Perceived Timing of Active Head Movements at Different Speeds

by

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Abstract

The central nervous system must determine which sensory events occur at the same time. Actively moving the head corresponds with large changes in the relationship between the observer and the environment, sensorimotor processing, and spatiotemporal perception. Numerous studies have shown that head movement onset must precede the onset of other sensory events in order to be perceived as simultaneous, indicating that head movement perception is slow. In addition, active head movement perception has been shown to be dependent on head movement velocity in that head movement perception is slower when the head moves faster. However, these findings were obtained between-subjects, so they can only be interpreted as participants who move their head faster than other participants require the head to move even earlier than comparison stimuli to be perceived as simultaneous. Previous findings cannot address the question of whether active head movement perception changes at higher speeds. The present study used a within-subjects design to measure the point of subjective simultaneity (PSS) between active head movement speeds and a comparison sound stimulus to properly characterize the correlation between the velocity and perception of head movement onset. Our results clearly show that i) head movement perception is faster when the head moves faster within-subjects, ii) active head movement onset must still precede the onset of other sensory events (Average PSS: -123 to -52 ms) in order to be perceived as occurring simultaneously even at the fastest speeds (Average peak velocity: 76° /s to 257° /s). We conclude that head movement perception is slow, but that this delay is minimized with increased speed.

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Chapter 1

Introduction

This section contains a brief, targeted literature review relevant to the sensory processing of the perceived timing of active head movements, details past studies on which the present study was based on, and outlines the present study objectives and hypotheses.

1.1 Overview

To create an accurate representation of the world, the central nervous system (CNS) processes incoming signals from different sensory modalities and determines how the information from these senses relate to one another. The ability to bind sensory information accurately in time is crucial for the CNS to make correct decisions about our environment and our movements in it. Since a single external event can stimulate multiple sensory modalities at different absolute times, the CNS must distinguish whether these stimuli originated from the same or separate events. Actively moving the head corresponds with large changes in the relationship between the observer and the environment, sensorimotor processing, and spatiotemporal perception. While quickly detecting the onset of head movement is crucial for reflexive behaviour and rapidly updating the representation of the world around us, past research suggests that perceptual awareness of active head movement onset is slower than passive movement of the head, as well as slower than comparison stimuli such as light, touch or sound [6, 7]

1.2 Perceived Timing of Sensory Information

Time relativity is not just unique to the world surrounding us. Our minds too view time as relative and our perception of time depends on many factors. The brain must compensate for processing time differences so as to create a veridical representation of the world, despite the differences in the timing of the individual stimuli. Different forms of energy travel at different speeds. For example, light travels faster than sound, so for a sensory event that includes both light and sound, the light will reach the eyes faster than sound will reach the ears. Furthermore, different sensory modalities have different transduction rates due to the unique properties of each sensory system. Hair cells in the auditory and vestibular system have very fast latencies of 40μs [22]. Photoreceptors, on the other hand, have transduction latencies that are far slower, at 15-93ms [57]. The CNS must also take into account the differences in axonal length between sensory receptors. A tactile stimulation on the foot will reach the CNS later than a tactile stimulation on the face [45]. A perception of true simultaneity despite these timing differences is called "simultaneity constancy" [55]. Exact temporal alignment is not necessary for the CNS to judge two events as simultaneous [37]. As long as the two stimuli fall within a specific window of time, they can still be perceived as simultaneous. The range of asynchronies considered as synchronous is defined as the temporal binding window (TBW). Two common ways of testing perceptual latencies are temporal order judgement (TOJ) tasks and simultaneity judgement (SJ) tasks. In temporal order judgement tasks, a participant is presented with two stimuli at different stimulus onset asynchronies (SOAs) and must then determine which stimulus came first [70]. By fitting psychometric functions to the probability of one stimulus appearing first as a function of the SOA, two indicators of performance are obtained: the point of subjective simultaneity (PSS), which is the SOA at which the participants perceives two stimuli as simultaneous, and the just noticeable difference (JND), which is defined as the minimum amount of time between two stimuli needed for the participant to judge the correct sequential order and which notes the participants sensitivity [46]. In SJ tasks, the participant is presented with stimuli at different SOAs and must then determine whether the stimuli were simultaneous or not [82]. Typically, a Gaussian curve is fitted to the responses, where the PSS is found at the point at which the participant is most likely to respond that the stimuli were simultaneous (i.e., the peak of the Gaussian), and the JND is the standard deviation of the Gaussian. Nevertheless, differences exist between these two tasks, and they may lead to different parameter estimates [60].

One large determinant of whether two stimuli will be bound together in time or be treated as separate events is their spatial and temporal proximity [32]. Other stimulus properties such as the duration [12], intensity [34] and stimulus envelope shape [50] have also been shown to affect timing perception of multisensory events. Longer stimulus durations, for example, shift PSS values to a common attractor value, and Boenke et al. [12] suggest that longer durations may stabilize the effect that bias towards one modality could have. Stimuli that have rising onsets and falling offsets are perceived to occur earlier than square shaped envelope stimuli [50]. Note that stimulus intensity is of particular interest for the purpose of this thesis and thus will be reviewed in greater detail in a later section. Lastly, perceived timing is highly dependent on cognitive factors such as attention, which may affect the perceived timing of multisensory events in the order of 17ms - 121ms [79]. Titchener [84] was the first to note the role of attention on the perceived timing of sensory events, and many studies have since confirmed it (for a review see [79]). Coined the law of prior entry, Titchener stated that attended stimuli come to consciousness faster than stimuli which we do not attend to [84]. Priming will make a stimulus more salient, and cause prior entry of that stimulus into awareness [83]. This demonstrates the importance of instructing participants to be equally attentive to both stimuli. Taken together, these results show that the perceived timing of sensory events is relative and can change depending on multiple factors.

1.3 Neuroanatomy of the Vestibular, Proprioceptive and Auditory Systems

Your sense of head position in space comes principally from three distinct sources of information that must be integrated in your brain: your vestibular system, your somatosensory - specifically your proprioceptive system, and your visual system. When you move your head, you engage all these systems, and it is important to understand the neuroanatomy underlying these systems in order to understand how they are integrated in the CNS. Although the sensory receptors that make up these systems are varied, all of these systems converge in the vestibular nuclei in the brain, the inputs to which are shown in Figure 1.1 and are further reviewed in Cullen [24]. The vestibular nuclei, which is at the first stage of central processing of vestibular signals, distinguishes itself by its highly multimodal nature, combining information from the vestibular organs, vision, neck proprioceptors, cutaneous somatosensory receptors, brainstem, cerebellum, and cortex [24]. Importantly, some of the cortical projections from the vestibular nucleus become important for the conscious perception of self-motion and decision making [24]. Of these cortical projections, the parieto-insular vestibular cortex is thought to be the most important in the perception of self-movement, spatial orientation, and body representation [24]. The following sections will detail the inputs to the vestibular nuclei for both the vestibular system and neck pro-

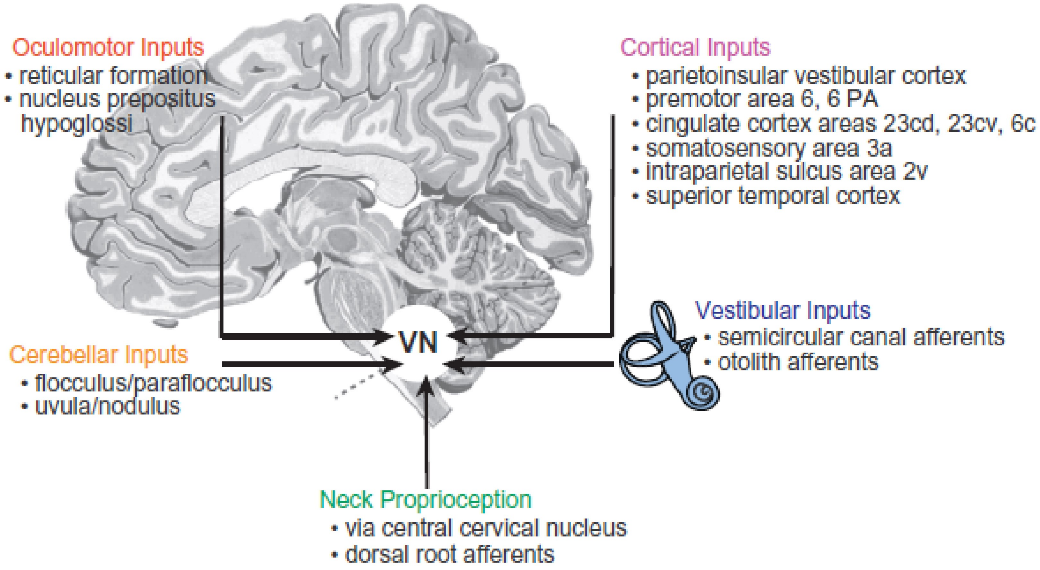

Figure 1.1: Inputs to the vestibular nucleus
This figure taken from [24] describes the inputs to the vestibular nuclei from sensory systems and other brain areas.

prioception as well as the higher brain areas which the vestibular nucleus projects to. Since the participants in our study conducted the experiment with their eyes closed, a review of the visual system is not included. Though visual information is available in natural head movements, it has been shown that visual information does not seem to change the perceived timing of an active head movement [20]. Although sound is used in our study, the auditory system is not reviewed here as the sound serves only as a comparison stimulus. It is chosen as a comparison stimulus because of the similarity of its sensory receptors with the sensory receptors of the vestibular system - both consist of hair cells.

