The Contribution of the Vestibular System to Temporal Attention

Saghi Arabi

School of Psychology, University of Kent

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Declaration

The research presented in this thesis was conducted at the School of Psychology, University of Kent, whilst the author was a full-time postgraduate student. The theoretical and empirical work presented is original work completed by the author under the supervision of Professor David Wilkinson, and the experiments were conducted with limited assistance from others. The author has not been awarded a degree by this, or any other University, for the work included in this thesis. Some of the data reported in Chapters 2 and 3 has been presented at the following conferences:

Conference Talks

Arabi, S., Wilkinson, D. T., (2019). Talk presented at the School of Psychology Annual Student Conference held at the University of Kent.

Conference Posters

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Abstract

The vestibular end-organ is phylogenetically old and placed deep inside the inner ear, detecting head movement and gravitational pull. The multiplicity of anatomical projections of the vestibular system, reaching cortical and subcortical brain regions, has proven to influence a wide range of higher-level functional relationships, including working memory (WM) and attention. The literature has established an association between the vestibular system and spatial attention, but little or no research has investigated the vestibular system's contribution to temporal attention in either normative or clinical groups. To this end, this thesis explores whether the periodicity of vestibular information can be used by visual and auditory temporal attention and thereon be utilised therapeutically. Chapter 2 examined whether visual and auditory attentional responses were enhanced if the presentation of visual and auditory stimuli coincided with the rhythmic presentation of vestibular pulses induced by Galvanic Vestibular Stimulation (GVS). Unexpectedly, synchronous vestibular signals were shown to inhibit rather than enhance visual response, more so when the vestibular waveform was sinusoidal (AC) than a square wave (DC) pulse. However, enhancement was observed when visual stimuli were replaced with auditory stimuli, although it did not matter if the Onset of the auditory stimuli was synchronised with that of the background vestibular stimuli. Chapter 3 moved on to show that the auditory enhancement was boosted when using an AC bilateral bipolar or AC bilateral bipolar with positive Offset instead of a DC bilateral bipolar signal. A group of participants with Specific Learning Difficulties (SpLDs), such as attention deficit hyperactivity disorder (ADHD), and dyslexia were recruited to investigate the therapeutic importance of any such improvement; however, the results were inconclusive. This chapter also showed that the visual inhibition seen in Chapter 2 was the product of the viewing conditions, which did not favour multisensory facilitation. Finally, Chapter 4 utilised a Rapid Serial Visual Presentation (RSVP) paradigm to assess the time course and

characteristics of the visual interference effect observed in Chapters 2 and 3. The experiments presented in this chapter found modest evidence of facilitation during GVS but did not cast light on the time course of the interference effect shown in Chapters 2 and 3. Together these thesis findings show that visual and auditory discrimination processes are sensitive to the temporal and morphological characteristics of the vestibular signal. However, this sensitivity differs across the visual and auditory senses and is constrained by task and the multisensory integration principles seen in other non-vestibular types of cross-modal interaction. The findings give further reason to understand how the brain exploits the high temporal fidelity of the vestibular system but do not yet support allied investigations into neuro-rehabilitative potential.

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Chapter 1 – General Introduction

1.1 Overview

This thesis aims to establish whether vestibular information can be utilised by visual temporal attention. Existing literature provides evidence regarding the impact of the vestibular system on human cognition (Wilkinson et al., 2005; Wilkinson et al., 2010; Gallagher et al., 2014). Most current research focuses on the autonomic functions and biological influences of the vestibular system. However, only a few studies in recent years have shed light on its non-biological and psychological aspects. These studies show that non-invasive stimulation could artificially and actively influence the vestibular system, potentially enhancing higher-level cognitive processes such as working memory and attention (Bigelow & Agrawal, 2015). While the relationship between the vestibular system and spatial attention has been well-established (Arene & Hillis, 2007; Gallagher et al., 2014), to my knowledge, no studies have yet examined its role in visual temporal attention. This is true for both normative groups and individuals with Specific Learning Difficulties (SpLDs) such as attention deficit hyperactivity disorder (ADHD) or dyslexia. I, therefore, aim to investigate the vestibular system's contribution to the higher-level cognitive processes of temporal attention and working memory.

