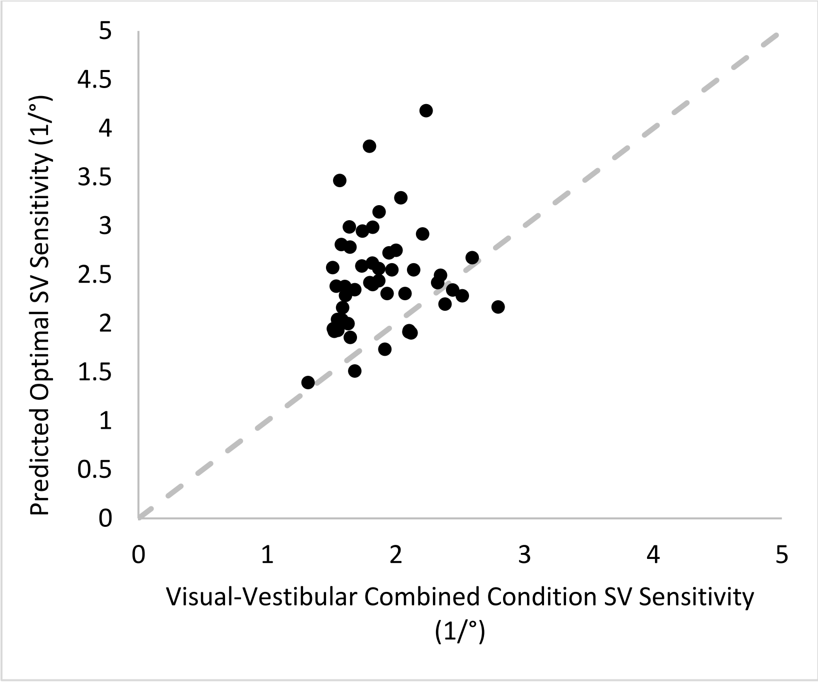


Figure 5.2: Scatterplot of predicted optimal SV estimate sensitivity and actual SV estimate sensitivity from the combined condition. Dashed gray line indicates a perfect correspondence between optimal and actual performance.

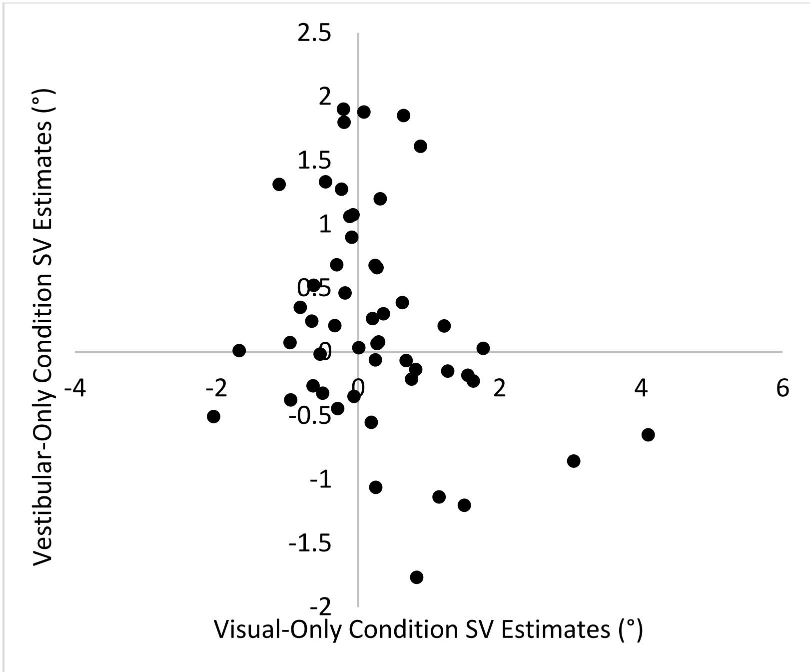


Figure 5.3: Scatterplot of SV estimates in single-cue conditions.

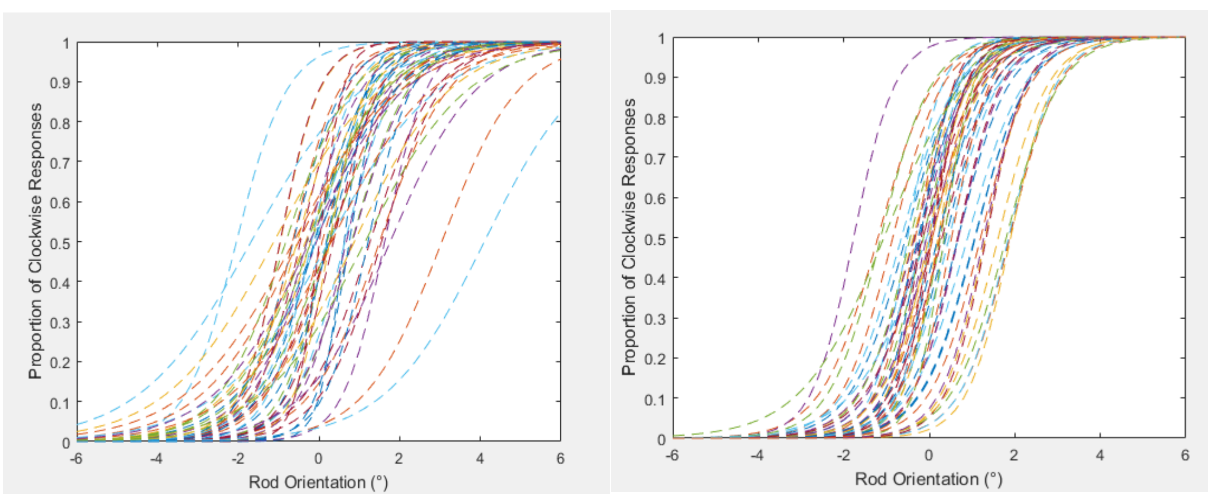


Figure 5.4: Individual fitted psychometric curves from SV discrimination tasks. Left: Visual-only condition. Right: Vestibular-only condition.