1.3.1 Vestibular System

The vestibular system is essential for functions ranging from the perception of self-motion and spatial orientation, to the motor coordination for maintaining balance and posture [2]. Your peripheral vestibular apparatus consists of 5 organs located inside the membranous labyrinth which itself is inside the bony labyrinth: the utricle and the saccule, together known as the otolith organs, and the lateral, superior, and posterior semicircular ducts,

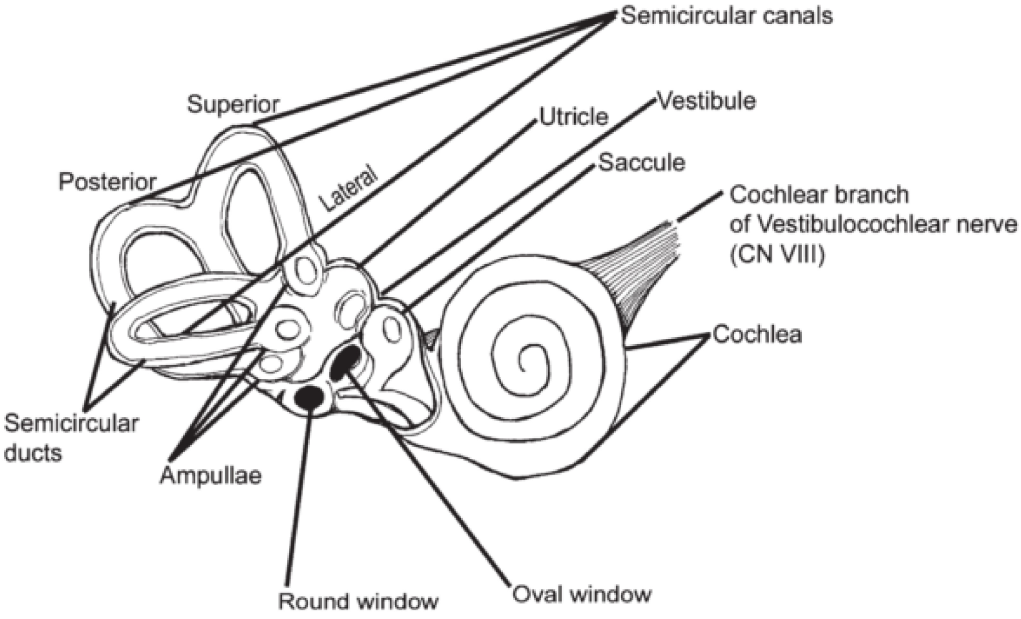

Figure 1.2: Anatomy of the bony and membranous labyrinth.
This figure is taken from [54] and shows the anatomy of the inner ear, including the vestibular system

known collectively as the semicircular canals. As seen in Figure 1.2, the utricle and saccule are located inside an oval cavity called the vestibule, whereas the semicircular ducts are located inside the semicircular canals. The otholith organs detect gravitational acceleration, and are therefore linear acceleration sensors [36]. While the utricle responds to motion in the horizontal plane, the saccule will sense motion in the vertical plane [54]. The semicircular canals, which are situated at right angles to each other, detect angular accelerations, or rotation [66].

Both types of neuroepithelium of the vestibular system, the macula of the utricle and saccule and the crista ampullaris of the semicircular canals, consist of mechanoreceptors called hair cells which respond to changes in head movement (for a review see [33]). There is a low frequency resting discharge in all of the organs, which either increases or decreases when a head movement occurs [39]. As reviewed in Khan [54], when head motion occurs, the hair cells shift, causing mechanical opening or closing of the transduction channel depending on the direction of the head movement. When the head moves in one direction, hair cells cause the opening of the transduction channel, leading to an influx of K^+ which then causes a depolarization of the Ca^{2+} channels at the base of the hair cell. This calcium influx causes neurotransmitter release into the synapses, and the afferent vestibular nerve fibres respond by increasing their firing rate. When the head moves in the other direction, the opposite occurs, with less K^+ influx, a hyperpolarization of C^{2+}, less neurotransmitter release, and a decrease in the firing rate of the afferent vestibular nerve.

The stimulus that acts on the semicircular canals is one of angular acceleration yet the neural output is the velocity of rotation. This is due to the increase in viscous properties of the contained fluid due to the small size of the canal [29]. This becomes relevant in later sections when discussing the perceived timing of vestibular stimulation.

After the stimulus reaches the vestibular organs, it is transduced by the vestibular nerve afferents. The vestibular nerve afferents are grouped based on the regularity of their resting discharge, where regular units have a lower variability in interspike intervals than irregular units [40]. The vestibular organs receive efferent input from vestibular efferent neurons which are located near the abducens nucleus in the brainstem, which may increase the sensitivity of the resting discharge of vestibular afferents. [39]. In high velocity rotations in primates, the vestibular afferents are modulated by the efferents, however, the role of this vestibular pathway is not clear [71]. The vestibular afferents travel via the vestiulocochlear nerve to reach the vestibular nuclei in the medulla [41]. The vestibular nuclei are subdivided into the superior (SVN), lateral (LVN), medial (MVN) and inferior (IVN) vestibular nuclei, and the minor e and γ group [24]. Horizontal and vertical semicircular canal afferents end in the MVN and SVN respectively, utricle afferents end in the IVN with projections being sent to the other three nuclei, and saccule fibers end in the LVN and IVN [17]. Furthermore, the MVN is important in coordinating the vestibuloocular reflex, which will be discussed in more detail later, and the vestibular spinal reflex [54]. Each of the vestibular nuclei has efferent connections to the other vestibular nuclei [41]. In addition to the direct vestibular afferent information it receives, the vestibular nuclei also receives input from the spinal cord, the visual system, and the cerebellum which provide it with extravestibular cues [41]. These extravestibular cues help the vestibular nucleus distinguish between different types of movements. For example, an active movement of the head and a passive rotation of the whole body will elicit similar responses in the vestibular organs, so the vestibular organs alone cannot distinguish these movements. With the addition of proprioceptive input or visual input, the vestibular nuclei knows whether only the head, or the whole body moved [64].

Our study involves moving the head along the yaw rotation. Head movement along the yaw rotation primarily engages the horizontal semicircular canal and the utricle, which are transduced to the MVN, and the IVN respectively. In monkeys, neurons that are sensitive to passive yaw rotations were found in the rostral MVN and ventro LVN [19, 25]. Neurons sensitive to pitch and roll were found in the SVN and MVN and the γ group [31].

The vestibular nuclei sends projections to the reticular and spinal centres, which are important for movement, the flocculo-nodular lobe of the cerebellum, and the thalamus. Of these, the flocculo-nodular lobe, also known as the vestibulocerebellum, is the primary recipient of vestibular nuclei afferent projections, both first and second order [86]. The vestibulocerebellum is divided into five main regions which receive vestibular input: the nodulus and ventral uvula (lobules X and IX), the flocculus and ventral paraflocculus, the oculomotor vermis of the posterior lob, (lobules VI and VII), lobules IV of the anterior lobe, and the deep cerebellar nuclei [24]. Each area plays a different role in processing vestibular information. Of these, three areas are especially relevant in the context of our study. The nodulus/uvula is connected bilaterally to the vestibular nuclei and plays a role in computing inertial motion [87]. Since our study assesses the temporal processing of an active head movement, it is likely that this area is involved. Lobules I to IV of the anterior lobe respond to both vestibular and proprioceptive signals [24]. The deep cerebellar nuclei receives primary and secondary vestibular neurons, and input from the cerebellar vermis [24]. About half of the neurons in the rostral fastigial nucleus, which is the most medial of the deep cerebellar nuclei, are responsive to both vestibular and proprioceptive input [16]. Since we look at active head movements, which involves the integration of vestibular and proprioceptive signals, these last two areas of the vestibullocerebellum become relevant in the discussion of our results.

Just like with other sensory systems, signals from the vestibular system pass through the thalamus before reaching the cortex (for a review see [59]). In an EEG study in the human cortex, stimulation of the vestibular nerve caused a response in five distinct cortical zones (prefrontal/frontal, ipsilateral temperoparietal, anterior supplementary motor area, contralateral parietal) within 6ms in human participants. These fast responses are trisynaptic, reaching the cortex after first synapsing at the vestibular nuclei, and then the thalamus. [30]. Temporal electrodes had a mean latency to onset of response at 3.5-6ms whereas frontal electrodes had a mean latency of 6-7ms. The mean latency to peak response was approximately 10ms in all electrodes, and significantly earlier in temporal electrodes (9.5ms) than for frontal (mean 10.7ms). Since the earliest response is seen in five different cortical areas within the same time frame, processing of vestibular information likely happens in parallel, which suggests that there is no distinct primary vestibular cortex which then distributes the vestibular signals to association areas, like in the auditory or visual system. Neurophysiological studies have shown vestibular related activity in area 2v of the intraparietal sulcus, area 3a of the sulcus centralis, the ventral intraparietal area, the medial superior temporal area, and the parietoinsular vestibular cortex (PIVC) [24]. However, the exact location of the human vestibular cortex is not fully resolved [59].

An activation likelihood estimation meta-analysis by Lopez [58] reviewed activation foci in 16 neuroimaging studies, and found that activations were mainly located in the bilateral insula, retroinsular cortex, inferior parietal lobule, superior temporal gyrus, the caudal part of the anterior cingulate gyrus, and the precuneus. In primates and in humans, the PIVC is generally regarded as the primary vestibular cortex [24]. Stimulation of this area in humans is well known for inducing vestibular sensations [63]. Nevertheless, further studies are needed to understand the mechanisms by which vestibular information is processed in the cortex.

Determining body position and balance involves not just the vestibular system, but also the proprioceptive, the visual system, and feedback from higher brain areas. The vestibular system distinguishes itself from other sensory systems due to its highly multimodal nature. Before the information gets to the cortex it is already integrated at the level of the vestibular nuclei, and it is then further integrated at the cortex [24] The early multimodal interactions that occur in the vestibular nuclei at the first synapse, and the central pathways following the vestibular nuclei are essential for regulating the reflexes involved in gaze and postural control [2]. Likewise, by differentiating active from passive movements, the vestibular nuclei ensure accurate motor control and maintains perceptual stability [24].

1.3.2 Proprioception

Proprioception (from the Latin 'proprius', one's own and 'recipio', to receive) [65] was first coined by Sherrington [75] and was originally defined as the receptors in the deep tissues where the stimulation on that receptor is caused by the organism itself. He referred to proprioception as the afferent information from the peripheral body used for postural regulation, joint stability, and conscious sensations of the muscles [68]. A related term, kinaesthesia, was coined by Bastian [9] as the "sense of movement", both active and passive.

There is considerable debate about the definitions of kinesthesia and proprioception in the present day and what they should include. The terms are used inconsistently, and as of yet, there is no general consensus on these terms [81]. The conventional view has been that kinesthesia refers to two senses: the sense of position and the sense of movement [65]. As reviewed by Han et al. [44], some consider kinesthesia as one of the submodalities of proprioception, whereas others see proprioception as joint position sense whereas kinesthesia is the conscious awareness of joint motion. Some have argued also that since joint movement and joint position are always associated with each other, these terms should be interpreted synonymously [44]. However, since there is evidence that the movement and position sense is processed independently in the CNS, Proske argues that both kinesthesia and proprioception should be restricted for muscle afferents that are involved in conscious sensations and not autonomic unconscious control of movement or posture [65]. Regardless of how proprioception and kinesthesia are defined, the present work involves changing the speed of active head movements where proprioceptive sensory input is provided to the CNS about head movement.