This chapter focuses on an in-depth investigation of the anatomical and physiological characteristics of the vestibular system. Furthermore, this chapter aims to elucidate the role of the vestibular system in cognitive processes, with particular emphasis on its implications for working memory and temporal attention. Finally, the chapter will present theoretical frameworks that underpin the experimental methodologies employed in the subsequent chapters.

1.2 The Vestibular System

Studies show that over 500 million years ago, a small yet complex organ was developed in ascidians to facilitate their survival by spatial localisation and movement detection within any environment (Smith & Geddes et al., 2010). This organ, known as the vestibular system, reached its advanced development around 100 million years ago, and there has been a minor change since (Smith & Geddes et al., 2010). The evolution of the vestibular system allowed vertebrates to sense, detect linear and angular motions, control movements, and orient themselves in three-dimensional spaces (Blazquez et al., 2004; Tascioglu, 2005).

The vestibular organ not only provides stability and postural structure (Scudder & Fuchs, 1992), but also contributes to autonomic regulations such as maintaining stable blood pressure (Yates & Bronstein, 2005) and affects cognition and higher cognitive processes (such as memory, perception, and attentional processes) and overall, the psychiatric wellbeing of individuals (Goldberg & Huxley, 2012). Cognitive deterioration goes hand in hand with vestibular dysfunction; for example, elderly individuals with the vestibular deficit are slow in tasks that contain decision making, memory, learning, and attention (Smith et al., 2005). The role and importance of the vestibular organ could become overlooked on a day-to-day basis until it becomes damaged (Scudder & Fuchs, 1992). The upcoming section further investigate how the vestibular system impacts cognition.

1.3 Vestibular Cognition

The vestibular system is essential to the sensorimotor system, detecting motion, maintaining balance, and orienting the head and body (Dent et al., 2020). This system merges information from the vestibular organs with visual and proprioceptive inputs, offering a comprehensive understanding of body position and movement (Cullen, 2012). Beyond regulating motor responses and assimilating data from other sensory systems, it

supports higher-order cognitive and perceptual functions like spatial awareness, navigation, self-motion perception, memory, attention, and decision-making (Dent et al., 2020). Vestibular dysfunction, manifesting as symptoms like dizziness and vertigo, has been linked to disruptions in the memory system and behavioural changes (Ossenkopp & Hargreaves, 1993; Brandt et al., 2005). Clinical findings also associate it with cognitive deficits, with patients often reporting memory loss and "brain fog" (Smith et al., 2009; Bigelow et al., 2015; Smith, 2022).

The vestibular system plays a pivotal role in interpreting and integrating signals related to spatial awareness and various other functions (Dieterich & Brandt, 2015), such as balance, posture regulation (Peterka, 2002), eye movement control (Leigh & Zee, 2015), spatial orientation (Angelaki & Cullen, 2008), motion perception (Goldberg & Fernandez, 1971), autonomic regulation (Yates & Bronstein, 2005), emotional regulation and cognition (Smith & Curthoys, 1989), and spatial learning and memory (Smith & Zheng, 2013). The vestibular system processes signals within crucial cortical regions, including the parietal cortex, insular cortex, prefrontal cortex, and the thalamus (Pfeiffer et al., 2014). The basal forebrain and hypothalamus also indirectly participate in this integration (Padova et al., 2022). The parietal cortex, known for its involvement in spatial cognition and multisensory integration, is especially significant in this process (Lopez et al., 2012). The thalamus, located within the diencephalon of the forebrain, serves as an essential hub for information (Kosif, 2016). Its ventral posterior nucleus directs vestibular data from the brainstem to the parietal cortex (Kosif, 2016). The insular cortex modulates emotional states influenced by vestibular inputs, impacting decision-making in emotionally charged situations (Ferrè et al., 2012). Additionally, the prefrontal cortex, foundational for executive functions, assimilates vestibular information, influencing cognitive aspects like attention and working memory.

Disturbances in the vestibular system can disrupt activity in the prefrontal cortex, potentially affecting decision-making capabilities (Hitier et al., 2014).