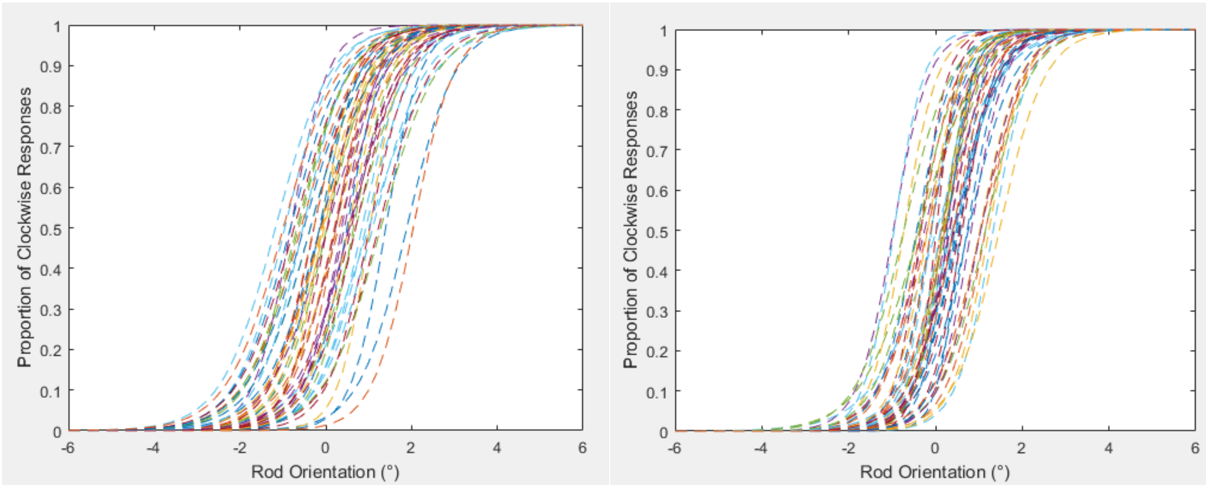


Figure 5.5: Individual fitted psychometric curves of combined SV estimates. Left: Visual-vestibular condition. Right: Bayesian optimal integration predicted estimate.

Using a three-way ANOVA among our experimental groups, we found no differences in SV biases across single or combined cued conditions, F (2, 96) = 0.04, p = .957. We did find differences in SV sensitivity across our conditions, F (2, 96) = 17.99, p < .001. Specifically, in the visual-vestibular condition (t (48) = 4.52, p < .001) and vestibular-only condition (t (48) = 4.83, p < .001) participants had a higher SV sensitivity than in the visual-only condition. The vestibular-only condition and the combined condition did not differ in sensitivity, t (48) = 0.49, p = .630.

Using the headtracking data, we found a positive correlation between head tilts in the vestibular-only condition and head tilts in the combined condition, r (30) = .534, p = .002 (see figure 5.6).

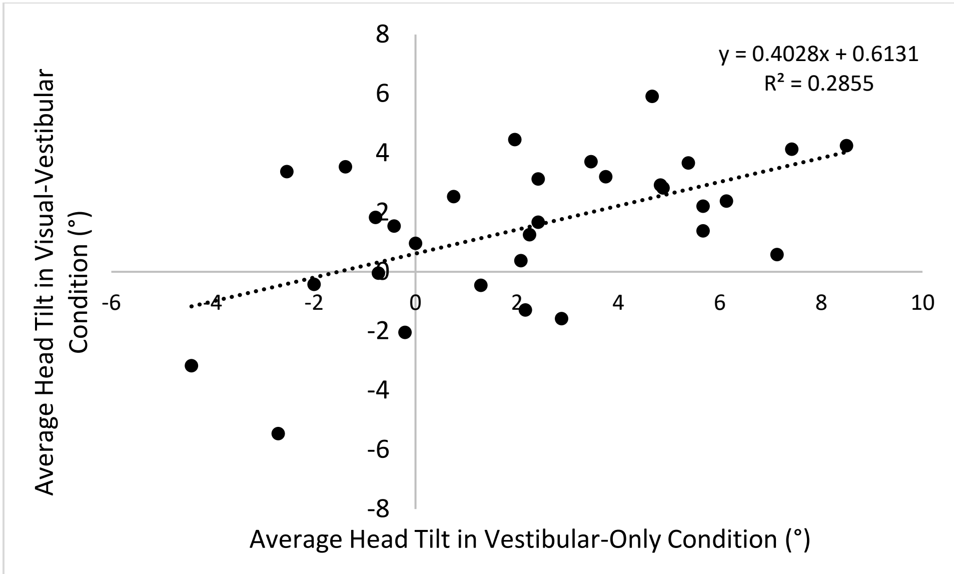
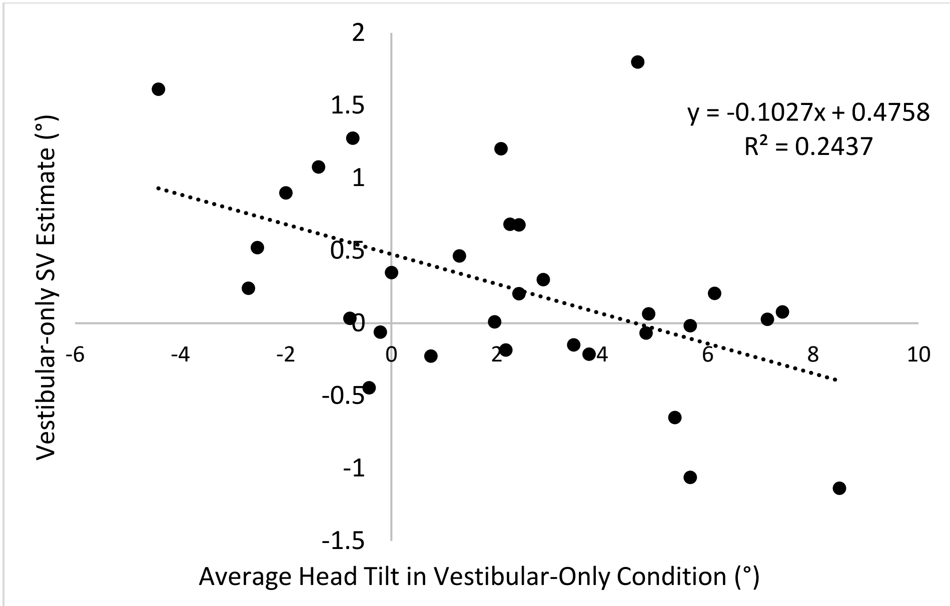