The vestibular system alone cannot distinguish whether only the head or the whole body is moving. The proprioceptors of the neck provide an important extravestibular cue, which helps the CNS encode body position in space [26]. The proprioceptor are muscle spindles and the golgi tendon organs, mechanoreceptors which are found in the fleshy part of musculotendinous tissue [67]. The former detect changes in the length of a muscle and the latter detect changes in muscle tension. Banks [4] showed that the greatest abundance of muscle spindles were found in the axial muscles (including neck muscles and those muscles that control head position) whereas the smallest abundance was found in the muscles of the shoulder girdle by fitting a regression of the logarithm of spindle number against the logarithm of muscle mass for different regional groups of muscles. This higher proportion of muscle spindles in the muscles controlling head position underscores their importance in providing necessary information about head movements, which has multiple degrees of freedom, relative to the trunk and eliciting the cervico-colic reflex for body posture and head stability [64]. Indeed, studies using neck muscle vibration have shown that neck proprioceptors affect human balance and self-motion perception as a whole [64].

Convergence of vestibular signals and neck proprioceptors have been investigated in the vestibular nuclei [1], the cerebellar vermis [61] the fastigial nucleus of the cerebellum [15], and the parieto insular vestibular cortex [76]. Based on the work of Anastasopoulos [1], the vestibular nucleus is a likely candidate for the integration of vestibular and proprioceptive signals. Here, half of the neurons in the caudal part of the vestibular nucleus in a cat that respond to horizontal semicircular canal stimulation also respond to stimulation of neck receptors during horizontal rotation of the trunk with a stationary head.

1.4 Vestibular Perception is Slow

Traditionally, the vestibular system was regarded as a very fast system due to the rapid transduction times of hair cells (40μs) and its role in generating quick reflexive behaviours, needed to maintain perceptual and postural stability. One such reflexive response is the vestibulo-ocular reflex (VOR), which is the compensatory movement of the eyes in response to head movement in order to stabilizes gaze. The VOR is composed of a three-neuron arc. Position-vestibular-pause (PVP) neurons in the vestibular nuclei receive direct input from

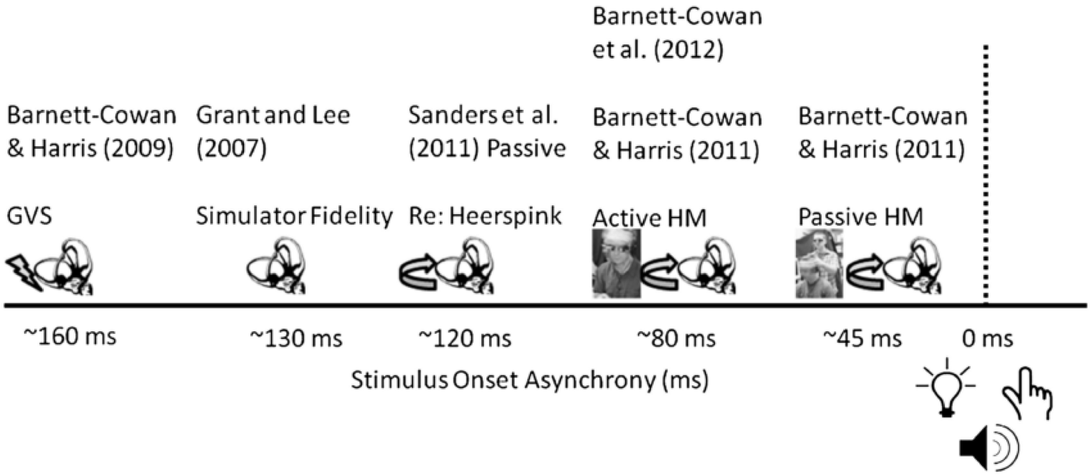

Figure 1.3: Vestibular perception is slow.
Taken from [5], this figure shows a summary of reviewed experiments where vestibular stimulation must lead a comparison stimulus for the two stimuli to be perceived as simultaneous.

vestibular afferents and project to and strongly inhibit ipsilateral abducens motoneurons and send excitatory projections to the contralateral abducens motorneurons. [24]. This neuronal architecture allows the VOR to respond quickly - within 5-6ms after vestibular stimulation in monkeys [49]. As noted previously, electrical stimulation of the vestibular nerve will result in an evoked response in different cortical areas as early as 6ms when measured with EEG [30]. As the physiological response to vestibular stimulation is extremely fast, one may reasonably assume that the perceived timing of vestibular stimulation is equally fast. Surprisingly, research has shown the opposite (for a review see [5]). Figure 1.3 shows a timeline of studies conducted up until 2013 which show that the perceived timing of vestibular stimulation is slow.

The first study that indicated the slow perception of the vestibular system was conducted in 2007, which looked at motion fidelity in a helicopter simulator and found that performance is best when the vestibular phase error threshold relative to visual motion is 133ms, with vestibular cues leading visual cues [42]. Since our vestibular system is so important in helping us maintain perceptual and postural stability, the finding that our perceptual awareness of our vestibular system is delayed is unexpected. The first study to directly assess the delay in vestibular stimuli perception in comparison to other stimuli was conducted by Barnett-Cowan and Harris [6]. Here, galvanic vestibular stimulation was presented at different SOAs relative to a light, touch, or sound. In order to appear simultaneous with light, touch or sound, galvanic vestibular stimulation had to be delivered first by about 160ms. However, this was a shorter time than what was expected from the difference in simple reaction times from vestibular and other stimuli. Therefore, there seems to be a partial correction for the vestibular timing perception (around 51% and 64%), but still, it remains delayed. In Barnett-Cowan et al. [8], it was thought that by matching the auditory stimulus temporal duration and envelope to that of an active head movement, one could perhaps resolve the temporal perceptual delay between these two senses. In this study, active head movement had to precede an auditory stimulus regardless of the duration of the auditory stimulus, both with a cosine shaped sound envelope, and a square shaped envelope. Although auditory stimuli with a cosine shaped sound envelope had to be presented earlier than brief sounds, the sound envelope and the stimulus duration itself could not resolve the temporal difference, with all conditions being significantly delayed when paired with an active head movement. Furthermore, the decrease in the temporal delay for the long square shaped sound versus the brief sound was linked to the time it took for the head movement to reach peak velocity. The brief sound stimulus caused participants to move their head faster and reach peak velocity quicker, which resulted in less of a perceptual delay. Since natural movement does not only stimulate the vestibular system, but also proprioceptive sense, subsequent studies looked at the effect of adding proprioceptive input on the perceived timing of that movement compared to other modalities. Several studies ([7, 8, 20]) have found that the delay in perceived timing of an active and passive head movement decreases from the delay obtained from galvanic vestibular stimulation only. However, the results from these studies remain so that an active head movement must occur approximately 80ms before an auditory comparison stimulus, and a passive movement 45ms, for the two modalities to be perceived as simultaneous. Sanders et al. [72] also looked at slow passive whole-body rotations and found that vestibular stimulation had to occur before the sound by 265ms for a TOJ task, and 230ms before a SJ task for perceived simultaneity.

Vision is one of the extra-vestibular cues that the CNS uses to distinguish between different types of movements. Chung and Barnett-Cowan [20] noted that past research studies on the perceived timing of active head movements conducted experiments with eyes closed, and therefore sought to examine the effect of adding visual input. In this study, participants tracked a LED target and performed temporal order judgement tasks between active head movement onset and a comparison sound while eyes were closed or opened. The LED target provided the visual cue which could improve the perceived timing of active head movements. They assessed the effect of visual cues on active head movements when the VOR is active by using an earth-fixed LED target, and where the VOR is suppressed and motion smear was present via a head-fixed LED target. In the eyes-closed condition, head movement onset had to precede a sound by 76ms. Although the remaining conditions had head onset lead times ranging from 48-70ms, which was smaller than the eyes-closed condition, there were no significant differences in the perceived timing of active head movement when the LED target was viewed in the light or the dark, whether the LED target was earth-fixed or head fixed, or when eyes were closed entirely. In short, adding visual information did not resolve the perceptual delay in active head movements.

Several theories have been put forward to account for the vestibular delay. Angelaki and Cullen [2] suggested that vestibular stimulation does not cause a separate and distinct conscious sensation because of the highly multimodal nature of the vestibular system, and because signals from the vestibular system become highly distributed when they reach the cortex [30]. Barnett-Cowan et al. [8] has suggested that it may be more important to respond to a vestibular perturbation than to be consciously aware of it. Support for this theory comes from a study by Berger et al. [10] where the vestibular information provided information for stability control faster than visual stimuli. Furthermore, the main purpose of the vestibular system is to relay information about acceleration [35], and yet, the signals coming from the vestibular system relay velocity. To know our head position, our CNS must then integrate the velocity over time, and the sampling time of this integration might contribute to the perceptual delay [5]. Lastly, it has been suggested that participants did not compare head movement onset as a cue to compare to the other sensory, but used another cue such as peak acceleration. Peak acceleration as a potential cue was addressed in Barnett-Cowan and Harris [7] which compared active and passive head movements. Here, the time it took participants to reach peak acceleration was the same in passive and active head movements, despite that different delay times were reported for active and passive head movements.

1.5 Active versus Passive Head Movements

An active movement refers to any movement which is self-initiated, whereas a passive movement is when your body is moved by your environment. To actively move the head, the CNS will first plan a motor command in the premotor cortex and the supplementary motor area, and will send that information to the primary motor cortex which will generate a motor command. In a yaw rotation, this motor command will activate the sternocleidomastoideus muscle (SCM) opposite to the direction of rotation, and the dorsal neck muscle group on the same side as rotation [64]. The SCM is innervated by the eleventh cranial (spinal accessory) nerve which has cranial and spinal components [3]. It may also receive innervation from the cervical plexus, mainly at C2 and C3 [13]. It is important for the CNS to distinguish between these two types of movements so that it can respond accordingly. For example, in an active head movement, the direction of gaze should change, whereas in a passive head movement, the gaze should remain the same [7]. To that end, the vestibulo-ocular reflex is suppressed in an active movement; PVP neurons pause or decrease their firing rate during vestibular quick phases during gaze redirection in studies on head-restrained monkeys [23].