The complex relationship between vestibular function, cognition, and the specific functional roles vestibular inputs play in cognitive processes remains an area of research. Anatomical studies have expanded our understanding of the complex neural pathways essential for processing vestibular information. These pathways connect the vestibular nuclear complex in the brainstem to the ventrobasal thalamus, integrating signals from joint sensory receptors and the vestibular system. Key cortical regions such as the parieto-insular vestibular cortex (PIVC) and the parietal cortex combine vestibular, visual, and somatosensory inputs. Theories suggest these complex vestibular projections enable information transfer to the hippocampus, with the parietal cortex acting as a mediator (Barmack, 2003; Sakka & Vitte, 2004; Tascioglu, 2005).

Several published case studies have shown a complex two-way interaction between vestibular disorders and their impact on cognition, mood, and personality (Smith, 2012). Furthermore, individuals with attentional loss, cognitive disorders, and anxiety also displayed issues with balance (Staab et al., 2003; Furman et al., 2006). Bigelow et al. (2015) connected vestibular loss with cognitive decline in the elderly, emphasising that those with vestibular disorders often face cognitive challenges.

Two primary theories offer insights into the potential mechanisms behind this vestibular-cognitive link: the Enabling Model and the Independent Projections Model, the pathways of interaction may differ (Ferrè & Haggard, 2020). The Enabling Model suggests that the vestibular system provides foundational input to basic brain circuits, particularly those related to autonomic control. In this model, the primary target of the vestibular system

is the autonomic domain, with sensorimotor and cognitive functions influenced indirectly, based on their dependence on a healthy autonomic system. This model correlates to the interaction to a series of dominoes: if one is affected, the others will follow. Based on this theory, disturbances in the balance system could directly impact cognition, primarily mediated by vestibular projections to the frontal lobes (Lopez et al. 2012; Eulenburg et al. 2012; Ferrè & Haggard, 2020). In contrast, the Independent Projections Model suggests that the vestibular system communicates directly with various brain regions, suggesting that its influence on autonomic, sensorimotor, and cognitive areas might not be interlinked and each could be impacted independently (Ferrè & Haggard, 2020).

The vestibular system is connected to brain areas like the hippocampus, which is central to spatial memory, and regions associated with voluntary motor control, such as the striatum in the basal ganglia (Smith et al., 2010). Bilateral vestibular dysfunction (BVD), marked by impairments in both inner ears, results in spatial memory deficits. MRI studies reveal individuals with this dysfunction have a bilateral hippocampal atrophy of approximately 17% (Smith & Zheng, 2009). Such damage to the vestibular system affects hippocampal activity, leading to observed memory impairments in tasks including the digit symbol and block design (Smith & Zheng, 2009). Vestibular deficits have also been associated with reduced outcomes on the Corsi block test and increased levels of depression and anxiety (Smith & Zheng, 2020).

From a neuroanatomical perspective, the hippocampus, vital for spatial memory and navigation, undergoes reduced activation and structural changes due to vestibular loss, impairing these abilities (Zheng et al., 2012). Behaviourally, individuals with vestibular dysfunction often rely more on visual cues for spatial navigation (Smith et al., 2005). This could lead to challenges in situations with limited visual cues.

Research emphasises role of the vestibular system in spatial navigation (Bigelow et al., 2015). It helps maintain awareness of head orientation and position. Animal studies highlight its contribution to environmental mental representations, aiding in successful navigation without visual cues (Yoder & Taube, 2014). In humans, loss of this function affects navigation. For example, those with vestibular neuritis require more time to walk familiar routes with their eyes closed (Guidetti et al., 2008). However, with rehabilitation and compensatory strategies, many can improve their navigation skills over time, suggesting the cognitive effects of vestibular imbalance are usually temporary (Cohen & Kimball, 2002).

Physiological methods such as transcranial magnetic stimulation (rTMS) have demonstrated bilateral activations in the superior temporal cortex linked to inhibited attentional shifts in the horizontal dimension of space (Karnath & Dieterich, 2005). These activations suggest these structures are part of a network for voluntary attentional control (Karnath & Dieterich, 2005). Moreover, the cortical activation pattern observed in healthy individuals during a visual exploratory task mirrors that seen in patients with hemi-spatial neglect.

