

Persistent perceptual delay for head movement onset relative to sound onset with and without vision

by

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**Authors Declaration**

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

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## **Abstract**

Knowing when the head moves is crucial information for the central nervous system in order to maintain a veridical representation of the self in the world for perception and action. Our head is constantly in motion during everyday activities, and thus the central nervous system is challenged with determining the relative timing of multisensory events that arise from active movement of the head. The vestibular system plays an important role in the detection of head motion as well as compensatory reflexive behaviours geared to stabilizing the self and the representation of the world. Although the transduction of vestibular signals is very fast, previous studies have found that the perceived onset of an active head movement is delayed when compared to other sensory stimuli such as sound, meaning that head movement onset has to precede a sound by approximately 80ms in order to be perceived as simultaneous. However, this past research has been conducted with participants' eyes closed. Given that most natural head movements occur with input from the visual system, could perceptual delays in head movement onset be the result of removing visual input? In the current study, we set out to examine whether the inclusion of visual information affects the perceived timing of vestibular-auditory stimulus pairs. Participants performed a series of temporal order judgment tasks between their active head movement and an auditory tone presented at various stimulus onset asynchronies. Visual information was either absent (eyes-closed) or present while either maintaining fixation on an earth or head-fixed LED target in the dark or in the light. Our results show that head movement onset has to precede a sound with eyes-closed. The results also suggest that head movement onset must still precede a sound when fixating targets in the dark with a trend for the head having to move with less lead time with visual information and with the VOR active or suppressed. Together, these results suggest perception of head movement onset is persistently delayed and is not fully resolved with full field visual input.

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## 1.0 Introduction

The vestibular system is essential for maintaining postural stability and coordinating self-motion to navigate the environment. It does so by monitoring changes in head movement, as well as detecting the position and orientation of the head in space relative to gravity. The vestibular system is constantly sending signals to the brain, even when the body is at rest on Earth (Angelaki & Cullen, 2008) due to the constant force of gravity. During locomotion, the vestibular system works together with other sensory modalities to properly control the body through expected and unexpected changes in motion. Relying on multiple sensory modalities increases the likelihood for the central nervous system (CNS) to detect the onset and change in motion. Crucially, the CNS must make sense of incoming sensory information that may arrive at different relative times. The main sensory modalities that contribute to this function along with the vestibular system are the somatosensory and visual systems. However, not much information is currently known about how the signals from these different sensory modalities are integrated together and processed in time.

When signals from the sensory modalities arrive to the CNS at different relative times, the brain has to decide whether those signals were the consequence of the same sensory event or not. Are they perceived separately and then integrated together afterwards or is there a specific time frame in which the brain waits to perceive all the signals? If it is the former reason, then during a multisensory event one would expect people to detect and perceive the temporally faster signals consistently before the slower. On the other hand, if it is the latter, then one would expect that even though the temporal processing of some signals are faster than others, they would be detected at the same time. There have been a considerable amount of studies revealing that the temporal processing of tactile, visual and auditory signals has different processing speeds, but can still be perceived as occurring simultaneously during a multisensory event (Barnett-Cowan & Harris, 2009). However, until recently there has been a

lack of research examining how the timing of vestibular information is perceived along with the other senses.

It was found that the perceived onset of head movement from galvanic vestibular stimulation (GVS) (Barnett-Cowan & Harris, 2009), as well as the perceived onset of passive and active head movements (Barnett-Cowan & Harris, 2011) are delayed compared to the onset of a light, a touch, or a sound. This means that the onset of vestibular stimulation needs to occur before the onset of other sensory stimuli in order for the CNS to perceive them as simultaneous. At the same time, there has been extensive research on the modulation of the vestibular system during eye and head movements in primates (Angelaki & Cullen, 2008; Cullen & Roy, 2004; Cullen, 2012). Single cell recordings of vestibular neurons suggest that head movements can significantly attenuate vestibular signals (Brooks & Cullen, 2014; Carriot, Brooks, & Cullen, 2013; Carriot, Jamali, Brooks, & Cullen, 2015; Medrea & Cullen, 2013; Roy & Cullen, 2001, 2004). What these studies have in common is that they are all observed during the generation of head movements, however they were also all conducted without vision or without accounting for visual information being present. The purpose of my thesis is to examine the perceived timing of active head movement onset with and without additional visual information.

## 2.0 Vestibular System and VO Pathway

The vestibular system is made up of three orthogonal semicircular canals, which sense angular acceleration and two otolith organs, which detect linear acceleration (Angelaki & Cullen, 2008; Cullen, 2012). Afferent fibers from these organs send sensory signals to the vestibular nuclei, which in turn projects to neural structures responsible for the control of eye movements, posture, balance, as well as higher level structures for computation of self-motion and body position (Cullen, 2012). The vestibulo-ocular reflex (VOR) is a reflex in which the vestibular system detects movements of the head and changes the direction and amplitude of the eyes in the opposite manner. This reflex is required in order to maintain and stabilize our gaze and our visual environment. What is unique about the vestibular system is that it is notably different from the other senses. It is highly convergent and strongly multimodal, where other sensory and motor signals are constantly integrated with vestibular inputs throughout the cortex (Angelaki & Cullen, 2008). The VOR has been well characterized in primates due to the relatively simple structure. It is comprised of a three neuron arc of vestibular afferent nerves entering the vestibular nuclei, which then project to extraocular motor neurons (Cullen, 2012).

The vestibular nuclei contain three different types of neurons. The majority of VOR neurons are called position-vestibular-pause (PVP) neurons, which are the main contributors to the direct VOR pathway (Cullen, 2012). A second class of VOR neurons called floccular target neurons (FTN) are responsible for the calibration of the VOR and also receive inputs from the flocculus of the cerebellum (Cullen, 2012). The last category of neurons is the vestibular-only (VO) neurons. These neurons do not project to oculomotor structures, but instead project to the spinal cord and higher order cortical structures and contribute to vestibular spinal reflexes for posture and balance, as well as detection of self-motion (Cullen, 2012). One of the main structures along the pathway is the cerebellum, more specifically the rostral fastigial nucleus (rFN), which is known to be the site for vestibular and



proprioceptive integration (Baumann et al., 2014; Brooks & Cullen, 2009; Cullen, Brooks, Jamali, Carriot, & Massot, 2011; Cullen, 2012).

A unique feature of the three-neuron arc for maintaining eye movement stability is that the second-order neurons (PVP, FTN and VO) are also premotor neurons; they directly project to motor neurons (Angelaki & Cullen, 2008). This allows for extremely fast transduction latencies of the vestibular signals. Indeed, Lorente De Nó (1933) found that when stimulating the vestibular nerve, the VOR responded with a latency around 200 ms using recording techniques with poor resolution. More recent work has shown the VOR to operate at a minimum latency of 5 to 6 ms in rhesus monkeys (Huterer & Cullen, 2002). These fast latencies could also be due in part to the kinetics of the hair cells that make up the vestibular system, which have latencies close to 40  $\mu$ s (Corey & Hudspeth, 1979). This makes sense because it is important that such a system is fast in order to maintain perceptual and postural stability. The most common problem in patients with vestibular deficiencies is frequent experiences of vertigo even with the slightest head movements (Cullen, 2012). Based on such rapid processing of vestibular information, it is reasonable to expect that the perception of vestibular stimulation should also be fast.

## 2.1 Slow Vestibular Perception

Contrary to this notion that vestibular stimulation should be fast the perceived timing of vestibular stimulation has been found to be slow. Barnett-Cowan and Harris (2009) measured the difference in reaction times (RTs) between GVS, light, touch and sound stimuli. They found that RTs to GVS were significantly slower by 197 to 241 ms compared to the other stimuli. These results were surprising because of the fast transduction latencies of the vestibular afferents. In addition, people do not perceive each of the individual senses separately, as one would expect with such a large discrepancy in RT. A possible explanation to this could be that there is a neural mechanism that synchronizes sensory signals that are perceived to be from the same event. This notion of a temporal binding window was first suggested by Von der Malsburg in the 1980s and more recently, a similar theory called “simultaneity constancy” by Kopinska and Harris (2004). These theories suggest that asynchronous signals are bound together or the delay between them is compensated for in effort to produce a veridical perception of a single event when the time difference between the signals falls within a temporal binding window.

The RTs here were measured separately, so what if they were presented together? Would they be temporally synchronized and perceived as simultaneous? Using temporal order judgments (TOJs) and synchronicity judgments (SJs), Barnett-Cowan and Harris (2009) revealed that when paired with a light, touch or sound, vestibular stimulation had to precede the other stimuli by approximately 160 ms to be perceived as simultaneous. This was less than the 220 ms predicted by the RT difference, but there was still a significant delay. This suggested a partial compensation to resynchronize the stimuli (Barnett-Cowan & Harris, 2009), however the size of the difference was too great to completely compensate for. Another possible reason suggested by the authors for the inability to completely synchronize the stimuli was because of the “unnatural” nature of the GVS. The reason for using GVS was to avoid any kinesthetic cues, however this form of vestibular stimulation may not have been recognized as a typical

sensory event. Therefore, experiments following this study were conducted to address this issue using whole-body and head-on-body movements as a more natural means of stimulating the vestibular system.