The brain can know about an active head movement before it occurs due to the efference copy. The efference copy refers to an internal copy of a movement signal in the CNS, which can affect other sensory areas in the CNS [85]. This way, sensory signals from the environment (exafference) can be compared to sensory signals from the actions of the organism (reafference). Although the vestibular system does not differentiate active and passive head movements at the level of the vestibular afferents [27], the vestibular nuclei do distinguish between these two movements, since semicircular canal activity is less active during an active head movement than during a passive one [26]. Those neurons in the rostral fastigial nucleus in the deep cerebellar nuclei that are responsive to both vestibular and proprioceptive input are unresponsive during active movement of the head or whole body in primates, which implies that an efference copy cancels out the responses to active movement in these neurons [16]. Then, the vestibular nuclei also receives input from the cortex, the cerebellum, and brain stem structures which may provide extra-vestibular cues with which the vestibular nucleus could differentiate active from passive head movements.

Lastly, neurons in area ventral intraparietal area 7 show differential activity in response to active and passive head movements including changes in the strength, timing, and direction selectivity of their responses under the two conditions [38].

1.6 Suppression of Active Movements - Past Studies

There is evidence that motor planning and execution areas could have a gating influence on sensory systems involved in perceptual decisions. Somatosensory feedback occurs during both passive and active movements, but evidence suggests that the transmission of somatosensory information is inhibited in stable active movement environments [14]. One study investigated somatic sensory evoked potentials and showed that the amplitude of these potentials are reduced in the dorsal column nuclei prior to an active movement, but are not reduced during passive movement which implies that the decrease in amplitude of sensory evoked potentials has a central mechanism of control and does not rely on reafferent input [52].

Two competing hypotheses exist in regards to active and passive head movements in humans. The first, known as the anticipation hypothesis, postulates that the availability of the efference copy would shorten the delay for active head movements. The second, known as the suppression hypothesis, suggests that the efference copy might suppress the vestibular nucleus activity, which would make active head movements more delayed than passive head movements. Barnett-Cowan and Harris [7] showed support for the suppression hypothesis, where passive head movements required 45ms lead time, whereas active head movements required 80ms lead time in order to be perceived as simultaneous with other comparison stimuli. This is in line with recent neurophysiological studies which have suggested that an efferent copy suppressed reafference in the vestibular nuclei [28]. This was also similar to research on active and passive touch, where active touch was also perceived slower than active touch due to sensory suppression [43].

Barnett-Cowan and Harris [7] also found that increased velocity of head movements resulted in greater perceptual delays (Figure 1.4). One theory attributed this to the suppression of the vestibular afferent signals found during higher movement velocities as recorded in monkeys [28], the rate of which was similar to the modulation of the point of subjective simultaneity (PSS) between the onset of active head movement and a comparison light, touch or sound stimulus for human temporal perception [7]. It was suggested that this suppression could stem from the efference copy. However, one issue with the findings of Barnett-Cowan and Harris [7] was that the results were from between-subjects data. Between-subjects data could not address the question whether increasing the velocity of active head movement in an individual would lead to a change in the perceptual delay of the movement. Asking a participant to move their head at a certain speed is subjective, in that a slow velocity for one participant could have the same magnitude as a fast velocity for another participant. Thus, their result that greater head movement velocities result in greater perceptual delays should really be interpreted as participants who move their head faster than other participants require the head to move even earlier than comparison stimuli to be perceived as simultaneous.

1.7 Current Study

In this study, we vary the velocity of an active head movement and analyse the data both between- as well as within-subjects. Participants performed TOJ tasks at different active head movement speeds paired with an auditory stimulus, using a within-subjects design. Our main hypothesis is that faster active head movements will lead to a larger temporal delay in perception when paired with a comparison sound stimulus. We compare our results

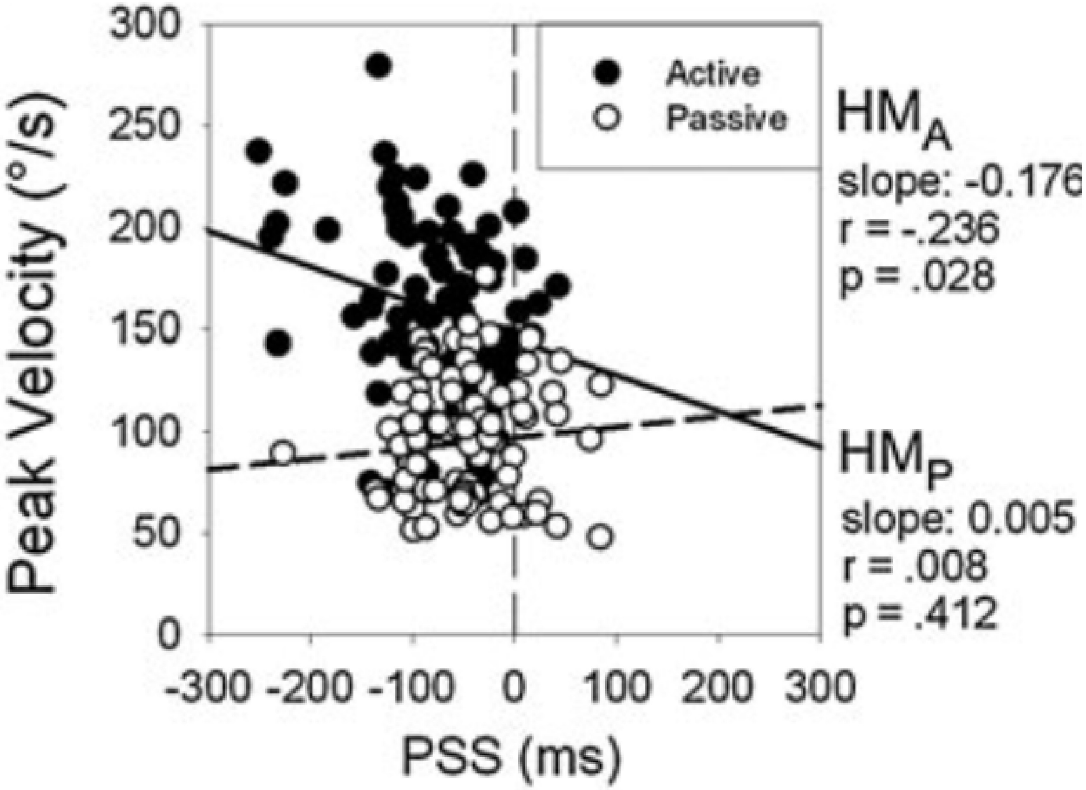

Figure 1.4: Linear regression of peak velocity and PSS
This figure is taken from [7] and shows the between-subject linear regressions for active and passive head movements.

to the findings of Barnett-Cowan and Harris [7] and discuss our results in the context of literature where the perception of more intense auditory, visual and vestibular stimuli is less delayed.

Chapter 2

Methods of Current Study

This section describes the methods of the completed study which was submitted to publication to Neuroscience Letters on February 1st. A pre-print is available at:
http://biorxiv.org/cgi/content/short/258590v1

2.1 Participants

20 participants (19-25y) who reported having no auditory, visual or vestibular disorders were remunerated $10 for one hour of testing. This study was carried out in accordance with the recommendations of Canada's Tri-Council Policy Statement: Ethical Conduct for Research Involving Humans (TCPS2) by the University of Waterloo's Human Research Ethics Committee with written informed consent from all subjects. All participants gave written informed consent in accordance with the Declaration of Helsinki.

2.2 Apparatus

Head movement was measured using the YEI 3-Space Sensor: Data-logging inertial measurement unit by Yost labs, which was mounted onto the back of the head using an elastic strap. The YEI 3-Space Sensor consists of a triaxial gyroscope, accelerometer, and compass. The measurements were recorded at 1000Hz using the Python API available directly through Yost Labs (https://yostlabs.com/3-space-application-programming-interface/). Python 2.7 was used to generate sounds, run the experiment and record data on a Dell Optiplex 725 intel Core 2 duo PC running Windows Vista. Participants responded via a keyboard by pressing the right or left arrow key and these responses were recorded using a custom-made python script.

2.3 Stimuli

Active head movement was self-generated by participants at the offset of a low pitch 200 Hz tone ‘go signal’ presented via headphones (Apple iPod earphones: MA662G/A). The duration of the go-signal ranged from 1-3s. The sound stimulus was a higher pitch 2000Hz tone presented for 50ms at a randomly generated time between 0ms and 650ms after the offset of the go signal. At the beginning of the study, participants were seated in a chair, blindfolded with their eyes closed, and instructed to practice rotating their head to the right and then back at different speeds before the actual trials commenced.

2.4 Procedure

Participants performed a temporal order judgement task in which they reported whether the onset of their head movement came first, or the onset of the high pitch sound stimulus came first. Each trial began with the onset of the low pitch go signal. The duration of the go signal was randomized to prevent participants from predicting the timing of the offset, and anticipating the start of the head movement (Figure 2.1). At the offset of the go signal, participants initiated head movement, and due to the response time delay between the offset of the go signal and the onset of the head movement, the comparison sound stimulus could occur before or after the head movement. Participants responded by pressing the left or right key on the computer keyboard, where the left key indicated that the onset of head movement came first, and the right key indicated that the onset of the sound came first. Once the participant selected a response, the next trial would begin immediately after. A schematic of a typical trial is shown in Figure 2.1. Participants performed 10 practice trials prior to the experiment which then consisted of three conditions in a block design with 100 trials within each block. Each block took approximately 10 minutes to complete with a break of 5 minutes in between blocks. For the three conditions, participants were asked to move their head at what they subjectively considered to be a slow, normal, or fast head movement, the latter being as fast as they could move their head. The order of the conditions across participants was randomized.

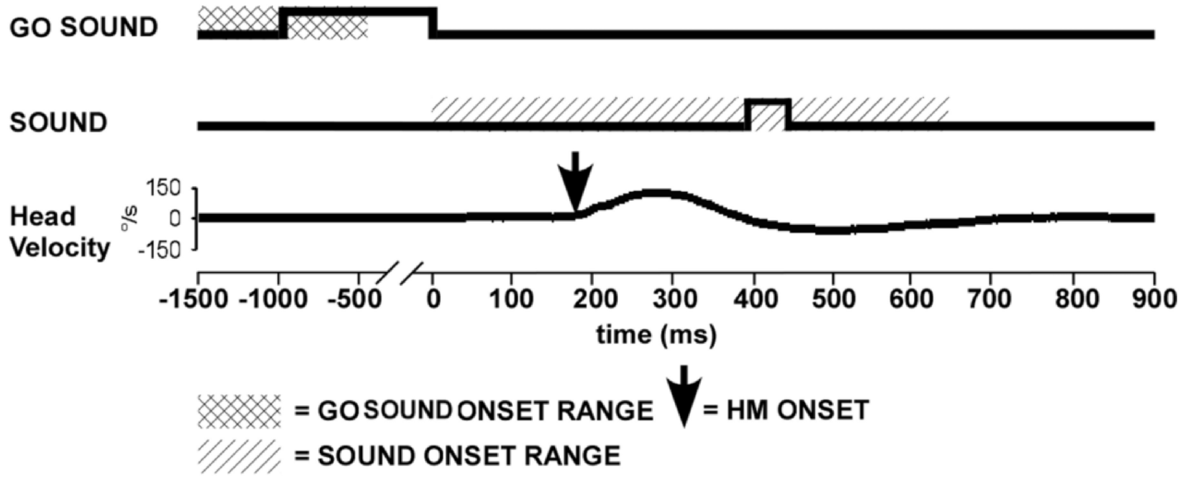

Figure 2.1: Example of a trial.