Figure 5.6: Scatterplot of average head tilts in the vestibular-only and the visual-vestibular conditions. Dotted black line indicates the line of best of fit.

Within the vestibular-only condition we found that participant's average head rotation negatively correlated with SV estimates, r (30) = -.494, p = .005 (see top panel of figure 5.7), such that SV estimates were made in the opposite direction of participants' head tilts. However, we did not find a significant correlation between average head rotation in the visual-vestibular condition and SV estimates in the visual-vestibular condition, r (30) = -.055, p = .768 (see bottom panel of figure 5.7).



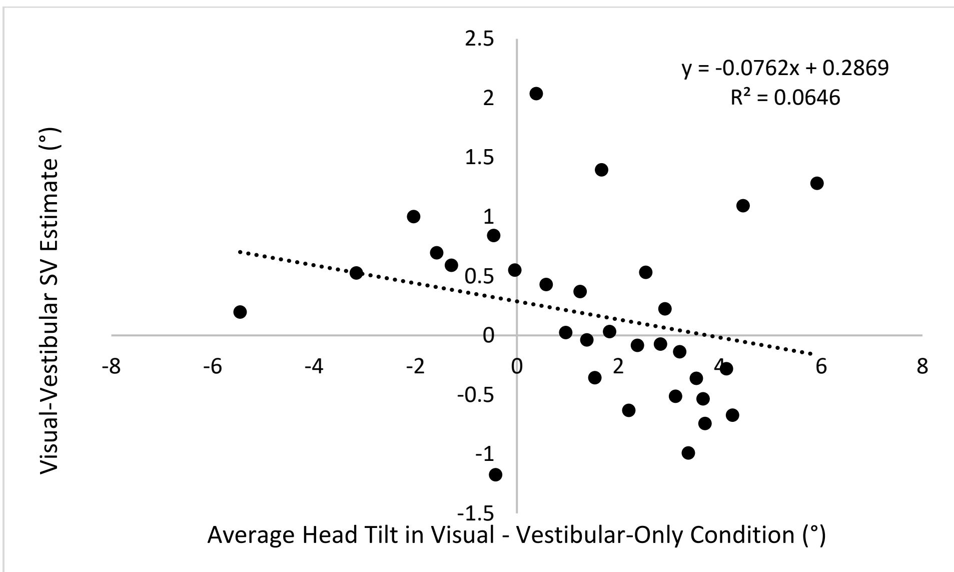


Figure 5.7: Scatterplot of average head tilt as measured by the VR headset and SV estimates in the vestibular-only condition (top panel) and the visual-vestibular condition (bottom pane). Dotted black line indicates the line of best of fit.

Within the vestibular-only condition, we found that participants used one of three types of head tilt strategies across their 6 body orientations. Participants either consistently either tilted their head (1) in a direction counter to the body orientation (n = 8), (2) in a direction congruent with their body orientation (n=10), or (3) in a static position that resulted half the trials to contain head tilts counter and half consistent with their body orientation (n=13). Using these categorizations, we then examined whether participants head-tilt correlated significantly with SV sensitivity in the vestibular-only condition. We confirmed our earlier finding that head tilt correlated with SV bias such that those that had counter head tilts had a significant negative correlation between head tilt and SV bias, r (7) = -.906, p = .002; those that had a congruent head tilt had a significant positive relationship between head tilt and SV bias, r (9) = .636, p = .048; while those that had a consistent static head tilt showed no relationship between head tilt and SV bias, r (12) = -.278, p = .358. However, we did not find any significant correlations between SV sensitivity and head tilt within any of these classifications. Furthermore, using a one-way ANOVA between head tilt groups, we did not find any group differences in SV sensitivity, F (2,28) = 0.312, p = .735, nor did we find a group difference in SV bias, F (2,28) = 1.244, p = .304. Furthermore, within each of these three head tilt groups, the significant difference between sensitivity predicted by the cue combination model and the combined condition remained robust, suggesting that head tilt was not a determining factor in this difference.