Sanders and colleagues (2011) tested the PSS of participants using slow passive whole-body rotations paired with auditory stimuli and found that vestibular stimulation had to occur roughly 265 (TOJs) and 230 ms (SJs) before the sound. As this value was expressed as a discrimination threshold, when corrected relative to the detection threshold the vestibular stimulation had to occur prior to the sound by 120 ms (Barnett-Cowan, 2013). So it appears that more natural movements allowed the stimuli to be bounded more closely compared to using GVS, but not completely. Conversely, active head movements had an even larger delay compared to passive head movements, possibly due to the efference copy suppressing the availability of the sensory signals. A problem with using head movements is the additional kinesthetic cues associated such as proprioception of the neck muscles. Von Holst and Mittelstaedt (1950) introduced the principal of reafference, in which a copy of the efferent motor command signal can be used to suppress the incoming sensory signal of the resulting movement. The purpose of the efference copy is to allow the nervous system to distinguish externally generated inputs from self-generated motions. However, for the purpose of studying the detection of a movement it is important to examine the difference between an externally produced passive movement and a self-generated active movement. For this reason, Barnett-Cowan and Harris (2011) paired both passive and active head movements with a light, sound or touch stimuli at various stimulus onset asynchronies (SOA). Both TOJ and SJ tasks revealed that for passive head movements, the head must precede the other stimuli by 45 ms, whereas 80 ms lead time was required for active head movements, for the stimuli to be perceived as simultaneous (Barnett-Cowan & Harris 2011). Even when matching the temporal envelope and duration of the sound with the head movement, the PSS remained around 73 ms (Barnett-Cowan, Raeder, & Bühlhoff, 2012). Notably, the use of natural head movements as opposed to

GVS (160 ms) and passive whole body rotations (120 ms) brought the point of subjective simultaneity (PSS) closer to true simultaneity (45-80 ms), however there still remains a significant discrepancy.

## 2.2 Vestibular, Proprioceptive and Visual Cues in Heading Discrimination

One of the key functions of the vestibular system is detecting acceleration of the head. This function is important for people to successfully navigate their environment during everyday activities. Another important sensory modality during self-motion is proprioception and the resulting feedback from the efference copy. When a person performs the motion of walking they are activating their lower body muscles, head movements require the activation of neck muscles and if required, ocular muscles from resulting eye movements. Visual information also contributes to motion detection through movement of objects and the environment, as well as through optic flow, which refers to the pattern of movement of the visual scene experienced during motion. The most common example is when adjacent vehicles start to move while sitting in stationary car, generating an illusory sensation of self-motion known asvection. One of the key differences between the visual and vestibular system in contributing to self-motion is that the vestibular system is signaled by changes in acceleration, whereas the visual system can better detect constant velocity (Berthoz, Pavard, & Young, 1975). Despite these differences, the contributions of vestibular and visual information for the perception of self-motion have yet to be fully characterized. In order to gain a better understanding of the contributions of the vestibular, proprioceptive and visual system during locomotion, studies have been conducted examining the effects of vestibular cues on perceived heading direction. The term heading will be used meaning the estimation of self-motion.

Royden and colleagues (1992) were one of the first to tease apart the effects of proprioceptive cues and visual cues during perceived heading. They had participants pursue a fixation point placed just above the ground horizon, generating horizontal eye movements and translational of the optic flow field of the ground. In a second condition, the fixation dot remained in the center while the flow field reproduced the identical motion on the retinal image, creating a “simulated” eye movement perception. They found that for rotations greater than 1 deg/s, participants were only able to accurately judge their

heading direction in the real eye movement condition. This suggested that people require extra-ocular or efferent information to accurately perceive the direction of their heading.

In a different study, Klatzky and colleagues (1998) had participants conduct a triangle-completion task in which they imagined, watched or physically walked a two segment path with a 90 degree turn in the between and then rotate themselves to face the direction of the origin. Participants were able to accurately update their perceived heading in the walking condition, but failed to do so in the remaining conditions. This study showed that people require proprioceptive and vestibular information in order to update their perceived heading during locomotion and visual information appeared to not be effective at all. Similarly, Bakker and colleagues (1999) reported that kinesthetic information was most crucial for maintaining orientation, followed by vestibular and then visual feedback. However, these studies involved movement of the whole body, so the results may have been biased towards proprioceptive cues due to the demands of the tasks. When examining head movements, there is a lot less proprioceptive information available; therefore, it is possible more emphasis will be placed on the vestibular cues.

The ability to discriminate motion presented visually can be influenced by vestibular and proprioceptive signals. When the head is actively tilted, the perceived direction of remembered moving random dot patterns viewed when the head was straight become deviated towards the tilt of the head (Ruiz-Ruiz & Martinez-Trujillo, 2008). Additionally, when visual information is reduced or unreliable, even more emphasis is placed on vestibular cues when detecting heading direction. Fetsch and colleagues (2009) demonstrated this by manipulating the motion coherence of optic flow patterns while passively translating both monkeys and human participants on a motion platform. They found that both monkeys and humans consistently relied more on vestibular information when the cues were conflicting and this bias increased as visual cue coherence decreased. Butler and colleagues (2010) reported the same results when vestibular and visual optic flow cues were conflicting in a similar heading

discrimination task. The mechanism for this bias has yet to be established, although there has been growing support that it fits a Bayesian optimal integration model for dynamic reweighting of the unimodal sensory cues (Butler, Smith, Campos, & Bühlhoff, 2010; Fetsch, Turner, DeAngelis, & Angelaki, 2009; Karmali, Lim, & Merfeld, 2014; MacNeilage, Banks, Berger, & Bühlhoff, 2007).

Another advantage the vestibular system has over the visual system is the precision of perceived heading. Karmali, Lim and Merfield (2014) demonstrated that the frequency response threshold of vestibular perception was lower than visual thresholds for discriminating roll tilt directions at a frequency greater than 2 Hz. Gu, DeAngelis and Angelaki (2007) also successfully trained rhesus monkeys to report their perceived heading direction and showed that they were able to discriminate differences as small as one to two degrees solely based on inertial motion cues. This is not surprising considering the vestibular system is primarily responsible for detecting changes in acceleration of the head and the sensitivity of the hair cell structures within the otoliths.

These studies maintain that vestibular cues are important for discriminating perceived heading directions and motion, however there has also been evidence to suggest that vestibular information may not be completely reliable. Omni (1996) found that when using a pointing task to indicate perceived heading direction, the variable errors of the vestibular estimates were almost double in comparison to the visual and proprioception conditions. Butler and colleagues (2006) also reported a high uncertainty level with vestibular estimates compared to visual estimates during a perceived heading discrimination task. In addition, the uncertainty in the vestibular condition remained constant for all heading angles, whereas the uncertainty for the visual condition was only high as the heading angle increased. It is interesting as to why the perceived headings based on vestibular cues are inconsistent when it has been shown to be the primary factor in the discrimination tasks. These results were reported under isolated conditions, so it is possible that the vestibular system requires some degree of visual and proprioceptive inputs in order to account for the uncertainty.

In earlier studies, researchers supported the peripheral dominance hypothesis in which peripheral vision had the dominant role for perception and control of self-motion over central vision as it was more ideal for detecting optic flow (Warren & Kurtz, 1992). However, later work examining the motion detection properties of the peripheral field found that it is not any more sensitive to motion or velocity of motion than central vision (Crowell & Banks, 1993; Fahle & Wehrhahn, 1991; Warren & Kurtz, 1992). In fact, Warren and Kurtz (1992) reported that central vision actually yields more accurate heading judgements than peripheral vision considering the higher density of photoreceptors and ganglion cells in the central retinal area. That is not to say that peripheral vision is not necessary still in perceived self-motion. An interesting finding by Berthoz and colleagues (1975) was that heading discrimination during linearvection in the periphery was better for forward motions than backwards. Fahle and Wehrhahn (1991) reported the same result and additionally found that detection of horizontal motion was superior than vertical motion in the peripheral field, while Crowell and Banks (1993) also reported that an observer's ability to judge heading depended on the pattern of the flow rather than the part of the retina stimulated. It was suggested that this bias was due to forward and horizontal motions being more natural and dominant in everyday experiences.

There has been some studies that have reported that visual information is more essential over vestibular input for perception of heading. Ohmi (1996) found that observers do not necessarily need vestibular input in a pointing judgment of heading direction, as long as there is sufficient visual and/or proprioceptive information. MacNeilage and colleagues (2007) reported that in a pitch-acceleration perception task, the availability of visual information helped participants more accurately perceive ambiguous accelerations on a pitched motion platform. Riecke and colleagues (2007) found that visual cues from a well-known natural scene are sufficient to induce spatial updating, regardless of any passive physical movements. In this study, they rotated participants while viewing either a natural scene or an optic flow pattern and then had to point to the location of specific objects in space of a scene viewed



prior to the rotation. The results showed that participants were more accurate in pointing to the remembered locations of the objects when viewing the natural scene during the rotation compared to when they just saw an optic flow pattern. This suggests that in addition to just optic flow, there are some dynamic visual information that is required during rotation of the body, to properly detect and update the orientation of the body in space.