Offset of the go sound is the signal to begin head movement (HM). The comparison sound is randomly generated between 0-650 ms after the go sound offset. Head movement can occur before or after the comparison sound stimulus due to the time it takes for the participant to perceive the go sound offset and initiate head movement.

2.5 Data Analysis

2.5.1 Data Cleaning

Raw recorded data was analysed using Python 2.7. Angular velocity, which was originally recorded in raw form by the gyroscope in YEI 3-Space Data-logging sensor, was converted to degrees by accounting for the sensitivity level of 0.07°/sec/digit for ±500°/sec. Displacement was obtained using the formula:

$$s = 0.5(v + u)t \tag{2.1}$$

where s is the final displacement, v is the final velocity, u is the initial velocity, and t is the time at the final velocity. Angular acceleration was calculated by taking the change in velocity over the change in time between two adjacent data points. Onset of head movement was calculated to be 5ms before the velocity of the head was greater than three standard deviations from the average head velocity sampled 100ms before the trial onset. Each individual trial was further examined visually by plotting the angular velocity signal using the MatPlotLib library in Python 2.7. In trials where the onset of head movement was not accurately determined by the algorithm due to local minima or a noisy signal, the trial was discarded. Trials which had an excessively noisy signal or signals which had multiple peaks were removed from analysis. Three participants were fully removed from the analysis since they had excessively noisy signals in over 20% of the trials within one or more of the original three velocity conditions.

2.5.2 Stratifying into four categories

Due to the subjective nature of the participants deciding what constitutes a slow, medium and fast head movement and participants poorly replicating their head movement trajectory trial-to-trial [16], there was significant overlap in the peak velocities for the three conditions. To correct for this, the peak velocities of each participant were artificially stratified into four equally-sized conditions according to increasing peak velocity and renamed velocity 1, 2, 3 and 4. There were two justifications for stratifying the data into four categories. Depending on the distribution of the data, a certain number of trials are necessary to create the sigmoidal curves from which the point of subjective simultaneity (PSS) is obtained, which describes the point at which participants view two stimuli as simultaneous. Having four instead of three velocity conditions resulted in a better fit for the within-subjects linear regressions. Goodness of fit of the sigmoidal curves was inspected visually. For a sufficient goodness of fit, there needed to be an overlap of responses where participants chose either sound first or head first as their response and we used a liberal approach to accept fits with an r^2 value of 0.068 or greater (see below for fitting details). The resulting sigmoidal curve had to have a visibly sigmoidal shape. It was not possible to stratify the data into more than four conditions without losing goodness of fit for the sigmoidal curves. Since stimulus onset asynchronies (SOAs) were not normally distributed, equally sized bins were used to stratify the data so that enough trials would be included in each new velocity condition to make the sigmoidal curves.

2.5.3 Extracting PSS and JND

Stimulus onset asynchronies (SOAs) were determined by calculating the difference between head movement onset and sound onset, with a negative SOA indicating that the head moved prior to the sound. A sigmoidal function (Eq. 2.2) was fitted to the participants responses for each of the four conditions as a function of SOA using SigmaPlot 12.5, with the inflection points of the sigmoidal function (x0) taken as the point of subjective simultaneity (PSS, Figure 2.3) and the slope of the function (b) as the just noticeable difference (JND; [1]). The average sigmoidal curve had an r^2 value of 0.525 (range: 0.068 to 0.917).

$$y = \frac{a}{\left(1 + e^{-\left(\frac{x - x_O}{b}\right)}\right)} \tag{2.2}$$

$$y = y_0 + a * x \tag{2.3}$$

2.5.4 Confirming the new stratified groups

All subsequent analysis was performed in R version 3.4.2. and included the use of the FSA library and the dplyr library. The Shapiro-Wilk test was applied to the peak velocity and time to peak velocity for all four stratified conditions to identify whether these measures were normally distributed. Peak velocity and time to peak velocity were not normally distributed so a one-way repeated-measures ANOVA on ranks (Kruskall-Wallis) was applied to peak velocity and time to peak velocity between the four stratified conditions to confirm that the different head movement categories were sufficiently significantly different from each other. Descriptive statistics and p-values were rounded to 3 decimal points. There was a significant difference for peak velocity between-subjects (H(3) = 45.236, p¡0.001) with medians of 71.667°/s (iqr=38.636) for velocity 1, 113.679°/s (iqr=37.095) for velocity

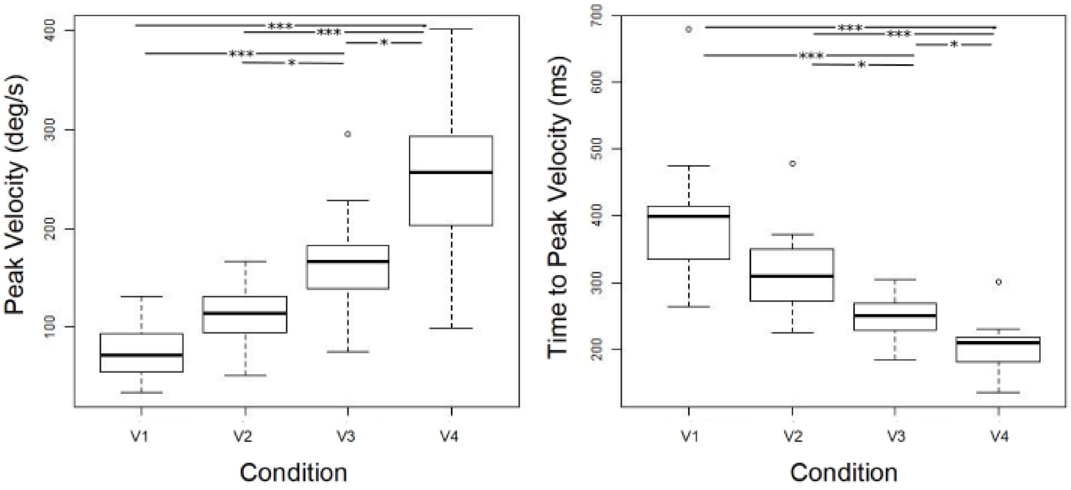

Figure 2.2: Head movement dynamics for each stratified condition.
a. peak velocity, b. average time to reach peak velocity. The bottom and top of the box represents the 25th (Q1) and 75th (Q3) percentile. The height of the box is the interquartile range (IQR). The middle line in the box represents the median. The ends of the whiskers are 1.5*IQR+Q3 for the upper whisker, and Q1-1.5*IQR. *=p¡0.05, ***=p¡0.001

2, 166.361 °/s (iqr=42.764) for velocity 3, and 256.768°/s (iqr=89.331) for velocity 4. Dunn's test were adjusted using the Benjamin-Hochberg method and revealed significant differences between velocities 1&3 (p¡0.001), 2&3 (p=0.023), 1&4 (p¡0.001), 2&4 (p¡0.001) and 3&4 (p=0.043). There was a significant difference for the time to peak velocity between subjects H(3) = 46.991, p¡0.001) with a median of 398.720s (iqr=79.522) for time to velocity 1, 310.004s (iqr=78.579) for time to velocity 2, 250.941s (iqr=41.167) for time to velocity 3, and 208.762s (iqr=38.296) for time to velocity 4. Dunn's test were adjusted using the Benjamin-Hochberg method and revealed significant differences between velocities 1&3 (p¡0.001), 2&3 (p=0.003), 1&4 (p¡0.001), 2&4 (p¡0.001) and 3&4 (p=0.037). These results, depicted in Figure 2.2, confirm that the categories are sufficiently different from each other so that they can be used in subsequent analysis.

2.5.5 Testing perceived timing of active head movement

Shapiro-Wilk test were conducted to the PSS values of each of the four stratified conditions to see whether the data was normally distributed. To compare the PSS of each condition to 0ms and confirm whether head movement must precede a sound stimulus for perceived simultaneity, one sample t-tests were used if the data in each individual condition was normally distributed, and the Wilcoxon signed-rank t-test was used if the data was not normally distributed. Descriptive statistics and p-values were rounded to 3 decimal points.

2.5.6 Testing effect of velocity on perceived timing of active head movement

To test whether there was a significant difference in PSS between conditions, a one-way repeated measures ANOVA on ranks was conducted between all four striated conditions and the Holm-Sidak method was used for pairwise comparisons. To test whether participants were differentially sensitive in each of the four velocity groups, a one-way repeated measures ANOVA was applied to the JND and the Holm-Sidak method was used for pairwise comparisons. To assess whether people who move their head faster require active head movement onset to occur earlier than a comparison sound stimulus (i.e., replicate [1]), we ran Pearson's r correlations (Spearman's ρ if not normally distributed) between peak head movement velocity and the PSS for each head movement condition, where a significant negative correlation for any head movement condition would replicate [1]. Lastly, to test the effect of the perceived timing of active head movements with a comparison sound stimulus as participants changed their head movement speed, a linear regression (Eq. 2.3) was fitted to each participant's PSS values for each of the four velocity conditions, and the slope and y-intercept was obtained for each participant's regression. The Shapiro-Wilk test revealed that the slopes and y-intercepts were not normally distributed. Therefore, to construct the average linear regression line, the median of the slope (a) and y intercept parameters (y0) for the individual regressions were used. A Wilcoxon signed rank t-test was applied to the slopes (a) relative to 0 (i.e., no change in the PSS relative to peak head movement velocity). A negative slope would confirm the hypothesis that the faster the head moves within-subject, the earlier active head movement onset must occur than a comparison sound stimulus. A positive slope would support the alternative hypothesis that an increase in active head movement speed reduces the PSS. Descriptive statistics and p-values were rounded to 3 decimal points.