5.4 Discussion

In the current study, we found that SV bias estimates did not differ from predicted optimal estimates. However, sensitivity to SV was significantly lower in the combined condition than the model predictions, suggesting that participants did not optimally integrate vestibular and visual cues. Fraser et al. (2015) found a similar difference in sensitivity between a combined condition and optimal predictions when they hadn't reduced the indirect effect of neck proprioceptive cues following the Clemens et al. (2011) model. We found that people were inconsistent in the ways in which they tilted their head in response to body tilt. We attempted to measure sensitivity and average head tilt by categorizing clockwise and counterclockwise head tilts that corresponded to each body tilt angle. Most people, at most body tilt rotated their heads clockwise, thus we were unable to fit a psychometric function of this type for almost all of our participants. However, considering most participants' vestibular SV estimates were tightly within $\pm 1°$, the degree of head rotations was overall small as well. Regardless, we found head tilt correlated with SV bias, but not sensitivity in the vestibular-only condition. Thus, our vestibular-only condition may in some ways be considered a vestibular/proprioceptive condition with any type of head tilt strategy informing the bias estimation in the absence of visual cues. Considering head tilts were correlated between the combined and vestibular-only conditions, suggests that whatever influence head tilt may have had on SV estimates, it was factored into the optimal predictions through the vestibular-only cue condition as well as into the combined condition to which we compared the optimal. Interestingly however, we did not find that head tilt correlated with SV estimates or sensitivity in the combined condition, suggesting that with the presence of visual cues, neck proprioception may have become less influential than vestibular or visual cues in bias estimates. These results together suggest that participants were not optimal in their SV estimates when combining vestibular and visual cues. There is a possibility that neck proprioceptive estimates may have indirectly affected sensitivities in either the calculation of the optimal estimates through the vestibular only condition or through the combined conditions. Correlation results using head tilt orientations obtained from the headset suggest that this was however unlikely. More research in this area is needed to determine the role of neck proprioceptive cues in this paradigm.

This study was the one of the few studies to investigate optimal cue combination in the estimates of SV using an optimal Bayesian cue combination approach with purely isolated single-cued conditions. Our study, following the example of Ernst & Banks (2002) and the model proposed by Clemens et al (2011), we used methodology that limited the single-cue conditions to estimates made in only the tested modality. Through this method we found limited results in optimal integration. These results however are not in conflict with Mittelstaed's (1984) and De Vrijer et al's (2008) findings. Like Fraser et al (2015), our results suggest that subjective vertical is estimated independently by vestibular and visual systems, however the combined condition yielded less than optimal results, suggesting that the compensation of one modality for the other can produce an accuracy/precision trade-off in which precision may be sacrificed for accurate SV estimates. Particularly, sensitivity to SV in the combined condition, in which all cues were available, was significantly lower than the model predictions based on single-cue conditions. The addition of a visual cue in this condition, may have enhanced estimation performance but may have also decreased precision. Further study should focus on the effects of proprioception in combination with vestibular and visual cues to produce estimates of SV and what might account for sub-optimal combination.

6 CHAPTER 6: General Discussion and Future Directions

In the previous chapters, we have discussed the various visual, vestibular and proprioceptive cues that aid in the perception of vertical measured by both visual and vestibular SV estimates. We have validated the use of a virtual RFT and have found similarities between using discrimination and the traditionally used alignment tasks, yet also important differences. Through the use of the virtual reality technology and software, we were able to begin to probe some of the various visual cues that may help to visually bias SV estimates, such as texture and object cues. We additionally investigated the role of vestibular cues on visual SV estimates using the VR headset in a supine position. We then probed vestibular input in the absence of head tilts to investigate the role of these afferents in the estimation of visual SV. Lastly, we validated our measure of vestibular SV through the rotation of the whole body using a custom-made tilt table. This served as our basis for gathering an independent measure of vestibular SV, without the influence of visual cues. We also tested various proprioceptive cues that may have influenced SV estimates in our study, finding that our use of a neck pillow may have decreased the use of proprioceptive cues in the visual SV estimates. Lastly, we tested how visual and vestibular SV estimates may combine to produce an integrated estimate of vertical. We did not find that participants optimally combined visual and vestibular cues in our experiment, however more research should be done to investigate the indirect role of neck proprioception per the model proposed by Clemens et al. (2011).

Overall, the studies outlined here serve as a jumping off point for various lines of research into visual, vestibular and proprioceptive contributions to body orientation and vertical. Additionally, we can begin to investigate how individual differences in sensory cue weighting may manifest particular maladaptive and debilitating ailments, such as motion sickness, vertigo, and acrophobia.

In the interest of understanding the etiology of these disorders and the malleability of the visual and vestibular sensory weighting system in the estimation of vertical. A key research area to pursue is how perceptual learning can affect the ability to use different sensory cues. Particular individual sensory weighting systems could have potentially interesting implications. As we have briefly mentioned previously, there are large individual differences found when looking at the biases produced by the RFT (Coelho & Wallis, 2010; Isableu et al., 2010; Isableu, Ohlmann, Cremieuz, & Amblard, 1998; Ji, Peng, & Nisbett, 2000; Willey & Jackson, 2014). When the RFT was first introduced, educational psychologists studied many correlates of these large individual differences among healthy participants. The scientific consensus at the time was that this test was indicative of a preferred educational learning style and interpersonal behaviors, such that those who were most influenced by the tilt of the frame were “visual field dependent” individuals and those who were least influenced by the tilt of the frame were “visual field independent” individuals (Rittschof, 2010; H. A. Witkin, Moore, Goodenough, & Cox, 1977; Herman A. Witkin & Goodenough, 1977). In many of these early studies, participants were split into these two categories using the median visual SV estimate and then measured on some other variable that would distinguish them between wholistic and individualistic learning and interpersonal styles. This construct is based on the idea that the tilt of the frame will bias the participant only to the extent that he/she can ignore it to perform the task. The more the tilt influences the estimate, the greater the visual dependence. However, being visually independent suggests that instead of overweighing available visual cues, the participant adapts to the context and more efficiently uses cues based on their reliability. This concept is similar to the idea of