### **2.3 Cue Integration and the MSTd**

The medial superior temporal area (MSTd) is known to be involved with processing visual stimuli and more specifically, it has been linked with analyzing information from optic flow to detect self-motion and rotation (Britten, Van Wezel, & Wezel, 2002; Perrone & Stone, 1998). So this raises the question of how this information is integrated together with vestibular and proprioceptive cues during locomotion. Evidence from primate studies has suggested that the information from both visual and vestibular modalities converges in the MSTd and that it is responsible for the early stages of integration (Gu, Angelaki, & DeAngelis, 2008; Gu, DeAngelis, & Angelaki, 2007; Gu, Watkins, Angelaki, & DeAngelis, 2006). A series of studies by Gu and colleagues (2008, 2007, 2006) showed that the MSTd neurons sensitive to optic flow information also responded during passive movements without visual input during a heading discrimination task. In addition, they found a population of neurons that displayed an improved sensitivity to combined visual and vestibular cue conditions, in which coincided with a greater precision in the discrimination task than in the single cue conditions (Gu et al., 2008). MacNeilage and colleagues (2007) was one of the first to show that heading discrimination improved when both visual and vestibular information was available in human participants. The MSTd has an important role in processing self-motion and it appears that it may be the convergence point for not only visual stimuli but also vestibular information.

### 3.0 Current Study

The purpose of this study is to determine why the perceived timing of vestibular stimulation is delayed and how to reconcile this delay. To do so, we need to further understand the mechanism of how vestibular information is integrated and the factors that are involved in the process. One of those factors is the availability of visual information. Visual cues have an important role in the detection of motion and previous studies comparing active and passive head movements have yet to take into account the effect of vision. There have been studies supporting and opposing the role of vision, suggesting that it may or may not affect the perception of self-motion.

In the previously mentioned studies, the focus was mainly on the contributions of each individual sensory modality. The goal was to create a model that can predict combined cue performances and cues were presented in a conflicting manner to probe how each relative sensory stimuli was integrated. There has been contrasting evidence, some suggesting that vestibular and proprioceptive information are dominant, while others argue the same for visual information. However, these studies did not explore how combined cue conditions could affect actual task performance. There appears to be an advantage to having visual cues in addition to vestibular and proprioceptive information (MacNeilage et al., 2007), although the relationship remains unclear. All that is known is that visual and vestibular information is integrated and processed together in the MSTd (Gu et al., 2008, 2007, 2006), but what role does this have in how people discriminate heading?

Another problem with these heading studies is that visual stimuli were provided through either a monitor display, head mounted display or a projector screen in order to manipulate the dynamics of the visual information. These apparatuses innately have limitations in their technical aspects such as field of view, refresh rate or latency and are presently unable to reproduce natural vision. Additionally, vestibular information was generated through either passive movement using motion platforms or active movements with walking. There was a lack of active movement conditions, in which the vestibular

system was isolated, such as in active head movements. It has been shown that there is a difference between active and passive head movements (Barnett-Cowan & Harris, 2011; Brooks & Cullen, 2014; Carriot et al., 2013; Roy & Cullen, 2001), however these studies were either conducted in the dark or they did not take into account the visual cues that were present. In order to properly assess cue integration, the conditions should be as near as possible to natural experiences to provide information that the sensory systems are accustomed to in normal circumstances.

For these reasons, our goal for the current study is to examine the effects of visual information on the perceived timing of motion generated by an active head movement. Participants performed a temporal order judgement task between the onset of an active head movement and a sound stimulus, in which they were asked to report which stimuli they perceived first (Barnett-Cowan & Harris, 2011). The heading information was provided either through vestibular and proprioceptive information alone (active head movement) or together with varying visual information, including a light emitting diode (LED) that was either viewed in the dark or in the light providing full field of vision. Because active head rotations elicit compensatory eye movements even when the eyes are closed (VOR), we included conditions in which the participants canceled their VOR by fixating on a head-fixed target (light moved with the head) or an earth-fixed target (light in a fixed position) to allow for the compensatory movements, which were both viewed in the dark and light.

In addition to cancelling the VOR, fixating a target that is moving congruently with the head causes the physically stationary environment around the target to move across the retina generating motion blur or smear (Tong, Patel & Bedell, 2006). Tong and colleagues (2005) showed that the degree of perceived motion smear of a laser diode moving in the same direction as a passive head rotation was greater when participants were fixating a head-fixed target compared to an earth-fixed target. Interestingly, they also found that the perceived motion smear of the diode was significantly greater when it was moving in the same direction as the head rotation compared to when it was moving in the

opposite direction while the VOR was suppressed, but in the earth-fixed condition with the VOR active, there was no significant difference. This suggests that when the VOR is suppressed, there is a different mechanism compared to when the VOR is active in order to accurately perceive the motion of objects in the visual environment. In another study by Bedell, Tong and Aydin (2010) found no significant difference in the perceived motion smear between a red diode that moved with or against the direction of visually induced self motion using an optokinetic drum. There was also no significant difference in the extent of perceived motion smear during the induced motion in comparison to when the drum did not move and there was no induced motion. This study further strengthens the role of extra retinal and vestibular signals and suggests that there is a separate component than just visual feedback in the perception of motion for when those signals are involved.

The head movement dynamics of participants' head movements were also measured, since the speed and degree of the head movements were not fully controlled. Barnett-Cowan and Harris (2011) found that peak velocity of the active head movements in their study had a significant negative correlation (slope = -0.18) with the PSS, suggesting that during an intermediate head velocity is when true simultaneity is accurately perceived. A comparable result was found in a following study by Barnett-Cowan and colleagues (2012), with a negative correlation between the peak velocity and PSS (slope = -0.39) when participants made active head movements matching a square- or raised- cosine-shaped auditory envelope. There was also an improvement in the perceived timing of vestibular stimuli when using high velocity head movements (45-80 ms) (Barnett-Cowan & Harris, 2011) compared to slow whole body rotations (120 ms) (Sanders, Chang, Hiss, Uchanski, & Hullar, 2011). These findings suggest that the velocity of the head movement provides an important cue for perceiving the onset of the movement.

We have three main hypotheses for this study. First, we expect to reproduce the findings from Barnett-Cowan and Harris (2011) and confirm that active head movements in the dark need to precede

paired sound stimuli by around 80 ms for them to be perceived as simultaneous. Second, we predict that the inclusion of visual input through the LED target and a full visual scene in the light should improve the perceived timing of the vestibular stimuli relative to the sound. We also predict that by suppressing the VOR in the conditions using a head-fixed target compared to an earth-fixed one, the visual system becomes more sensitive to the motion due to the increased amount of motion smear and we would expect to see performance in the head-fixed conditions closer to zero than the earth-fixed conditions. Lastly, we predict that the just noticeable difference (JND) should be lower in the conditions with the lights on and with the head-fixed target, due to the increased amount of visual information present.

## 4.0 Methods

### 4.0.1 Participants

A total of 19 participants (8 males, 11 females) aged 19 to 25 participated in the study. All participants reported having no auditory, visual or vestibular disorders and gave their informed written consent in accordance with the guidelines of the University of Waterloo Research Ethics Committee. Six of the participants were volunteers, while the remaining participants were remunerated \$10/h for their participation.

### 4.0.2 Apparatus

Head movement was measured using the Chronos Inertial Tracking System (C-ITS 6000) which was mounted on the Chronos Eye Tracking Device (C-ETD) (Chronos Vision GmbH, Berlin, Germany). It consists of two triaxial sensors around each of the three orthogonal axes: one for measurement of linear acceleration and one for angular rate. The measurements were recorded at 400 Hz using the provided online recording software, ETD (Chronos Vision GmbH, Berlin, Germany). The signal from the sensor blocks are connected to a signal conditioning box containing buffer amplifiers with factory-set gain and offset via a 42-pin D subconnector powered by a 5 V power supply unit, which is then connected via a 37 pin connector to analog-to-digital converter (ADC) in a standard IBM compatible PC on Windows XP. Sound stimuli was generated using MathWorks MATLAB (R2015a) on a Dell Precision T1700 PC running Windows 7 Professional and fed into the ADC board on the IBM PC via a 3.5mm stereo auxiliary cable and recorded at 8000 Hz on the software ETD. Target light stimuli were presented on a custom board in which five red light emitting diodes (LEDs) powered by a 120 V power supply unit were mounted in cardinal positions 10 cm apart on a 25.5 cm x 22 cm black wooden board. The board was then mounted onto a wall via Velcro, allowing the height to be adjustable. Another red LED was mounted on a 36.5 cm long rod attached to the front of the frame of the eye-tracking device. Participants inputted their responses on a Sony PlayStation 3 controller that was recorded through MATLAB on the Dell PC.