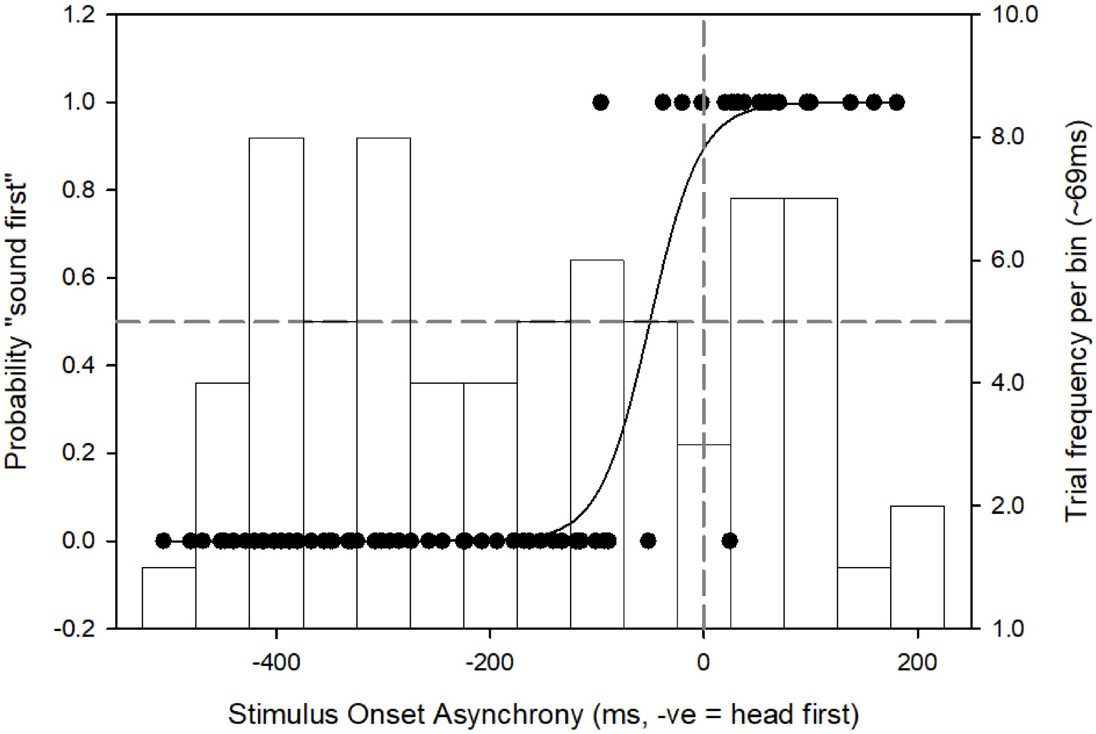

Figure 2.3: Sample TOJ data from an average participant from the fastest condition. Positive SOAs represent sound occurring first, whereas negative SOAs represent head movement occurring first. An SOA of 0ms represents true simultaneity and is represented by the dashed vertical line. The PSS occurs at a probability of 0.5 and is represented by a dashed horizontal line. A frequency distribution of SOAs binned for each 10% of trials is also shown on the right y-axis.

Chapter 3

Results

This section details the results from the current study.

3.1 Descriptive Statistics for Peak Velocity

In total, 17 participants were included for analysis. Four artificial, equal-sized conditions were created by sorting the peak velocity of each participants from the lowest to highest velocity and then grouping the trials into four equally-sized conditions. These conditions are referred to as Velocity 1 (median: 71.67°/s, iqr = 38.64), Velocity 2 (median: 113.68°/s, iqr = 37.09ms), Velocity 3 (median: 166.36°/s, iqr = 42.76ms), and Velocity 4 (median: 256.77°/s, iqr = 89.33ms). The global median was -84.47ms (iqr = 92.37ms). The descriptive statistics for all velocity groups are found in table 3.1. In total, 6.47% of trials were removed due to anticipatory head movement, excessively noisy data, or two peaks being present in the velocity signal.

3.2 Active Head Movement Perception is Slow

Figure 3.1a-d shows the results of fitting the sigmoidal curve function to each individual participant's data (grey lines and dots) as well as a representation of the average sigmoidal curve constructed from the average slope and PSS value for each condition (black lines and dots). Figure 3.1e shows the individual (grey dots) and median (black dot with standard error bars) PSS values for each condition. The PSS for Velocity 1 was significantly

Velocity Conditions	Velocity 1	Velocity 2	Velocity 3	Velocity 4
Mean (°/s)	76.46	110.42	167.47	256.78
Median (°/s)	71.67	113.68	166.36	256.77
Standard Error (°/s)	6.42	8.13	12.30	19.75
Standard Deviation (°/s)	26.475	33.540	50.701	81.446
Min-Max (°/s)	34.2 - 131.3	52.0 - 166.3	75.6 - 294.9	99.0 - 400.4
Interquartile Range (°/s)	54.6 - 93.2	94.7 - 131.8	139.3 - 182.1	203.1 - 292.4
Median Peak Vel. Time (ms)	398.7	310.0	250.9	208.8
IQR Peak Vel. Time (ms)	335.1 - 414.7	271.7 - 350.3	227.9 - 269.0	180.1 - 218.4

Table 3.1: Descriptive statistics for all velocity groups

Velocity Conditions	Velocity 1	Velocity 2	Velocity 3	Velocity 4
Mean (s)	-122.506	-110.938	-66.574	-52.134
Median (s)	-100.338	-103.524	-51.694	-41.387
Standard Error (s)	18.32	20.60	22.19	22.76
Standard Deviation (s)	75.529	84.923	91.490	93.859
Min - Max (s)	-34.2 - -294.3	-3.9 - -356.4	94.2 - -258.4	87.3- -264.0
Interquartile Range (s)	-163.5- -68.3	-117.4 - -58.3	-125.0 - 10.4	-100.7 - 5.6

Table 3.2: Descriptive Statistics for Point of Subjective Simultaneity

before 0ms (t(16)=-6.688, p¡0.001). The PSS for Velocity 2 was significantly before 0ms (median=-103.524, Wilcoxon Z=-3.621, p¡0.001). The PSS for Velocity 3 was significantly before 0ms (t(16)=-3.000, p=0.009). The PSS for Velocity 4 was significantly before 0ms (t(16)=-2.290, p=0.036). The global median for all PSS conditions was -84.47ms (iqr = -92.37). Descriptive statistics for PSS values can be found in Table 3.2. Together these results support previous work which has shown that the perceived timing of an active head movement is slow compared to a comparison sound stimulus [1,16,17].

3.3 Between-Subjects Analysis

To examine the hypothesis that participants who move their head faster require the active head movement to occur even earlier when paired with a comparison sound stimulus, a one-way repeated measures ANOVA indicated significant differences in PSS values between subjects (F(3,67)=9.386, p¡0.001). Holm-Sidak pairwise comparisons revealed significant differences between V1&V4 (p¡0.001), V2&V4 (p=0.002), V1&V3 (p=0.003), V2&V3 (p=0.020). A one-way repeated measures ANOVA on ranks revealed no significant difference for the JND values between the four conditions ($\theta 2 = 3.141$, df = 3, p = 0.370) (Figure 3.1f), meaning that the participants' precision did not differ as the velocity of head movement changed. Correlations between peak velocity and time to peak velocity versus PSS were run separately for each velocity condition and are depicted in Figure 3.2. Peak velocity had no significant relationship to the PSS for Velocity 1 (Pearson's r = 0.157, p=0.548), Velocity 2 (Spearman's $\rho = 0.061$, p = 0.817), Velocity 3 (Pearson's r = 0.086, p = 0.741), or Velocity 4 (Pearson's r = 0.068, p = 0.794), or the overall peak velocity versus PSS (Pearson's r = 0.0311). Neither did time to peak velocity have any significant relationship to the PSS for Velocity 1 (Spearman's r = 0.191, p = 0.461), Velocity 2 (Spearman's $\rho =$ 0.123, p = 0.639), Velocity 3 (Pearson's r = 0.256, p = 0.321), or Velocity 4 (Pearson's r = 0.325, p = 0.203), or the overall peak velocity versus PSS (Pearson's r = 0.173), suggesting that the speed of the active head movement does not have an influence on the PSS. We find no further evidence that peak velocity has an effect on PSS between-subjects in this dataset.

3.4 Within Subject Analysis

To test whether increasing the peak velocity within an individual participant has an effect on the PSS our third hypothesis, linear regressions of peak velocity versus PSS were applied individually for each participant (average r^2: 0.577, s.e.: 0.321), and are shown in Figure 3.3a. From the slopes and intercepts of these linear regressions, an average regression line was obtained from the median slopes and y-intercepts, to describe the overall trend within-subjects (Figure 3.3b and 3.3c). The average regression line had a median slope of 0.892. (interquartile range = 0.906) A one-sample signed-rank test confirmed that the regression slopes are significantly different from zero (Median=0.892, Wilcoxon Z=2.49, p=0.011). Outliers were defined as any data point more than 1.5 IQRs below the first or the third quartile. This revealed one outlier with a slope of -3.54. After removing this outlier, the average regression slope had an even higher median of 0.992. These results suggest that within-subjects, an increase in active head movement velocity leads to a smaller PSSs.