Bayesian cue combination discussed in the previous chapter. Some studies suggest that there may even be cultural effects in the RFT, suggesting that more collectivist cultures such as in East Asia may have greater errors on the RFT than Western cultures. They suggest that East Asian cultures analyze a visual scene as a whole, rather than individual parts, and thus are more influenced by the tilt in the peripheral frame (Ji et al., 2000).

It was not until recently that visual perception and multisensory researchers began to use this in order to study how individuals utilize varying kinesthetic and visual cues for movement and navigation (Crajé, Van Der Kamp, & Steenbergen, 2008; Isableu et al., 2010; Isableu, Ohlmann, Crémieux, & Amblard, 2003; Isableu et al., 1998). These differences in how people may be weighing different sensory cues can have drastic consequences. For example, the degree to which people are visually field dependent have been shown correlated with the likelihood of being fearful of heights (Coelho & Wallis, 2010; Willey & Jackson, 2014), exhibiting different propensities for vertigo and motion sickness (Cian, Ohlmann, Ceyte, Gresty, & Golding, 2011; Isableu et al., 2010), adopting different navigational styles (Boccia, Piccardi, D'Alessandro, Nori, & Guariglia, 2017). The bias created from the tilted frame has also been correlated with the susceptibility of other visual illusions (Willey & Jackson, 2014). These studies can help to shed light on how modalities involved in estimates of subjective vertical may calibrate their weighting system through learning. Isableu, Ohlmann, Cremieuz, & Amblard (1998) was the one of the first to show that a tilted frame not only biases SV but also induces a postural tilt towards the frame tilt. This effect was only significant within in those who are deemed as visually dependent than those who are visually independent. Coelho & Wallis (2010) also found that participants' postural sway during a static stance was highly correlated with the amount of bias found during the RFT. They also found these two variables to be significant predictors of severity of a fear of falling. Willey & Jackson (2014) found that those who had greater errors towards the tilt of the frame tended to have greater overestimations of vertical distances in addition to have a greater fear of falling from a height than those who had fewer SV biases. Other studies have found that performance on the RFT also varied by sports training. In one study, researchers found that a group of Judoists and dancers showed no effect of head tilt on the RFT while untrained participants did (Golomer, Guillou, Testa, Lecoq, & Ohlmann, 2005). They also found that the expert groups tended to be more visually dependent while the untrained participants were more visually independent. Another study investigated performance on the RFT in tennis players compared to gymnasts and found that while tennis players tended to be more visually dependent, gymnasts tended to be more visually independent (Guillot, Collet, & Dittmar, 2004). Given the types of bodily movements that each must perform, it may make sense that gymnasts have learned to be less reliant on visual information in relation to vestibular and proprioceptive cues (Croix, Chollet, & Thouvarecq, 2010). These studies seem to suggest that training or perceptual learning may be able to reduce reliance on visual cues when visual cues are not helpful in determining vertical.

One disorder in particular that could benefit from better understanding of visual, vestibular, and proprioceptive integration is cervical dystonia. Cervical dystonia is a movement disorder in which patients have painful contractions of neck muscles. Mostly thought to be a disorder affecting the basal ganglia, sensory integration at the level of the cerebellum have also been implicated (Avanzino & Fiorio, 2014; Avanzino, Tinazzi, Ionta, & Fiorio, 2015; Bove, Brichetto, Abbruzzese, Marchese, & Schieppati, 2004; De Pauw et al., 2017). The weighting of sensory systems, which work together to control head movement, varies among patients with cervical dystonia, while also uniquely contributing to each patient's symptoms. In particular, patients with cervical dystonia have marked issues with proprioception. If there is an indirect neck proprioceptive pathway that aids in the detection of vertical through head and body estimates, we could be able to identify if this was the source of maladaptive integration in cervical dystonia patients. This individual variation in pathophysiology may limit the ability to determine effectiveness of a PT treatment across a group of cervical dystonia patients but opens the door for individualized sensory-based physical therapies for each patient. This is an area of great interest for future research.

Along these lines in future studies, we wish to address the many potential consequences of overreliance on visual cues and other possible maladaptive visual and vestibular cue weighting. Given the studies that suggest a disruption of vestibular functioning in the presence of a visual tilt bias, it would be assumed that reducing the reliance on visual information may also result in better static postural stability. The opposite may be tested as well. That is, if we train people to use vestibular cues more effectively in order to detect when there is postural instability, would we also witness a decrease in errors on the RFT and thus a decrease in the reliance on visual information to make the subjective vertical estimate? This aspect of training in order to change the relative weight of cues used in a task has not be previously investigated. Indeed other researchers have paved the way for testing for optimality of SV estimates in the RFT (Alberts et al., 2016; Vingerhoets et al., 2009) based on the reweighting of these cues. Thus, follow-ups to the present study could include how sensory reweighting can be a result of training in one of the relevant sensory modalities to estimating subjective vertical.