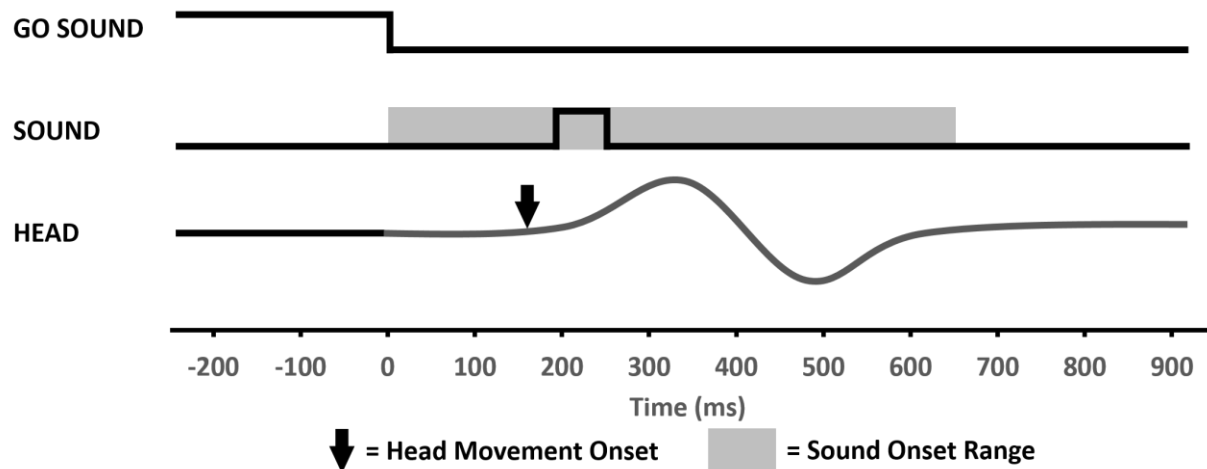
#### 4.0.3 Stimuli

Active head movement was self-generated by participants at the offset of a 200 Hz tone go signal presented through headphones. Participants were instructed to rotate their head to the right and then back at a specified degree and angular velocity and practiced with the experimenter at the beginning of the study. The comparison sound stimulus was a 2000 Hz tone presented for 50 ms at a random generated time between 0 to 650 ms after the offset of the go signal. Visual stimuli consisted of a red LED either attached to the frame of the head mount or the LED board on the wall. Participants were seated so that their eyes were 57 cm in front of the led board and the height of their seat and the board was adjusted so that their eyes were in line with the central LED. In the conditions with the lights on, the room environment in the participants' field of view was also part of the visual stimuli.

#### 4.0.4 Procedure

Participants performed temporal order judgements (TOJ) in which they reported whether the onset of their head movement was before or after the sound stimuli. Each trial was initiated by the onset of the 200 Hz tone. At the offset of the go signal, participants initiated their head movement and because of the reaction time before the head movement commenced, the comparison sound stimuli could be presented before or after the head movement (Barnett-Cowan & Harris, 2011). The onset of the sound stimuli was randomized between 0 to 650 ms relative to the offset of the go signal. An example of a typical trial is illustrated in Figure 1. The duration of the go signal was also randomized so participants could not predict the timing of the offset and preemptively start their head movement. Participants responded by pressing the left (square) button to indicate that their head moved before the sound or the right (circle) button to indicate that their head moved after the sound. The next trial would initiate after participants made their response.





**Figure 1.** Example of a trial. Offset of the go sound signaled participants to start their head movement. The comparison sound stimuli was randomly generated between 0 to 650 ms from the go sound offset and because of the reaction time for the head movement the sound could be presented before or after the movement.

The experiment consisted of five conditions in a block design with 110 trials within each block. Each block took approximately 10 minutes to complete and there were five minute breaks in between each block. In the vestibular and proprioceptive condition (eyes closed), participants performed the task with their eyes closed and in the dark. In the head-fixed LED conditions, participants completed the task while maintaining their fixation on the target in the dark (head-fixed dark) and in the light (head-fixed light). They also performed the task while maintaining fixation on the wall-mounted LED in the dark (earth-fixed dark) and in the light (earth-fixed light). The order of the conditions across participants was randomized.

#### 4.0.5 Data Analysis

Statistical data was analyzed using MATLAB, SigmaPlot 12.5 and JASP version 0.7.5.6. One participant was excluded from the data analyses due to the inability to follow the task instructions. The angular velocity of the head movement was recorded in Volts and then converted into deg/s using

the provided formula (Eq. 1) from the factory calibrations. Onset of head movement was defined as occurring 5 ms before the velocity of the head was greater than three standard deviations from the average head velocity sampled 100 ms before and after the trial onset. Trials in which the head movement onset was less than 100 ms or greater than 1000 ms from the go signal offset were removed. Sound recording was down sampled from 8000Hz to 400Hz to match the head movement recording and graphed overlapping with the head velocity. Go signal onset, offset and sound offset were determined using an algorithm which traced along the signal for changes in the signal and marked them on the graph (Figure 2). Stimuli onset asynchronies (SOAs) were determined by calculating the difference between the head movement onset and the sound onset relative to the trial onset, with a negative SOA meaning that participants judged the head moved prior to the sound. A three parameter Gaussian function (Eq. 2) was fitted to the SOA data with the participants' responses, with the inflection points of the cumulative Gaussians ( $x_0$ ) taken as the point of subjective simultaneity (PSS) (Figure 3) and the slope of the function as the JND (Barnett-Cowan & Harris, 2011).

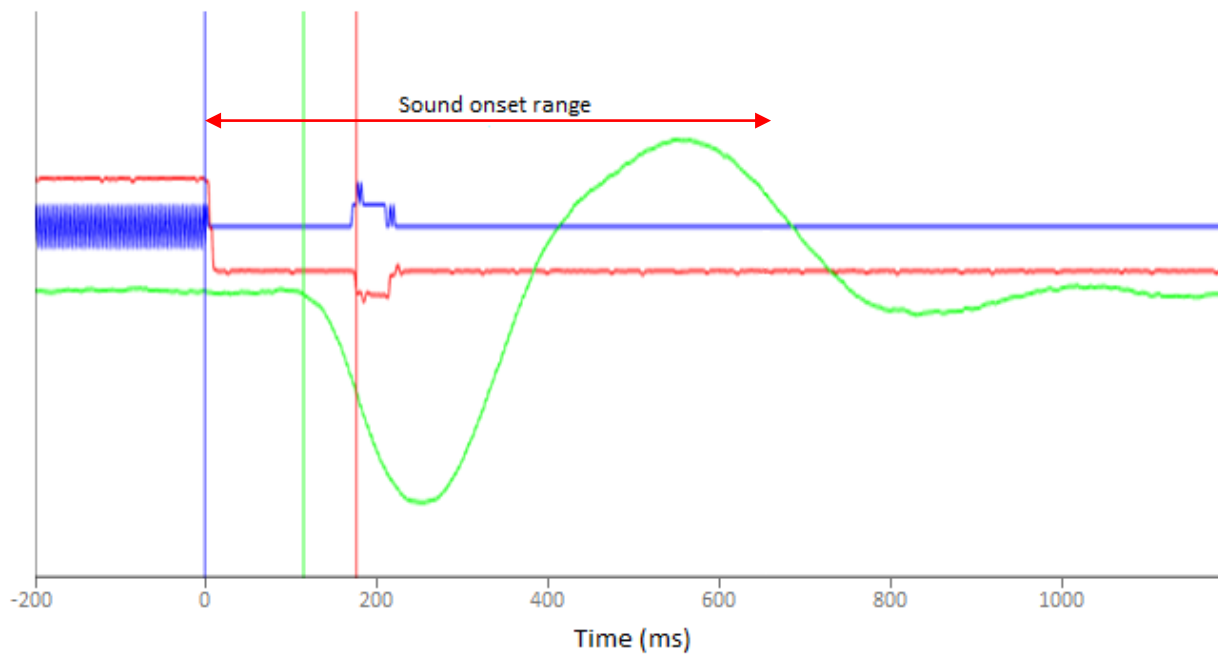
$$y = 207.28x + 1.4235 \quad (1)$$

$$y = \frac{a}{1 + e^{-\left(\frac{x - x_0}{b}\right)}} \quad (2)$$

For the first hypothesis, a one-sample t-test was conducted comparing the average PSS of the condition with the eyes closed and the previous finding of -80 ms from Barnett-Cowan and Harris (2011), to replicate their finding that the head onset has to occur before the paired sound stimuli to be perceived as simultaneous. For the second and third hypothesis, a one-way repeated measures ANOVA was conducted comparing the average PSS between the five conditions, as well as paired sample t-tests comparing each condition with the eyes closed condition, as we expected to find the largest difference between the eyes closed and head-fixed light condition. Additionally, a two-way repeated measures ANOVA was conducted to test for any interactions or main effects of just one of the manipulations of

the room lighting or fixation target. Similarly, for the last hypothesis a one-way repeated measures and paired sample t-tests were conducted comparing the average JND of the five conditions.