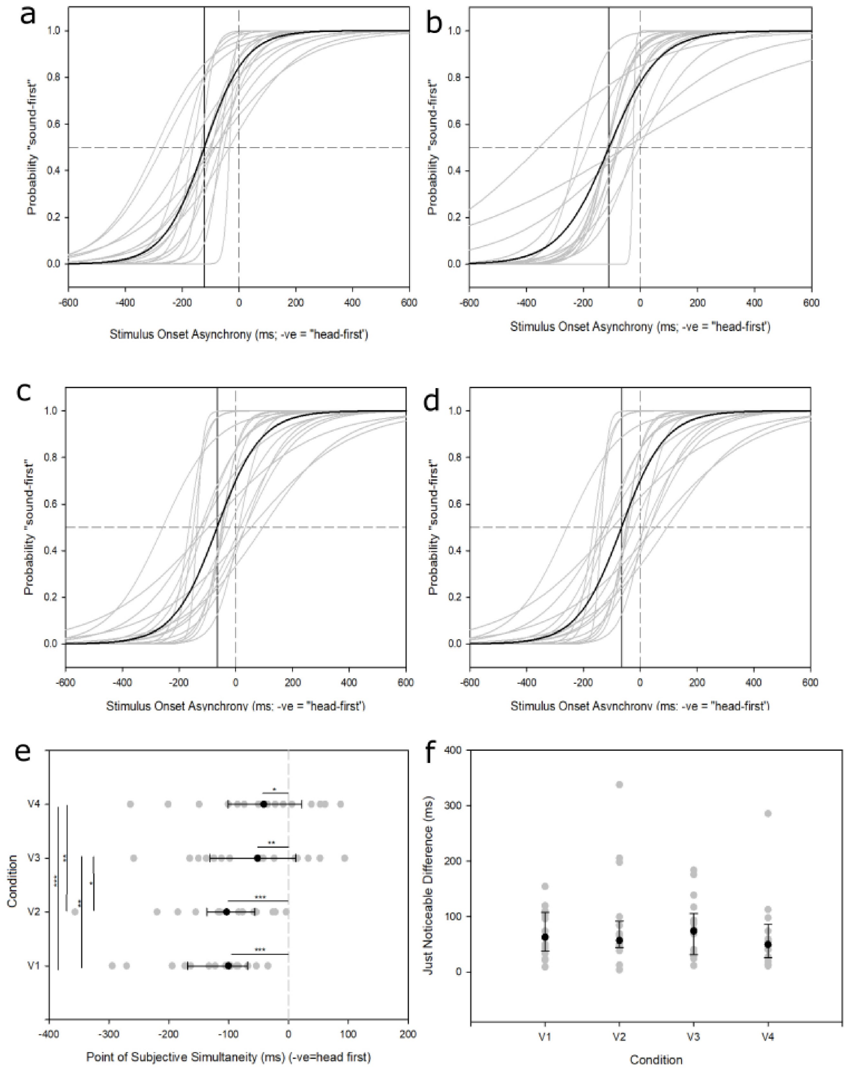

Figure 3.1: Average TOJ, PSS and JND data for all four stratified velocities. a. Slowest velocity (V1) TOJ data, with gray curves representing individual participants, and the black curve representing the average logistic function. b. Second-slowest (V2) TOJ data. c., Second-fastest (V3) TOJ data. d, Fastest (V4) TOJ data. e. Average PSS data for all four stratified conditions. Grey dots represent individual participants and black dots represents the median PSS for each condition, with error bars representing the 25% and 75% quartiles. f. JND data for all four stratified conditions. Grey dots represent individual participants and black dots represent median JND value for each condition. Error bars are 25% and 75% quartiles. *: p¡0.05, **: p¡0.01; ***: p¡0.001

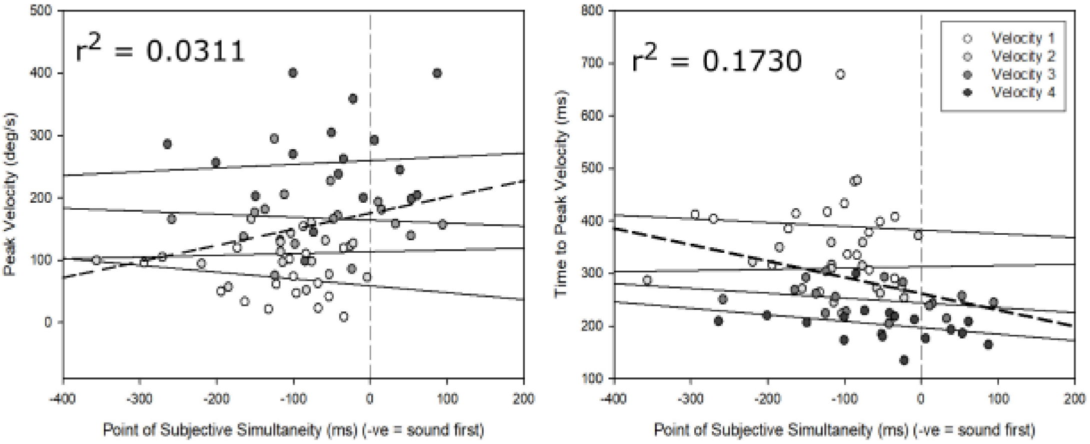

Figure 3.2: Correlations for peak velocity and time to peak velocity versus PSS
a. peak velocity versus PSS and b. time to peak velocity versus PSS. Different shades of dots represent different velocity groups

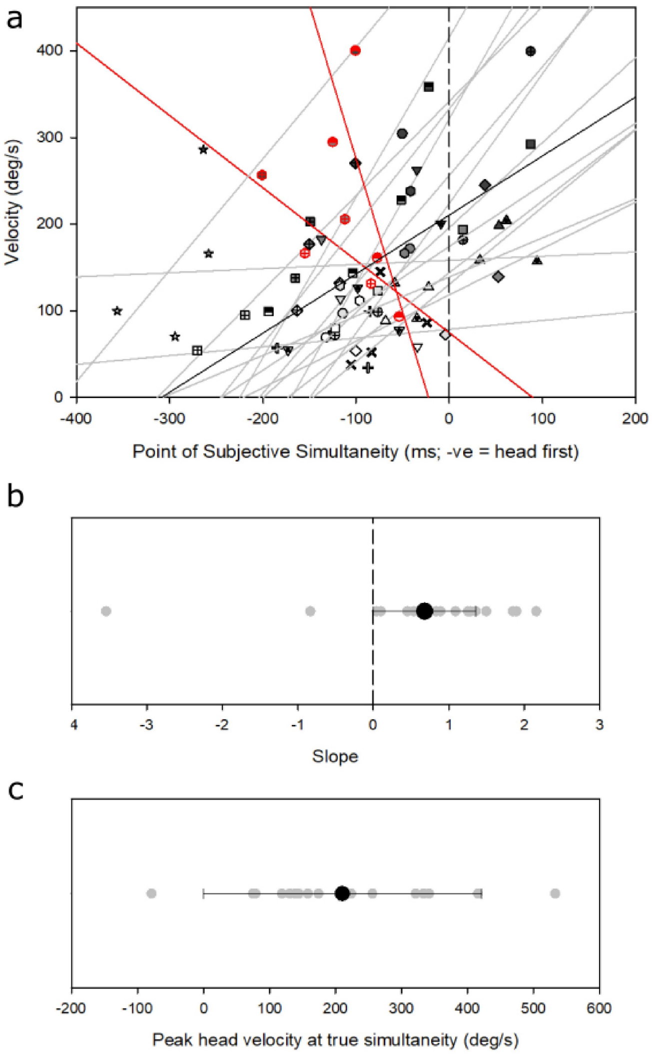

Figure 3.3: Overall within-subjects data for PSS versus peak velocity
a. Individual linear regressions for each participant for all four velocity conditions. Different symbols represent different participants. Thicker black line is the median linear regression which represents the average participant. Dashed line shows the point of true simultaneity. Red dots and line represent linear regression for participants with a negative slope b. Slopes and c. r-squared coefficients for within-groups linear regressions. Each gray dot represents one participant, the black dot represents the median. Red dots represent participants with a negative slope. Error bars are 25% and 75% quartiles. *: p¡0.05.

Chapter 4

Discussion

4.1 Overview

In the present study, we investigated whether the velocity of active head movement will influence the perceived timing of the head movement using a within-subjects design. We provide further evidence that the perceived timing of active head movements is slow when paired with a sound stimulus. This delay, which had a global median of 84ms for all conditions is similar to the 80ms delay previously reported [7, 8, 20]. Contrary to the predictions of our second hypothesis, the results showed that a greater peak velocity did not lead to a significantly greater delay in the PSS between-subjects. Most importantly, the individual regressions of the within-subjects data revealed that an increase in peak head movement velocity is significantly correlated with a reduction in the delay of the PSS. Barnett-Cowan and Harris [7] reported an increased lag in the perceived timing of active head movements as the velocity of head movement increased, in a between-subjects design. We find no further evidence of this in our study and quite convincingly show that higher velocities cause a decrease in the lag of the perceived timing of an active head movement, and not an increase.

4.2 Head Movement Dynamics

Multisensory temporal judgements are subject to a lot of individual variability [80]. In Figure 3.3a most linear regression slopes cluster around 1, but in the case of two participants there was a negative slope value, meaning that as head velocity increased the timing to perceive the movement also increased. Given that most participants had slopes that were relatively close to one another, it is possible that the results from these two participants are not indicative of the typical participant. These negative slopes may be a result of the small number of data points that were used to make the linear regressions, a result of the constraints in the number of trials that could be conducted for each participant, and the minimum number of trials that were necessary to create the corresponding sigmoidal functions. Alternatively, there may be characteristics in certain participants which cause them to behave in an opposite way, or they performed the experimental task differently. Subsequent studies should investigate what factors may be responsible for this individual variability.

From the within-groups analysis, it is suggested that true simultaneity of audio-vestibular stimuli would be reached at around 200°/s. However, it is important to note that the within-groups comparison only contained four data points per participant for each linear regression. This limits any analysis on the dynamics that head movement velocity has on PSS. We cannot conclude whether the behaviour is linear, or non-linear, and importantly how these change across individuals. A visual analysis of the within-group regression seems to indicate a more exponential relationship. Future studies could include more trials per participant on multiple testing days to avoid fatigue and habituation, so that the velocities can be stratified into more than four conditions. This would allow for a closer analysis of the dynamics of this effect.

We made the decision to stratify the data into four categories in order to obtain more PSS data points for the within-subjects linear regressions. By doing so, we pooled data into categories where one participant's subjective slow and normal trials could be mixed. It should be noted that if there was as cognitive bias in how participants made their decisions for the temporal order judgements based on instructions of moving the head at slow, normal or fast speeds, then such a bias would not be accounted for in our stratified data. We note that analysing the data based on the original categories without stratification yielded similar results to when we stratified the data into four conditions. In future studies, participants could be instructed to freely move at a range of speeds without being instructed to move at a predetermined speed prior to the begin of the trial. In addition, future studies should monitor the role of fatigue in repeated head movements on the perceived timing of head movement onset. Furthermore, since there were more trials in which the head moved first, it is possible that the distribution of SOAs could have an effect on the resultant PSS. Future studies should force the SOAs to follow a normal distribution. Note, however, that previous work on the perceived timing of active head movements did not find that shifts in the distribution of SOAs can account for change in the PSS or JND [20].