APPENDIX A: INFORMATION SHEET FOR VISUAL AND TILT TABLE SV EXPERIMENTS (ORAL CONSENT)

UNIVERSITY OF CALIFORNIA LOS ANGELES

STUDY INFORMATION SHEET

Vestibular, Visual, and Proprioceptive Tilt Perception

Chéla Willey and Zili Liu from the Department of Psychology at the University of California, Los Angeles (UCLA) are conducting a research study.

You were selected as a possible participant in this study because you are at least 18 years old and are enrolled in the Department of Psychology's participant pool. Your participation in this research study is voluntary.

Purpose of the Study

This study seeks to understand how postural and visual cues combine to aid in estimating gravitational vertical.

Participation in the Study

If you volunteer to participate in this study, the researcher will ask you to do the following:

- Determine the orientation of a presented visual stimulus using a virtual reality headset.
- Determine the orientation of your own body while being tilted using a tilting platform.
- Identify pressure differences applied via inflating arm bands.
- Answer a general questionnaire aimed at identifying susceptibility to maladaptive symptoms concerning visual-vestibular integration (e.g. motion sickness, vertigo, etc.). This questionnaire also includes questions regarding mental health, smoking, alcohol consumption, and citizenship of family members

Length of the Study

Participation in this study will take a total of about 2 hours.

Potential Risks or Discomforts

There is a small risk of mild discomfort and motion sickness while in the virtual environment but these effects are short-lived after taking off the headset. The virtual environment used in this study contains low level visual stimuli, reducing the chance of motion sickness greatly. Regardless, scheduled breaks throughout the experiment are included to reduce any risks of motion sickness and general fatigue. However, you are welcome to take a break at any point during the experiment. Please inform the researcher should you feel any motion sickness or if you'd like to take a break outside of the scheduled breaks.

Potential Benefits

You will not directly benefit from your participation in this research. The results of the research may help us to understand how visual and vestibular systems are integrated to produce a sense of the direction of gravity in relation to the body. This research has a wide range of implications, from improving augmented and virtual reality systems to understanding how different rehabilitation therapies might influence perceptual integration. This study can also inform us how individual characteristics such as susceptibility to motion sickness may arise or give rise to visual and vestibular perceptual differences between individuals.

Alternatives to Participation

You have the option of choosing alternatives to participating in this research study to fulfill research participation credit. You have the opportunity to participate in any other research experiment or write a paper on a journal article in order to receive your course credit.

Compensation for Participation

You will receive 1 course credit per hour of participation towards a selected course via the Psychology Department's participant pool.

Privacy and Confidentiality

Any information that is obtained in connection with this study and that can identify you will remain confidential. It will be disclosed only with your permission or as required by law. To maintain confidentiality, we never use identifying information to collect your data. All data will be collected under a non-identifying participant ID number. Your information will only be used in order to grant you credit within the Sona-system.

Rights as a Participant in Research

- You can choose whether or not you want to be in this study, and you may withdraw your consent and discontinue participation at any time.
- Whatever decision you make, there will be no penalty to you, and no loss of benefits to which you were otherwise entitled.
- You may refuse to answer any questions that you do not want to answer and still remain in the study.

Contact Information

- **The research team:**

  If you have any questions, comments or concerns about the research, you can talk to the one of the researchers. Please contact:

  Chéla Willey, PhD Candidate

  cwilley@ucla.edu

  Zili Liu, PhD

  zili@psych.ucla.edu

- **UCLA Office of the Human Research Protection Program (OHRPP):**

If you have questions about your rights as a research subject, or you have concerns or suggestions and you want to talk to someone other than the researchers, you may contact the UCLA OHRPP:

Box 951406

Los Angeles, CA 90095-1406.

(310) 206-2040;

participants@research.ucla.edu

APPENDIX B: SCREENING SCRIPT FOR GVS EXPERIMENTS

UNIVERSITY OF CALIFORNIA, LOS ANGELES

CONSENT SCRIPT TO SCREEN FOR RESEARCH

Study: Subjective Vertical and Tilt Biases

I need to ask you a few questions in order to determine whether you may be eligible for the research. I will ask you about aspects of your medical history in order to ensure that you are eligible for the procedures in this study. So, before I begin I would like to tell you a little bit about the research.

We are interested in looking at the perception of vertical that arises from your visual and balance systems. In order to do this, this study will involve wearing a virtual reality headset to perform a simple discrimination task in which you will determine whether a presented 3D rod is tilted clockwise or counterclockwise from vertical. We may ask you to perform this task in different visual scenarios and during vestibular stimulation. Galvanic Vestibular Stimulation is a method of administering a weak current at very low intensity indirectly to the vestibular nerve through the skin behind your ear. The intensity is comparable to the intensity of a flashlight powered by a 9-volt battery. The stimulator used is widely available to patients to use at home for medicine delivery through the skin. Our use of the stimulator is for research purposes only. The electrodes will be placed directly behind your ears and will remain there throughout the experiment. GVS is considered painless and the procedure is usually well tolerated by our volunteers. The duration and intensity of stimulation are well within the safety criteria limits. This screening does not signify consent to participate in the research described above and is only used to determine eligibility for the study described above.

Would you like to continue with the screening? The screening will take about 1-5 minutes. You may feel uncomfortable answering questions about your personal medical history. You do not have to answer any questions you do not wish to answer and you may stop at any time. Your participation in the screening is voluntary. A decision whether or not to participate in the screening will not affect your relationship with UCLA. You will not directly benefit from the screening.

Your answers will be confidential. No one will know the answers except for the research team. If you are not eligible for this study, your answers will be destroyed. If you are eligible for the study, the general outcome of this screening (yes or no) will be kept with the research record to document your eligibility if you decide to participate and sign the research informed consent form.