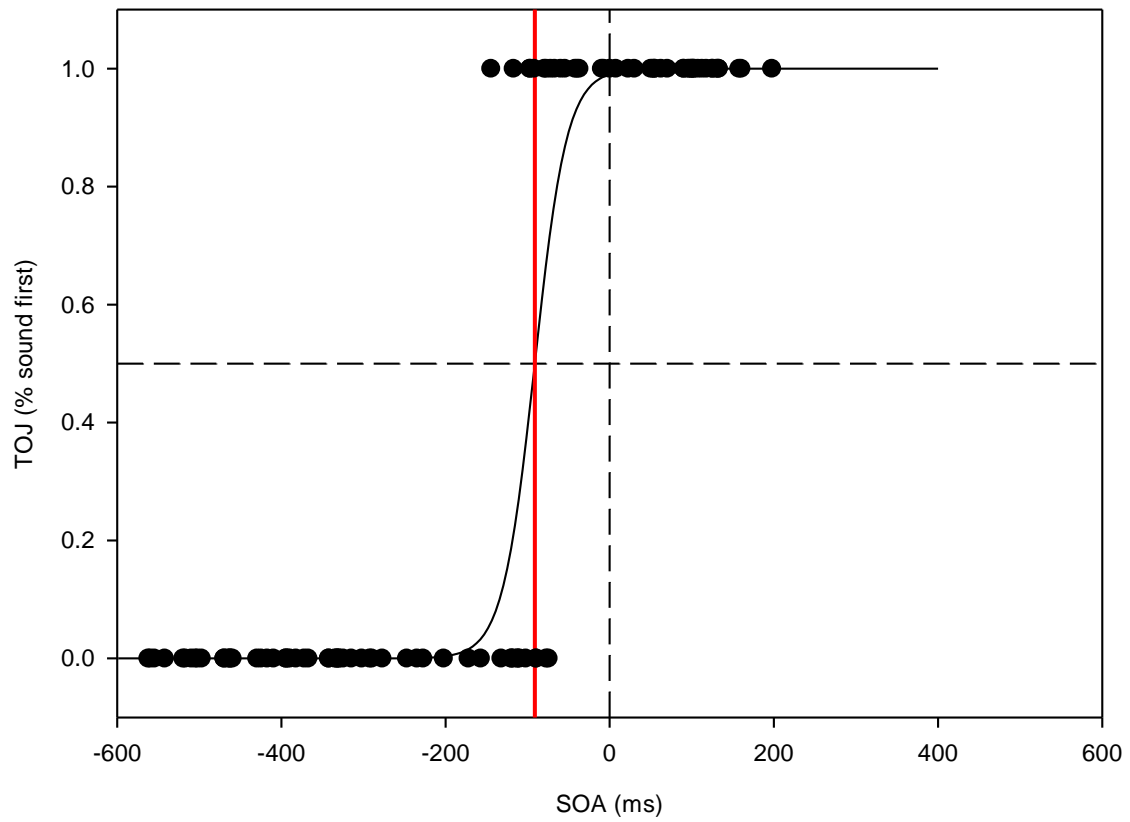
For the head movement dynamics, the angular velocity data was integrated to find the position and derived to find the acceleration of the head, which were then plotted along time. The plots were analyzed using MATLAB to identify the peak velocity, position, acceleration of every trial, as well as the time to reach each respective peak relative to the onset of each trial. The values were then tested for significant using paired sample t-test between the each manipulation and the eyes closed condition, as we expected the head-fixed light condition to have the largest difference similar to what we predicted with the PSS. A repeated measures ANOVA was also conducted to test for a main effect across conditions and a one-way ANCOVA was used to test covariance with the PSS.



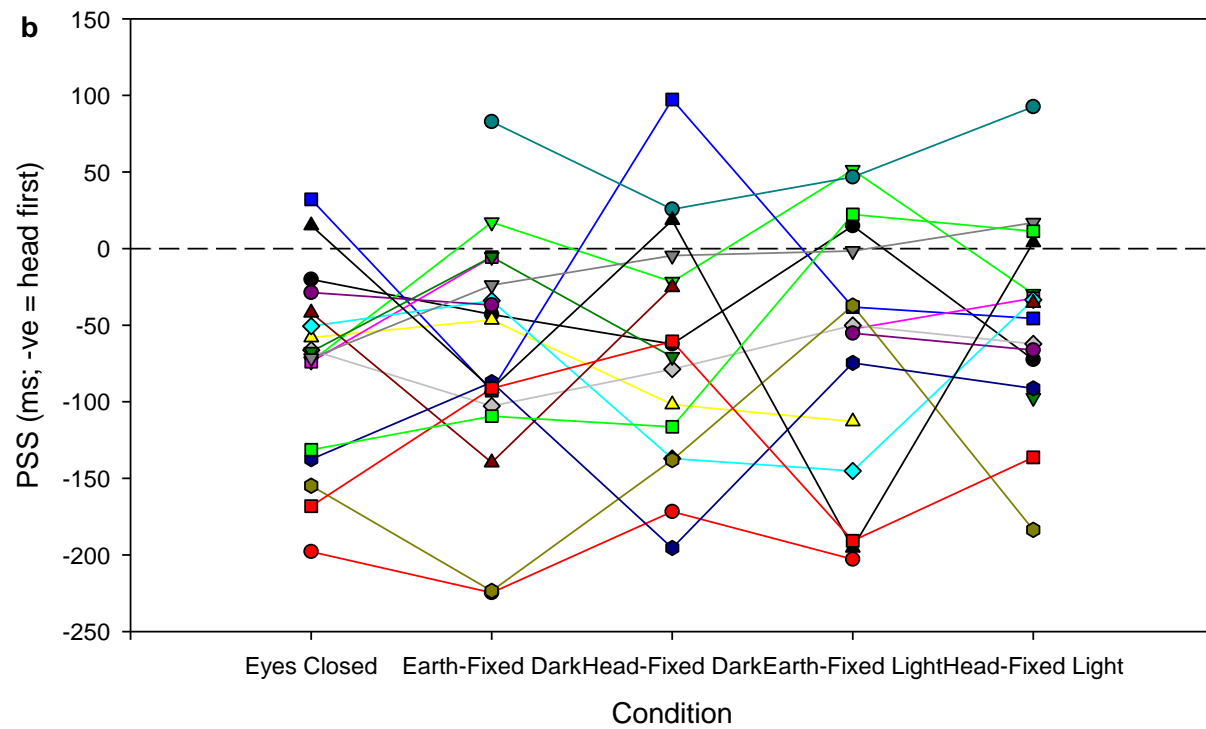
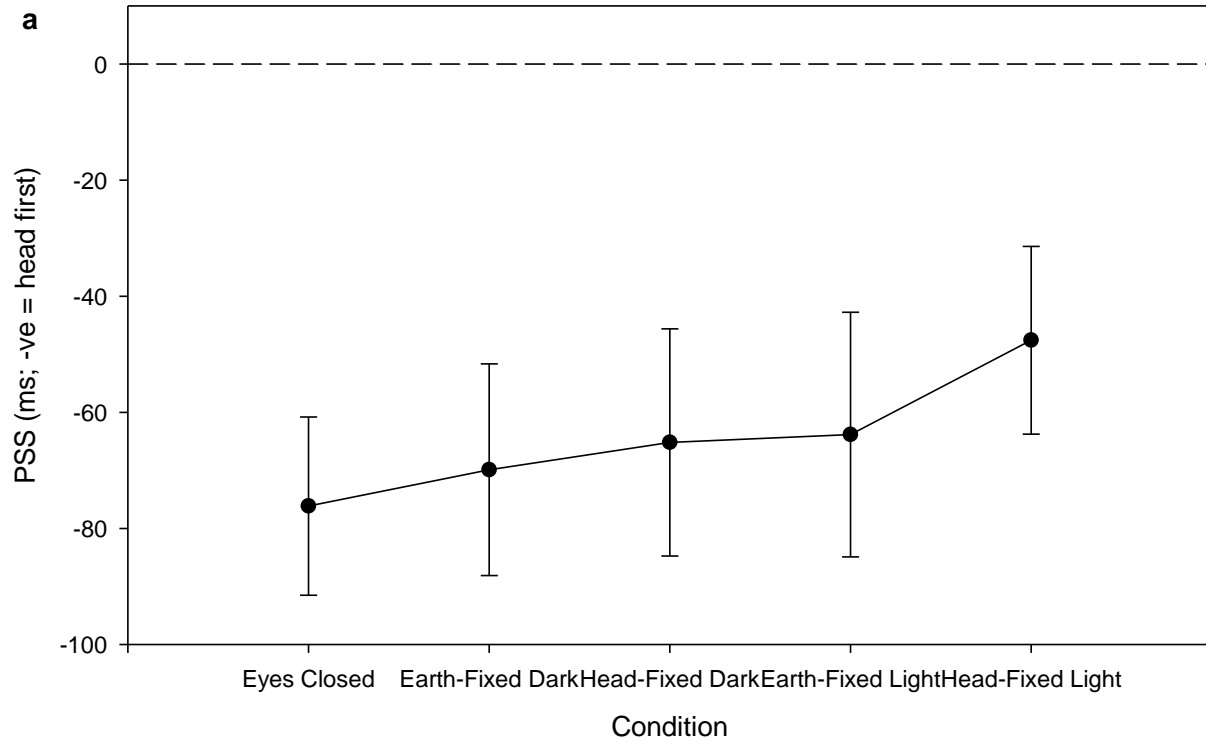
**Figure 2.** Example of a trial analysis. The blue trace represents the trial onset signal and sound onset, although the red trace was used as the true indicator of the sound onset because it was recorded in sync with the head movement, which is represented by the green trace. Sound stimuli onset can vary from 0 to 650 ms from the trial signal offset. The y-axis is arbitrary.