4.3 Effect of Stimulus Intensity

From Bigland and Lippold [11], we know that the velocity of shortening in a muscle corresponds to an increase in integrated electrical activity. This increase in excitation is related to the quantity of active motor units and their frequency of firing. To generate fast head movements, an increased number of motor units will be recruited in order to quickly generate enough force to overcome the inertia of the head over a shorter period of time. Importantly, active head movements are internally derived stimuli but lead to external stimulation of the vestibular and proprioceptive organs, primarily the horizontal semicircular canals and the neck muscle spindles and golgi tendons. Deflections of hair cells will cause an increase or a decrease in the baseline firing rate with larger deflections resulting in a larger change in firing rate as more calcium channels open or close [22]. In the auditory system, stimulus amplitude, which corresponds to the intensity of the sound, is encoded by an increase in the spike rate in the auditory nerve fibers [47]. Goldberg and Fernandez [35] recorded the responses from single units in the semicircular canal afferents of squirrel monkeys while the monkeys were exposed to different velocity conditions. Here, at velocity frequencies between 0.1°/s and 2.0°/s, the responses in single units increased linearly as the velocity increased. In our study, peak velocity was reached after approximately 200-400ms. This would correspond to a frequency of 0.8°/s - 1.6°/s and falls within the linear portion of Goldberg and Fernandez [35]. Within this range, the hair cells in the semicircular canals encode the speed of velocity with an increase in a firing rate, much like the hair cells in the auditory nerve. From these results, we can conclude that an increase in active head movement speed corresponds to an increase in stimulus intensity in the semicircular canal.

Our within-subjects result that the perceived timing of active head movements becomes less delayed at increasing head velocities are in agreement with other literature on stimulus intensity. Most studies that have investigated the effect of stimulus intensity on the perceived timing of sensory stimuli involve audiovisual tasks or comparing two visual events. As early as 1933, Smith [77] reported that stimuli of higher intensity were perceived earlier than lower intensity, in an audiovisual temporal order judgement (TOJ) task where the intensity of stimuli was varied. Roufs [69] showed that bright flashes of light are perceived earlier than synchronous dim flashes. When two flashes were shown simultaneously with different intensities between 10-1000 trolands, observers reported an apparent movement of the flash in the direction of the dimmer flash, due to the longer perceptual delay of the weaker flash. A study by Efron [34] paired a light stimulus with a shock stimulus under four sets of conditions, where either stimuli could be weak or strong. If both stimuli were strong, there was less of a deviation from true simultaneity than if both stimuli were weak. Additionally, if either stimulus was weak, the weaker stimulus had to be presented before the stronger stimulus in order for the observer to subjectively rate them as occurring simultaneously. Neumann [62] varied stimulus intensity in an audiovisual task, where for most trials the auditory stimulus had to be presented first in order to be perceived as simultaneous. This effect could be reversed, however, when the intensity of light was decreased and the intensity of sound was increased. These results suggest that intensity can influence the order in which stimuli from different modalities are perceived. More recent studies confirm that higher intensity stimuli in audiovisual tasks are perceived earlier in time [12], and that higher intensity stimuli are less likely to be reported as synchronous than lower intensity stimuli in simultaneity judgement tasks [56]. With respect to the vestibular system, a study by Chang [18] found that the PSS between the onset of passive self-motion and sound is significantly shorter during passive whole-body rotations when the rotation frequency increases from 0.5 Hz to 1 Hz (˜170 ms difference) and as the angular velocity increases from 5°/s to 60 °/s (˜133 ms difference). An intensity effect involving passive self motion and sound was also observed in a previous study by Sanders [72]. Here, when the rotation frequency and the angular velocity increased, the PSS between the onset of the passive self-motion and sound grew significantly shorter. Taken together, these findings suggest that an active head movement velocity (stimulus intensity) should result in less time required for the head to move prior to other stimuli to be perceived as simultaneous. An intensity effect could also explain why we only observe a significant difference in the within-subjects data as we can only compare the varying intensity within individuals, due to the subjective nature of what constitutes a slow or fast head movement for a participant. It remains to be seen whether the intensity effect will hold true for passive active head movements.

4.4 Alternate Explanations

Studies such as Jaskowski [51] have shown that stimulus duration has an effect on the perceived simultaneity in an audiovisual task, where the shorter stimulus can shift towards the offset of the longer stimulus. Others, such as Boenke et al [12] showed that longer stimulus durations shift the PSS to a common attractor value. Since a faster head movement corresponds to a shorter stimulus duration, it is conceivable that duration, not intensity, could be driving the effect seen in our study. In Barnett-Cowan et al. [8], the temporal envelope duration and shape of an auditory stimulus was matched to the active head movement stimuli to investigate whether the differences in the perceived timing of vestibular and auditory stimulations could be attributed to the stimulus characteristics (e.g. stimulus rise time, sound envelope shape, duration, etc). It was found that head movements paired with long square sounds were not significantly different than head movements paired with short cosine sounds. Though head movements paired with a long-raised cosine sound needed to be presented earlier than brief stimuli for participants to judge them as simultaneous, this effect was driven by the longer time it took for the participants to reach peak head movement velocity in the long cosine condition. Because a slower rise in velocity denotes a slower detection of head movement onset, shorter times to peak velocity corresponded to a smaller perceptual lag. Taken together, these results showed that matching the duration or shape of the auditory and vestibular stimulus did not resolve the perceptual lag of vestibular stimulation. Although the study by Barnett-Cowan et al. [8] does not rule out that the duration of an active head movement could have an effect on the perceived timing of the events, the present study cannot address this question, and it therefore remains open area of investigation for future studies.

Faster head movements correspond to a faster time to reach peak velocity. Faster times to peak velocity means that the detection of head movement onset will also occur earlier. In our study, there is a significant difference among the time it takes to reach peak velocity for the four velocity conditions, and it could be argued that this would affect the results. However, it should be noted that the threshold of detection for rotation of the head is as small as 1°/s [78]. All of our conditions passed this threshold rapidly, meaning that the influence of faster head movement onset detection at faster speeds is likely negligible.

Participants were asked to compare a sound to the onset of their own active head movement, but the average time to peak velocity occurs much later, at 200-400ms. However, the motor cortex and supplementary motor area encode the kinematics of the planned movement prior to it occurring [21, 53] and are therefore aware of the peak velocity of the movement before the onset of the active head movement begins.

4.5 Suppression of Active Movements

It is known that when an efferent signal is sent from the motor cortex to the muscles, an efference copy is created, and the resulting corollary discharge gets routed to other parts of the sensory cortex [85]. The efference copy allows the CNS to predict the sensory consequences of an action. By comparing the sensory reafference to the efference copy, the CNS can then adjust its subsequent commands and predictions. The comparisons of sensory consequences to the motor command are hypothesized to occur in the cerebellum [74, 48].

In the previous study by Barnett-Cowan and Harris [7], passive head movements were perceived earlier than active head movements, and this supported the suppression hypothesis of active head movements. One possible mechanism for suppression is that the efference copy of the active movement suppresses the vestibular nucleus and delays the perceived timing of the head movement.

If the vestibular signal is suppressed, the time it takes for that neural mechanism to make a decision will take longer. Here, it is possible that the neural mechanisms that underlie the perceived timing of active head movements must accumulate enough evidence in order to decide that a head movement has taken place, and this may explain the delay. However, a general feature of studies which investigate the perceived timing of active head movement is that participants themselves initiate their own movement, and that the addition of this secondary task requirement may increase the delay in comparison to passive movements where participants are not instructed to engage in the movement itself. Another reason why suppression might be occurring is because participants anticipate the start of the movement, but must suppress that movement until the offset of the low-pitched sound. Seki and Fetz [73] investigated cutaneous sensory evoked potentials in the spinal cord, primary somatosensory, motor cortex, and premotor cortex in monkeys performing a delay tasks. Here, they found that evoked responses were suppressed in the motor cortical area prior to the movement occurring with the suppression correlating with the reaction time of that movement. Because of the possible influence of suppression due to movement anticipation during the experimental task, future studies should consider an experimental design where the movement cannot be predicted by the participant prior to the onset of the active head movement.

4.6 Comparison to Barnett-Cowan and Harris (2011)

Based on their finding that a greater head movement velocity was correlated with a larger delay in PSS, Barnett-Cowan and Harris [7] postulated that the suppression mechanism described earlier could be velocity based. Their results were similar to the findings of vestibular nucleus suppression during active head movements in monkeys [28]. If increasing speeds of active head movements increase the delay in perception, it would provide further evidence for velocity-based suppression. In our study, increasing the speed of active head movement decreases the delay in perception within-subjects, so our results do not support a velocity-based suppression mechanism. Why was an effect of velocity on PSS found between-subjects in Barnett-Cowan and Harris [7], but not in this study? There are several key differences between these studies. Participants in Barnett-Cowan and Harris [7] were asked to move their head as fast as possible for all trials, whereas in our study, participants were asked to move their head at slow, medium and fast speeds. As a result, peak velocities in Barnett-Cowan and Harris [7] ranged from 70°/s - 280°/s, whereas peak velocities in this study ranged from 34°/s-400°/s. Furthermore, this study had 310 trials, whereas Barnett-Cowan and Harris [7] had 110 trials in total. The effect found in Barnett-Cowan and Harris [7] may be attributable to sampling error due to the lower range of peak velocities and lower number of trials. It should be noted that two studies since Barnett-Cowan and Harris [7] have found no effect of head movement velocity on the PSS between-groups [8, 20] . Further studies should look at the effect of velocity with active and passive head movement to determine whether the findings of Barnett-Cowan and Harris [7] can be replicated when explicitly controlling for the velocity of head movement. Future experiments should also look at the relative role of neck proprioception versus vestibular stimulation.

Chapter 5

Conclusion

From the results of this experiment, we conclude that the perceived timing of active head movement is slow in comparison to an auditory stimulus, replicating previous research on the perceived timing of active head movements. Furthermore, we conclude that an increased active head movement velocity shortens this perceptual delay within the responses of each individual participant. This is in line with literature where more intense auditory, visual and vestibular stimuli are perceived earlier in time. We failed to replicate the results from Barnett-Cowan and Harris [7] where an higher velocities of active head movements led to an increase in the perceptual delay when paired with a comparison auditory stimulus. Our study was not designed to test the suppression hypothesis, and as such, our results do not refute the suppression hypothesis that was previously reported, where an efference copy of the active head movement delays the perceived timing of the head movement via suppression of the vestibular afferent signals [7]. However we do provide evidence against a velocity-based suppression mechanism. Instead, our results may suggest a stimulus intensity effect, where increasing the velocity of the head movement and thus providing a greater stimulus intensity, leads to a decrease in the perceptual delay.

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