Would you like to continue with the screening?

[*If yes, continue with the screening*].

[*If no, thank the person and end conversation*].

Please do not answer the following questions individually. I will ask several questions as a group. When I am done asking the group of questions, you may say "yes" if any of the questions in the group apply.

Here is the first group of questions:

Are you an English speaker?

Do you have normal or corrected-to-normal vision?

[*If YES, continue screening*].

[*If NO, say "Thank you but you are not eligible to participate in this study at this time*."].

Second group of questions:

Do you have any metal implanted in your body other than dental fillings?

Do you, or have you, suffer from a seizure disorder?

Do you have a history of serious head trauma?

Are you or could you possibly be pregnant?

Are you under eighteen years old?

Do you have any active, unstable or untreated medical, second neurological or psychiatric diagnoses?

Have you had electric convulsive therapy within the past 6 months?

[*If person answered "YES" to this group of screening questions, say* Thank you for your time, but you are not eligible to participate in this study at this time]:

[*If person answered "NO" to all screening questions, say "*Thank you for your time, but you are not eligible to participate in this study at this time." *continue with screening*]:

Thank you for answering the screening questions.

In this experiment, you will be asked to stand for periods of up to 10 minutes at a time on a foam mattress, while wearing our study equipment. Out of our last 200+ subjects, we had one episode of fainting. As such, please inform the researcher if you are prone to fainting spells or have a history of fainting in instances of prolonged standing. We will ask you to make sure you have eaten and are hydrated before coming to our study.

Thank you again for your interest in our study and your willingness to answer our questions.

Do you have any questions about the research screening?

You will now be given an informed consent that you should read and understand for deciding to participate. You will be required to sign this informed consent sheet before you participate in any part of this study. Your participation is completely voluntary and you can choose not to participant with no adverse effects.

If you have questions about your rights as a research subject, please call the UCLA Office of Protection of Research Subjects at (310) 825-5344.

APPENDIX C: SIGNED CONSENT FORM FOR GVS EXPERIMENTS

UNIVERSITY OF CALIFORNIA, LOS ANGELES

CONSENT TO PARTICIPATE IN RESEARCH

Study Title: Tilt Bias and Subjective Vertical

Allan Wu, MD and *Zili Lu, PhD* from the departments of Neurology and Psychology at the University of California, Los Angeles (UCLA) are conducting a research study. You were selected as a possible participant in this study because you are a healthy individual with normal or corrected-to-normal vision and possess normal hearing. Your participation in this research study is completely voluntary. Please read the information below and ask questions about anything you do not understand before deciding to participate. You are required to sign this formed consent if you are to participate in this study.

Purpose of the Study

We are interested in understanding how visual cues and standing balance cues interact to determine the perception of the direction of true vertical. Additionally, this study aims to identify individual differences that relate to differential weighting between visual and balance cues.

Procedures

If you volunteer to participate in this study, the researchers will ask you to take part in all the testing sessions that you signed up for, which may be up to three 3-hour sessions on separate days. Long-term follow-up may involve a phone call in 6 to 12 months after completion of initial participation. At each session the investigators may ask you to take part in some or all of the following tasks:

Subjective Vertical Task: You will be asked to put on a virtual reality headset and in a series of trials, you will be asked to determine if the 3D line presented is counterclockwise or clockwise from true vertical. During some of these trials, there will be a surrounding 3D frame that may or may not be rotated. The trials may be performed while standing or lying down (supine) on a memory foam mattress. We may apply vibration to the mattress while either standing or lying supine. We may also ask you to place a vibrating travel neck pillow around your neck during trials. This task can take up to 1 hour to complete all experimental blocks. We have scheduled breaks within the task, however you can take a break at any point during the task.

Galvanic Vestibular Stimulation (GVS): The GVS procedures will be delivered via a 9-volt battery powered direct current stimulator through a pair of two 5 x 7 cm electrodes (saline soaked sponges). The two sponges will be positioned on the bones directly behind your ears. A cloth or rubber cap or strap will be positioned over your head to hold the sponges in place and they will remain there throughout the experiment. We may ask you to perform subjective vertical tasks during stimulation or to maintain standing passively without performing any task. During GVS, you may experience a mild tingling or pricking sensation. The device will be turned on at a very low intensity (maximum of 4 mA). This stimulator is widely bought and used by patients at home to deliver medication through the skin. The use of the stimulator in this experiment is for research purposes only. The duration and intensity of stimulation are well within the safety criteria limits described in the Risk/Benefit Assessment section below.

Questionnaires: You will be asked to fill out a general questionnaire concerning your susceptibility to balance related problems, anxiety around heights and your daily activities. We will also ask you to answer questions concerning how cervical dystonia impacts your cognitive and motor functioning.

Please ask the researchers if you have any questions concerning any procedures involved in this study.

Potential Risks and Discomforts

There are no anticipated physical, psychological, social, legal, or other long-term risks to you in this experiment.

The virtual environment contains low level perceptual cues with all stationary objects (no moving objects) which minimizes risks of motion sickness. There is a small risk of slight discomfort and motion sickness while in the virtual environment but these effects are short-lived after taking off the headset. Scheduled breaks throughout the experiment are included to reduce any risks of motion sickness. However, you are welcome to take a break at any point during the experiment.