#### 4.1 Results

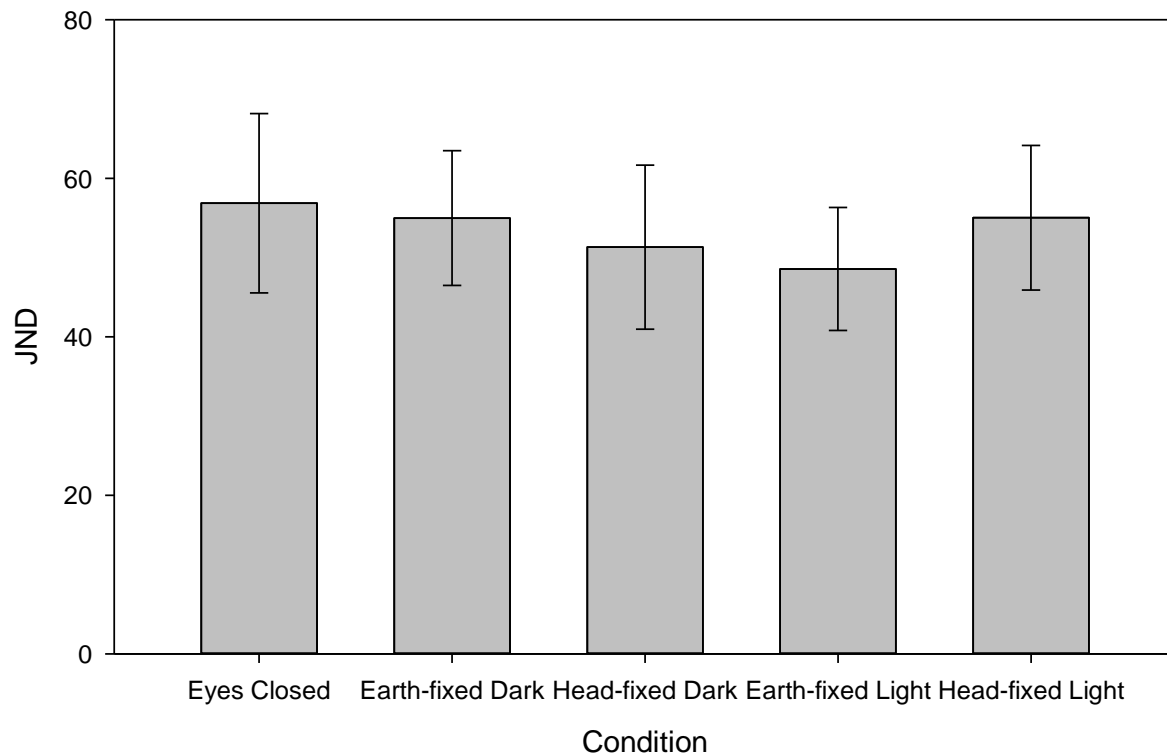
There was a total of 3.15% data loss due to head movement onset outside of the specified range of 100 to 1000 ms or signal detection error. In the eyes closed condition, the average PSS was -76.15 ms (SD = 63.28),  $t(16) = 4.96$ ,  $p < 0.001$ , meaning that the onset of head movement had to precede the comparison sound stimuli by 76.15 ms in order for participants to perceive them as simultaneous events. One sample t-tests were also conducted for the remaining conditions showing significant differences from zero: earth-fixed dark (M=-69.88, SD = 77.37),  $t(17) = 3.83$ ,  $p = 0.001$ , earth-fixed light (M = -63.83, SD = 84.30),  $t(15) = 3.03$ ,  $p = 0.008$ , head-fixed dark (M = -65.18, SD = 78.25),  $t(15) = 3.33$ ,  $p = 0.005$  and head-fixed light (M = -47.58, SD = 64.69),  $t(15) = 2.94$ ,  $p = 0.01$ . These average PSS means for each condition are plotted in Figure 4a and the raw data from each individual is shown in Figure 4b. Compared to the finding of Barnett-Cowan and Harris (2011) of -80 ms, a one sample t-test showed no significant difference  $t(16) = 0.25$ ,  $p = 0.805$ , confirming our first hypothesis in replicating their findings that the perceived timing of the onset of head movement is delayed when compared to a paired sound stimulus with the eyes closed.



**Figure 3.** Sample figure of TOJ data of one condition from one participant. An SOA of 0 ms represents true simultaneity highlighted by the dashed-line, while the PSS of the participant is highlighted by the red line. A positive SOA represents the sound occurring first, whereas a negative SOA for the head occurring first.



**Figure 4 a.** Average PSS data for each condition with standard error bars. A PSS value of zero represents true simultaneity of the stimuli. **b.** Individual average PSS data across each condition.



**Figure 5.** Average JND data for each condition with standard error bars. There were no significant differences between the conditions, meaning the manipulation did not affect the participants’ precision in the task.

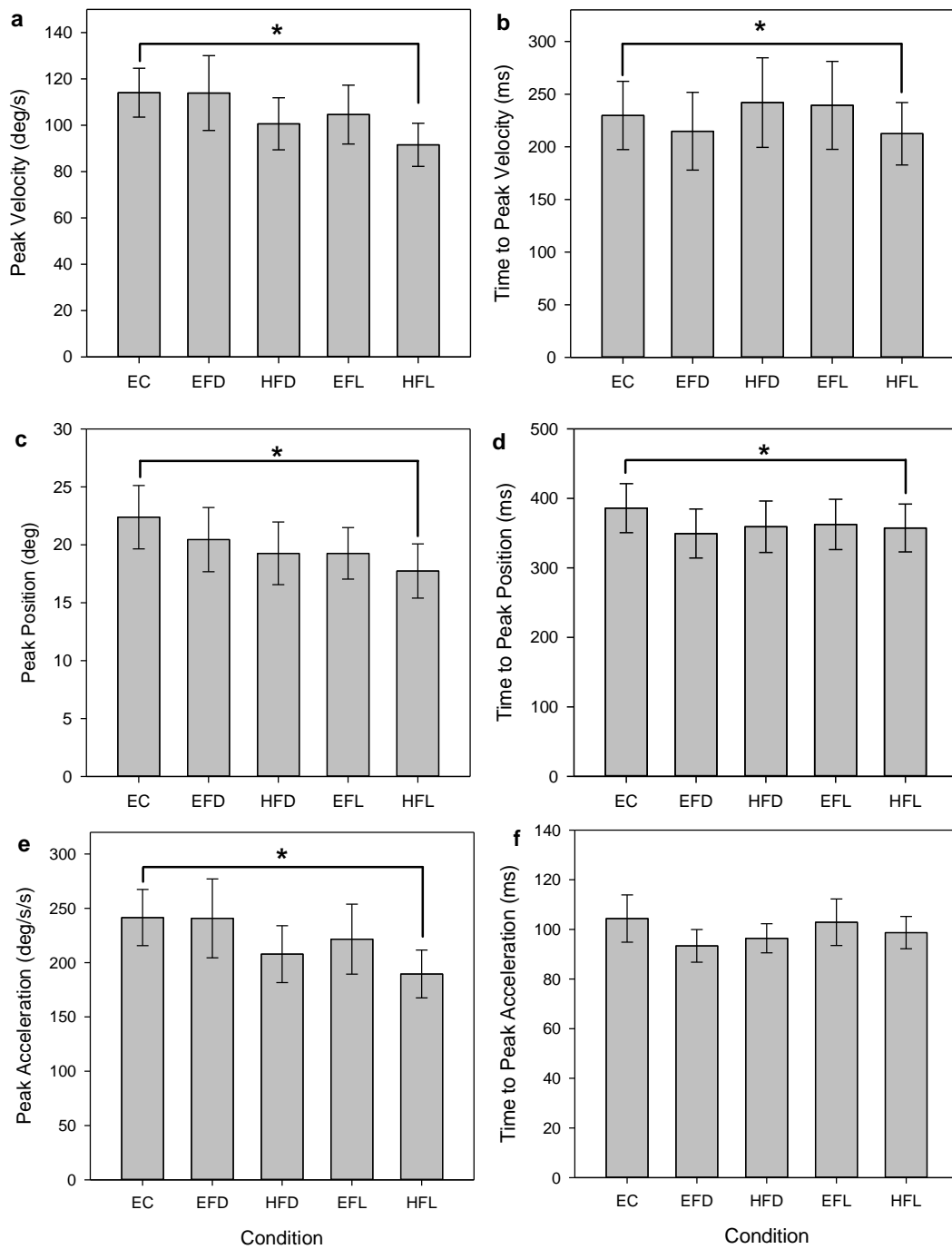
For our second and third hypothesis, we compared the average PSS between all the conditions. Paired-sample t-tests revealed that there were no significant mean differences for each condition compared to the eyes closed condition: earth-fixed dark ( $M = -2.72$ ,  $SE = 16.28$ ),  $t(16) = 0.17$ ,  $p = 0.87$ , earth-fixed light ( $M = -7.82$ ,  $SE = 24.43$ ),  $t(14) = 0.32$ ,  $p = 0.75$ , head-fixed dark ( $M = -8.22$ ,  $SE = 13.48$ ),  $t(14) = 0.61$ ,  $p = 0.55$  and head-fixed light ( $M = -12.31$ ,  $SE = 14.65$ ),  $t(14) = 0.84$ ,  $p = 0.42$ . For the ANOVA, there was a loss of 7.78% of the conditions due to the missing data and in order to get a proper psychometric fit, these missing values were replaced with the average value of the corresponding condition. A one-way repeated measures ANOVA showed no significant main effect across all five conditions,  $F(4,68) = 0.68$ ,  $p = 0.61$  and a post hoc analysis using Tukey’s procedure showed no

significant mean differences between any pair of conditions. Similarly for the JND, there was no significant differences in the paired t-tests and no significant main effect across all five conditions using a one-way repeated measure ANOVA,  $F(4,68) = 0.26, p = 0.91$  and no significant mean differences were found in the post hoc tests, meaning the participants precision did not differ between conditions (Figure 5). Lastly, a two-way repeated measure ANOVA revealed no significant main effect of whether the room light was on or off,  $F(1,17) = 0.91, p = 0.35$ , or whether the target was earth-fixed or head-fixed,  $F(1,17) = 0.53, p = 0.48$ , as well as no significant interaction between the two factors  $F(1,17) = 0.19, p = 0.67$ . Taken together, these results indicate that there was no difference in the perceived timing between whether the LED target was earth-fixed or head-fixed and whether it was viewed in the light or in the dark.