Following a discussion of the contributions of physiological methodologies to the comprehension of attentional control, it is imperative to further explore the neural transmitter systems that form the foundation of these cognitive processes. In animals with vestibular lesions, there's a documented decline in the cholinergic system, which relies on the neurotransmitter acetylcholine for signal transmission within the nervous system (Tai et al., 2011; Aitken et al., 2016). Acetylcholine is crucial for memory, learning, and attention, acting as a chemical messenger between nerve cells (Gould et al., 2015; Pepeu & Giovannini, 2016). A decrease in cholinergic activity, especially in the medial septum and diagonal band of Broca in the basal forebrain, can disturb the neurotransmitter balance needed for cognitive

performance (Schliebs & Arendt, 2017). When combined with changes in the hippocampus, this can lead to significant memory declines (Brandt et al., 2005; Zheng et al., 2009). Neurophysiologically, beyond the hippocampus, regions like the parietal and prefrontal cortices, integral for spatial attention and working memory, show altered activation in those with vestibular dysfunction (Dieterich & Brandt, 2015). These shifts could be behind the cognitive and attentional deficits seen in these individuals.

Data from 102 patients with vestibular dysfunction indicated that 85% displayed signs of memory and attentional deficits, accompanied by anxiety and depression symptoms (Smith & Darlington, 2013). Risey and Briner (1990-1991) found most of their vestibular dysfunction patients had difficulties with tasks like counting backward (Hitier et al., 2014). Furthermore, Sang et al. (2006) reported that patients with high rates of depersonalisation and derealisation symptoms, along with compromised attention, generally had vestibular impairments (Smith & Darlington et al., 2010). This observation is supported by subsequent research, including a study examining data from over 3,000 participants in the National Health and Nutrition Examination Survey (NHANES), which reaffirmed the strong connection between vestibular dysfunction and cognitive impairment (MacLean et al., 2013).

Furthermore, body tilt information, a component of the vestibular system, has been found to influence cognitive tasks, especially in visual perception. In a study conducted by Daiber and Gnugnoli (2023), variations in visual clarity based on body orientations were observed. This revelation confirms that changes in body position can affect visual task performance, emphasising the influence of the vestibular system on higher cognitive functions such as memory.

Beyond its role in cognition, the vestibular system significantly influences attentional processes. An impaired system necessitates more cognitive resources to maintain balance, leading to reduced cognitive availability for other tasks (Kahneman, 1973). Building on this foundational understanding, earlier research offers further insights. Kahneman's Capacity Model of Attention (1973) suggests individuals have a limited capacity for mental tasks. Experimental findings support this theory, indicating declines in mental performance for those with vestibular issues, especially when multitasking with balance and attention-driven tasks (Abernethy, 1998; Bigelow et al., 2015). Interestingly, individuals with poor baseline balance exhibit improved posture during mental tasks (Yardley et al., 2001).

Expanding beyond these fundamental cognitive effects, the importance of the vestibular system also reaches into the academic domain. Taking into account the association between the vestibular system and cognitive faculties, its implications on academic ability become evident. Vestibular dysfunctions can lead to challenges in communication and learning (Emami et al., 2012). A study by Franco and Panhoca (2008) has shown a relationship between vestibular anomalies and academic underperformance in some students. However, the specific connection between vestibular dysfunction and communication difficulties requires further investigation as a direct cause-and-effect relationship between lower academic performance and vestibular impairments cannot be definitively established based on current research. Other sensory impairments, such as auditory processing difficulties (Jack et al., 2010) and visual dysfunction (Maguire et al., 2006), can significantly disrupt learning efficacy. Therefore, a more comprehensive evaluation that considers the full spectrum of sensory systems is essential for accurately identifying the underlying factors at play.