The GVS method used in this study has been used in a number of research laboratories worldwide for the last 30-40 years for purposes. Even though this study utilizes safety procedures outlined by the established research and the device manufacturer, the following possible effects may occur:

- Mild tingling: During the initial application of tDCS, the most common reported effect is a mild tingling or burning sensation under the electrodes.
- Redness or skin irritation: After stimulation, it is common to have redness at the site of the electrodes. This effect is short-lived (lasting approximately an hour after stimulation) and can be soothed with application of topical lotion or aloe vera.
- Dizziness, mild nausea or vertigo: During or immediately after stimulation, you may feel mild dizziness or nausea. You can stop or pause the trials at any time or extend the scheduled break periods. You or the researcher may stop the experiment at any time if these symptoms become too severe. Water is available upon request to help alleviate any feelings of motion sickness. If vertigo becomes too severe there is a small chance of vomiting. However, note that stimulation in this study will only occur in 2-3 min intervals, thus drastically reducing the risk of moderate or severe dizziness and nausea.

During this study, you will be asked to wear virtual reality and GVS equipment while standing on foam for up to 10 mins at a time. Due to the increased load of this equipment and nature of standing on the foam mattress, there is a small risk of fainting, particularly if you are prone to such fainting spells. Please inform the researcher if you are concerned with your risk of fainting in this study and if you have a history of fainting. We ask that while standing on the foam please do not lock your knees as this will increase this risk. Our research assistants will reiterate this during the experiment and are trained in recognizing signs of fainting and in basic first aid in the event of a fainting spell. Additionally, we have an on-call medical physician that will medically assess your symptoms in the event of a fainting spell.

To minimize potential risk, you will be asked some questions about you and your family's medical history. You will be excluded from the study if you have any of the following:

- *Any type of metal in your head* (except dental fillings).
- *Any serious or active medical, neurological, or psychiatric illness*.
- *You are or may be pregnant*.
- *Cannot stand stationary for up to 10 minutes without experiencing a fainting spell*

Potential Benefits

You will not directly benefit from your participation in the research. The results of the research may help us to understand how cervical dystonia impacts the use patient's visual and vestibular systems, which may potentially help with new treatments. Additionally, this study can inform us how individual characteristics such as susceptibility to motion sickness may arise or give rise to visual and vestibular perceptual differences between individuals.

Alternatives to participation

Participation is entirely voluntary. You may choose not to participate in this study. You are free to choose another study listed on the Sona-Systems website as an alternative to participating in this study or you have the option of writing a research paper for course credit.

Payment for participation

You will receive 1 course credit per hour for participating towards a participating course.

Privacy and Confidentiality

The researchers will do their best to make sure that your private information is kept confidential. Information about you will be handled as confidentially as possible, but participating in research may involve a loss of privacy and the potential for a breach in confidentiality. Study data will be physically and electronically secured. As with any use of electronic means to store data, there is a risk of breach of data security. It will be disclosed only with your permission or as required by law. Data is de-identified and stored on a University encrypted computer. Paper data will be kept locked in a filing cabinet that only the investigators will have access to.

When the results of the research are published or discussed in conferences, no information will be included that would reveal your identity. Your data will be labeled with an alphanumeric code and stored electronically or in a locked filing cabinet.

Participation and withdrawal

Your participation in this research is VOLUNTARY. If you decide to participate, you are free to withdraw your consent and discontinue participation at any time without consequences of any kind. You may also refuse to answer any questions you do not want to answer and still remain in the study.

Withdrawal of the participation by the investigator

The investigators may withdraw you from participating in this research if circumstances arise which warrant doing so. The investigators will make the decision and let you know if it is not possible for you to continue. The decisions may be made to protect either your health or safety. The investigators may also stop your participation at any moment if they feel that you do not follow the directions of the study and if it might lead to risk for your safety in this research.

If you stop participating because an investigator asks you to (rather than because you have decided on your own to withdraw), you will be paid in proportion to the completed part of the study.

Rights as a Participant in Research

You can choose whether or not you want to be in this study, and you may withdraw your consent and discontinue participation at any time. Whatever decision you make, there will be no penalty to you, and no loss of benefits to which you were otherwise entitled. You are not waiving any legal claims, rights or remedies because of your participation in this research study. If you wish to ask questions about your rights as a research participant or if you wish to voice any problems or concerns you may have about the study to someone other than the researchers, please call the Office of the Human Research Protection Program at (310) 825-5344 or write to Office of the Human Research Protection Program, UCLA, 11000 Kinross Avenue, Suite 102, Box 951694, Los Angeles, CA 90095-1694.

The Research Team: In the event of a research related injury or if you experience an adverse reaction, please immediately contact one of the investigators listed below. If you have any questions or concerns about the research, please feel free to contact the investigators.

Chela Willey, PhD Candidate

cwilley@ucla.edu

Monica Skordilis, MD

Voicemail: 310-206-3426

mskordilis@mednet.ucla.edu

Zili Liu PhD

zili@psych.ucla.edu

Allan Wu, MD

310-206-3356

SIGNATURE OF RESEARCH SUBJECT

I have read the information provided above. I have been given an opportunity to ask questions and all of my questions have been answered to my satisfaction. I have been given a copy of this form, as well as a copy of the Subject's Bill of Rights.

BY SIGNING THIS FORM, I WILLINGLY AGREE TO PARTICIPATE IN THE RESEARCH IT DESCRIBES.

____

Name of Subject

_______________________________________ _____________________________

Signature of Subject or Legal Representative *Date*

SIGNATURE OF INVESTIGATOR

I have explained the research to the subject or his/her legal representative, and answered all of his/her questions. I believe that he/she understands the information described in this document and freely consents to participate.

____

Name of Investigator

_______________________________________ _____________________________

Signature of Investigator *Date (must be the same as subject's)*

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