For the head movement dynamics, paired sample t-tests did show significant mean differences between the eyes closed and head-fixed light conditions in peak velocity ( $M = 22.81, SE = 8.43$ ),  $t(14) = 2.70, p = 0.017$  (Figure 6a), time to reach peak velocity ( $M = 27.57, SE = 11.75$ ),  $t(14) = 2.37, p = 0.034$  (Figure 6b), peak position ( $M = 5.32, SE = 1.63$ ),  $t(14) = 3.26, p = 0.006$  (Figure 6c), time to reach peak position ( $M = 44.74, SE = 16.68$ ),  $t(14) = 2.68, p = 0.018$  (Figure 6d) and peak acceleration ( $M = 49.29, SE = 17.16$ ),  $t(14) = 2.87, p = 0.012$  (Figure 6e). There was a significant difference in a one-way repeated measures ANOVA between all five conditions in peak acceleration,  $F(4,68) = 3.46, p = 0.012$ . However, the same analysis for the remaining properties revealed no significant differences: peak velocity,  $F(4,68) = 2.46, p = 0.054$ , time to reach peak velocity,  $F(4,68) = 0.97, p = 0.43$ , peak position,  $F(4,68) = 1.63, p = 0.087$ , time to reach peak position,  $F(4,68) = 1.32, p = 0.27$ , and time to reach peak acceleration,  $F(4,68) = 0.57, p = 0.68$ .

Furthermore, a one way ANCOVA was conducted testing for significance between the average PSS of each condition with each of the head movement parameters as covariates. There were no significant differences between the PSS depending on the peak velocity,  $F(4,73) = 0.34, p = 0.85$ , time to





**Figure 6.** Average head movement dynamics with standard error bars for each condition and significant differences from paired sample t-tests indicated **a.** Average peak velocity **b.** Average time to reach peak velocity **c.** Average peak position **d.** Average time to reach peak position **e.** Average peak acceleration **f.** Average time to reach peak acceleration.

reach peak velocity,  $F(4,69) = 0.18$ ,  $p = 0.95$ , peak position,  $F(4,69) = 0.16$ ,  $p = 0.96$ , time to peak position,  $F(4,69) = 0.20$ ,  $p = 0.94$ , peak acceleration,  $F(4,69) = 0.64$ ,  $p = 0.63$  and time to reach peak acceleration,  $F(4,69) = 0.38$ ,  $p = 0.82$ . These findings indicated that we were unable to explain the lack of difference in PSS using the head movement parameters and confirmed that there was no significant difference in the perceived timing of the head movements between the conditions.

## 5.0 Discussion

In the present study, we investigated the perceived timing of an active head movement with the inclusion of varying visual input. We were able to successfully reproduce the findings from Barnett-Cowan and Harris (2011) that an active head movement compared to a paired sound stimulus is delayed by around 80 ms. Contrary to our predictions, the results showed no significant differences between whether the LED target was viewed in the dark or in the light. Additionally, the placement of the LED target did not influence the perceived timing, as there were no significant differences between the conditions in which the LED was earth-fixed or head-fixed. None of the conditions were significantly different from when the eyes were closed, suggesting that visual input had no influence on the perceived timing. Lastly, there was no difference in the participants' precision in the task between the conditions.

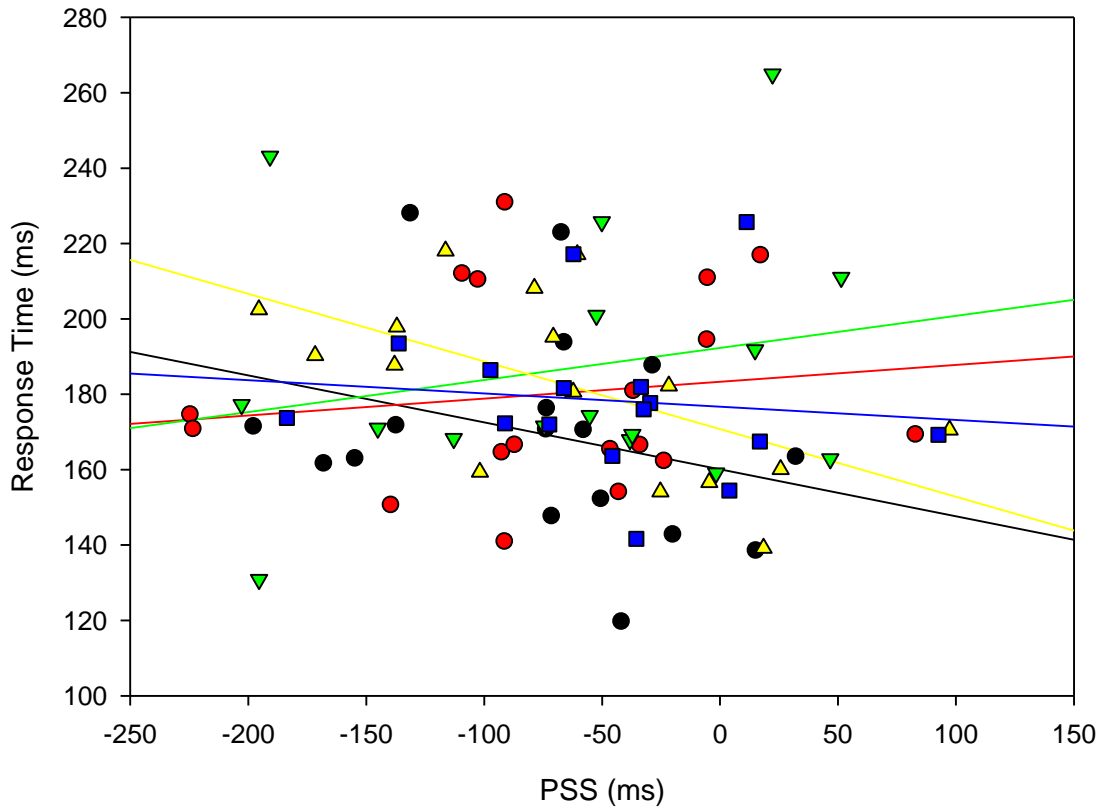
Although there were no significant differences in all the conditions, the PSS was still far from zero, meaning that there was a delay present in the perceived timing of active head movements. We originally hypothesized that during VOR suppression, the visual system becomes more sensitive to the increased amount of motion smear and vision having a greater role in detecting the perceived onset of the motion, then we would expect to see performance in the head-fixed conditions closer to zero than the earth-fixed conditions. Instead, there were no significant differences between the two conditions. This result is similar to previous findings in primates, where there were also no differences between fixating an earth-fixed target and a target that moved with its head during passive whole-body rotations (Roy & Cullen, 2004) and passive head rotations in the dark (Gu et al., 2007). These findings indicate that the cancelling of the VOR and signals from the ocular muscles have no effect in determining head motion. However, we did observe a trend where the head-fixed conditions were closer to zero, although we were unable to determine the exact relationship due to the large amount of variability. This suggests

that there may have been an effect from the inclusion of vision, but it was buried under the large fluctuations between participants.

One possible explanation to the variability could be differences in head movement velocity between individuals, as it has been shown that the PSS is correlated with peak velocity (Barnett-Cowan & Harris, 2011) and time to reach peak velocity (Barnett-Cowan et al., 2012). However, in this study there was no significant main effect of peak velocity or time to reach peak velocity, so we are unable to explain the variability using these factors. Additionally, there were no significant main effects of peak position, time to peak position and time to peak acceleration. There was however, a significant main effect of peak acceleration between conditions and paired t-test showed significant mean differences between the eyes closed and the head-fixed light conditions for peak velocity, time to peak velocity, peak position, time to peak position and peak acceleration. This further strengthened the trend that we observed with the PSS and the idea that there might have been a difference underneath the variance, but further PSS analyses using the head movement parameters as covariates did not reveal any significant differences.

Additionally, we examined the response times of participants' head movements as a possible factor for the variance or PSS. There was a positive trend across the conditions, with the lowest average response time in the eyes closed condition (170.1 ms) to the highest in the head-fixed light condition (205.3 ms), however this difference was not statistically significant. We also performed a linear regression with the response time plotted as a function of the PSS (Figure 7), however there were no significant results as well. This poses as a limitation as there is a lot of variation between participants, as seen in Figure 7 and it is difficult to determine the relationship between the response time and PSS without being able to control for the way in which participants move their head. Another important limiting factor that could have a role is attention. If participants were distracted from the go signal offset or comparison sound stimuli onset it could have greatly influenced their head movements and

subsequent responses to those trials. We also observed that closer to the end of the experiment, the participants' head movements were slower and to a lesser degree. Future studies should try to account for these factors and control the participants' head movements.



**Figure 7.** Linear regression of head movement response time plotted against PSS. Each point represents the average of one individual participant. The black trace represents the eyes closed condition, red trace for earth-fixed dark, green trace for earth-fixed light, yellow for head-fixed dark and blue is for the head-fixed light condition.

Another possible explanation as to why visual input had no affect could be the reweighting of sensory cues in this particular task. It was previously reviewed that there is a fast growing support for a reweighting model of unimodal sensory cues during head discrimination tasks (Butler, Smith, Campos, & Bühlhoff, 2010; Fetsch, Turner, DeAngelis, & Angelaki, 2009; Karmali, Lim, & Merfeld, 2014; MacNeilage, Banks, Berger, & Bühlhoff, 2007). In a majority of these studies, they reported that vestibular and

proprioceptive information tend to dominate the visual input throughout a range of passive and active motions. It may be that in our task the visual information is being out weighed, thus regardless of whether the participant is viewing the target in the light or in the dark the visual input becomes suppressed. This could explain why we did not observe any difference between the conditions with visual input and with the eyes closed.

It is perplexing that visual input would be ignored when it is commonly paired with active movements in everyday activities. One reason could be that in this particular task, the vestibular and proprioceptive input is sufficient in determining the motion of the head. However, if this was the case then why do we find this 80 ms delay in the perceived timing? The cancellation of the reafferent signal along with the attenuation of VO neuron (Brooks & Cullen, 2014; Carriot et al., 2013; Cullen, 2012; Medrea & Cullen, 2013; Roy & Cullen, 2001, 2004) could be one possible mechanism, as there is no advantage for the CNS to perceive the consequence of an expected motion over unexpected stimuli. Barnett-Cowan and Harris (2011) included passive head movements in their study and found that the perceived timing was better than during active head movements, but it was still significantly delayed. Additionally, it has been shown that there is a 133 ms vestibular phase error threshold relative to visual motion under virtual reality (Grant & Lee, 2007). There have also been reports that the vestibular system is not completely reliable during perceived heading discrimination with high levels of uncertainty (J. Butler, Smith, Beykirch, & Bühlhoff, 2006; Ohmi, 1996). Indeed, we observed in our results that there was a high degree of variability in every condition. Although we are not certain of the factors that are responsible for the variability, the reliability of the vestibular and proprioceptive systems could be one of the factors.

The response of VO neurons in rhesus monkeys during active gaze shifts (combined eye and head movement) were on average attenuated by 70% compared to passive whole body rotations and passive head on body rotations (Roy & Cullen, 2001). They also examined whether the VO neurons

would still respond to passive movements that occurred while the monkey was generating active head movements and found that the neurons would still reliably encode the passive motions. Even though the responses from the active movements were suppressed, they were not entirely cancelled or there is a different pathway that detects unexpected perturbations. To ensure that the neurons were not just responding to neck afferent activation, Roy and Cullen (2001) also passively rotated the monkeys' body under a restrained head and the VO neurons were not suppressed, meaning the cancellation is not due to the input from the neck muscles. They also demonstrated that the knowledge of the self-generated movement was not responsible for the attenuation of the VO neurons through a novel task in which the monkeys steered their head and body on a turntable. Taken together, this indicated that a motor command of an active head movement or an efference copy was specifically required in order for the attenuation to occur.

In a follow up study, Roy and Cullen (2004) further characterized the attenuation of the VO neurons during active head movements. They confirmed that passive movement of the body under a restrained head did not affect neural responses and that neuron sensitivities were reduced during active gaze shifts. However, they also found that generation of a neck motor command while the head was restrained did not reduce the activity of the neurons. This contradicted their previous hypothesis that a motor command or efference copy of the neck muscles was required to attenuate the response of the vestibular neurons. Instead, they discovered that in order for the activity to be reduced, the actual activation of the neck proprioceptors had to match an internal model of the expected sensory consequences of the head movement (Roy & Cullen, 2004). They showed this by passively rotating the monkeys' body in the opposite direction of its active head movement, causing the neck motor command and resulting proprioceptive activation to match. Brooks and Cullen (2014) successfully reproduced this finding and also further characterized this effect by adding a torque to perturb the monkeys' head movements to have both active and passive head movements concurrently and found that neurons

robustly encoded both movements when there was a discrepancy between the actual and expected proprioceptive feedback. They also reported for the first time that not only were the VO neurons attenuated for active head movements (73% reduction), but also for active whole body rotations (71%).

Since then, similar findings have also been reported with vestibular stimulation of the otolith organs during translations. Carriot and colleagues (2013) found that VO neurons were significantly attenuated by about 76% during active head translations compared to passive ones. Similarly, they found that passive translation of the body with the head restrained did not contribute to the cancellation of the signal and neither did neck motor commands without the resulting proprioceptive consequences. In a different study by Medrea and Cullen (2013), they reported vestibular neurons in mice encoded passive translation linearly, meaning the neurons modulation was predicted by the linear sum of its sensitivity of vestibular and proprioceptive stimuli when applied in isolation. However, during self-generated motions, the neuronal responses were attenuated and less than what the linear model predicted. Carriot and colleagues (2015) reported the exact same findings, but in rhesus monkeys and not only for translational movements but for rotations as well. They also found an overall 70% reduction of activity in the VO neurons during both active types of movement consistent with previous findings (Carriot et al., 2013; Roy & Cullen, 2001). These studies provide strong evidence for a cancellation or suppression of vestibular neuron activity during active motions. Furthermore, the similarities in the degree of attenuation suggests that there is a common mechanism.

Another possible reason why visual input had no effect could be that the visual information that was presented was irrelevant. There have been studies showing the importance of visual input during heading discrimination tasks (MacNeilage et al., 2007; Ohmi, 1996; Riecke, Cunningham, & Bühlhoff, 2007), so it has a role under specific circumstances. It may be that certain visual scene dynamics are required for the task we used and the visual information that we provided was irrelevant in this context. With the proper visual dynamics to match the given task, the visual input could gain more weight and



improve the timing perception. There has also been evidence suggesting that there is no difference in the ability to detect motion and discriminate heading direction in the central or peripheral vision (Crowell & Banks, 1993; Tynan & Sekuler, 1982; Warren & Kurtz, 1992). This could potentially explain why there was no difference between viewing the LED target in the light or in the dark, if all that was required to precisely detect the motion was the LED in the central fixation.

Lastly, the lack of affect from the inclusion of visual information may provide some insight as to the location in the CNS where active head movements are perceived. The two leading sites that are hypothesized to integrate vestibular information are the rostral fastigial nucleus (rFN) and the medial superior temporal area (MSTd). The integration of vestibular and proprioceptive information has been highly linked to a population of neurons in the cerebellum, the rostral fastigial nucleus (rFN) as it has been known to be the site for receiving inputs from the vestibular nuclei and contributing to the generation of vestibulospinal reflexes (Baumann et al., 2014; Brooks & Cullen, 2009; Cullen et al., 2011; Cullen, 2012). However, few have actually measured activity of these neurons and how they respond to head and body motions until recently. Brooks and Cullen (2009) were one of the first to discover that the neurons can be divided into two classes: unimodal and bimodal neurons. They found that unimodal neurons only responded to vestibular input from head motion and bimodal neurons responded to the activation of neck proprioceptive input from rotation of the body under a stationary head and also combined passive head and body rotations.

To further characterize the activity of the neurons during voluntary self-motion, Brooks and colleagues (2015) monitored the response of the unimodal neurons during active head movements in rhesus monkeys. They reported that compared to passive motions, the sensitivity of the rFN neurons were attenuated by around 70% during active motion, consistent with reports in the VO neuron (Carriot et al., 2013, 2015; Roy & Cullen, 2001). However, when an unexpected load was applied to the active head movement, leading to the expected proprioceptive outcome to not be produced, there was a spike

in neuron activity. As the monkeys learned and adjusted to the torque, the activity diminished and spiked again when the load was unexpectedly removed (Brooks, Carriot, & Cullen, 2015). This indicated that the rFN neurons robustly encoded reafferent sensory input when there is a discrepancy between expected and resulting motor outcome or unexpected movements. These findings are in agreement with those found with the VO neuron, in which an attenuation of the signal only occurs when the active motion matches the resulting motor outcome and provides further evidence for the link between two areas. They also suggest that the rFN is highly involved in encoding vestibular and proprioceptive inputs, although further research is required to determine how the information is integrated. It remains unclear whether the rFN is directly responsible for controlling the cancellation signal or it may just act as a relay center for other neural correlates.

The rFN region has been shown to encode vestibular and neck proprioceptive information and has been directly linked to the VO neurons (Brooks et al., 2015; Brooks & Cullen, 2009), while the MSTd area has been identified as a site for visual and vestibular stimuli integration (Gu et al., 2008, 2007, 2006; MacNeilage et al., 2007). Since visual information does not have an effect on the perceived active head movements, this suggests that the rFN may likely be the region responsible for encoding the motion. It also suggests that the site for perceiving the information is along the pathway of the rFN and further research could explore neural correlates of these neurons to determine the exact location.

## 6.0 Conclusion

This experiment showed that there were no significant differences in the perceived onset of an active head movement between whether the eyes were closed or open in the dark and in the light. Additionally, there were no differences between whether the participants were fixating an earth-fixed target and activating the VOR or suppressing the VOR by fixating a head-fixed target. There was a large amount of variability between participants and an observed trend that suggested there may have been an effect, although using the differences in head movement parameters were not successful in explaining the trend or variance. We have discussed some alternative explanations as to why the addition of visual information had no effect, but it is still unknown whether the large variability was due to the experimental conditions or just individual differences. Future studies could aim to use more visually enriching environments or manipulating the movement of the visual scene using virtual reality for example, to try to tease apart the possible underlying mechanism of the presence of visual feedback.

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