Shifting focus from general academic impacts, it is crucial to explore the vestibular system's connection to specific neurological disorders, such as Specific Learning Difficulties (SpLDs). Given the vestibular implications, it becomes essential to initiate an exploration of its intersections with specific neuropsychological disorders, notably ADHD. This is particularly significant when considering executive function—a foundation of cognitive processing. Embodying pivotal abilities such as planning, problem-solving, and self-regulation, executive function is not only vital for everyday tasks but can also evolve over time. However, it is susceptible in conditions like ADHD and other Specific Learning Difficulties (SpLDs) including Dyslexia, Dyspraxia, and Auditory and Visual Processing Disorders (Barkley, 2010; McLuckie et al., 2018). Investigations centred on the sensory contributions to postural capabilities in individuals with ADHD suggest that specific postural capabilities, particularly balance control, require attentional resources. This is an essential sensorimotor skill that appears to be impaired in the ADHD population when compared to the normative group (Zang & Qian, Wang et al., 2003). Such impairments establish a link between ADHD and vestibular function (Woollacott & Shumway-Cook, 2002; Bucci et al., 2014). Furthermore, some ADHD symptoms mirror those found in disorders such as Traumatic Brain Injury and spatial neglect, which also share similarities with vestibular function. These similarities emphasise the idea that issues like spatial neglect could have roots in vestibular disorders at the cortical level (Karnath & Dieterich, 2005, Karnath & Dieterich, 2006). It is further supported by neuroimaging findings, which show the involvement of the superior temporal cortex in attentional orientation and spatial navigation (Karnath & Dieterich, 2005).

Given the association between the vestibular system and various cognitive functions, an examination of its influence on individuals diagnosed with ADHD and dyslexia provides a compelling opportunity. Such an exploration can deepen our understanding of its impact on

cognitive processes, lay the groundwork for potential therapeutic interventions, and provide targeted interventions, empowering individuals to overcome these temporal attentional challenges and improve their quality of life. Beyond specific disorders, these interactions have broader implications for how the human brain functions. The findings discussed shed light on the capacity of the human brain to manage multiple information streams and prioritise them. They expand our understanding of the complex relationship between sensory systems and higher cognitive functions, especially in conditions with compromised cognitive abilities. Cognitive performance challenges are not solely due to competition for specific resources, but indicate broader cognitive capacity limitations (Chari et al., 2022). The magnitude of cognitive impairments correlates with the attentional demands of tasks (Shumway-Cook et al., 1997; Yardley et al., 2001). The relationship between the vestibular system and cognitive performance highlights the impact of sensory systems on cognitive processes. When vestibular function is disrupted, the brain prioritises attention and resources to maintain balance, potentially at the expense of cognitive task performance, to prevent falls (Wallace & Lifshitz, 2016) based on the "orientation-first" principle (Gresty & Golding, 2009).

The connection between vestibular function and spatial attention is well-established in the literature. However, its link with temporal attention is less explored. Nevertheless, research suggests that cross-modal integration can enhance spatial attention (Lepecq, 2006; Mast, 2010; Volkening et al., 2014; Ferrè et al., 2015), leading to the hypothesis that similar mechanisms might bolster temporal attention. This hypothesis is grounded in the Dynamic Attending Theory (DAT), aligned with this thesis's central idea suggesting attentional processes can increase efficiency by leveraging the regularity of the vestibular system. Using this framework, interventions for populations with attentional deficits might explore the

potential for artificial vestibular stimulation to influence temporal responses, thereby improving cognitive functioning.

To summarise the breadth of this discussion, the vestibular system's impact on cognition arises from its interactions with cortical areas processing spatial, emotional, and executive information. Disturbances in this system underline the complex relationship between our sense of balance and overall cognitive abilities.

1.4 Physiology of the Vestibular System

The forthcoming section will concentrate on describing the physiology and operations of the vestibular system. Furthermore, it will expand on the association between the vestibular system and cognition, serving as the fundamental basis of this thesis.

The vestibular system can be broadly divided into the central and peripheral systems. The peripheral vestibular system is located in the inner ear, specifically in the petrous part of the temporal bone (see Figure 1.1). This system comprises sensory organs such as the otolith organs (saccule and utricle) and three semicircular canals, which detect linear and angular accelerations of the head, respectively. These organs aid in maintaining balance and spatial orientation. The bony labyrinth, a component of the peripheral system, consists of the cochlea (primarily responsible for hearing), vestibule, and the semicircular canals (Colclasure & Holt, 2004). It is filled with a fluid known as perilymph (Smith & Darlington et al., 2010). Inside the bony labyrinth is the membranous labyrinth, which contains alternative fluid called endolymph. On the other hand, the central vestibular system relays to parts of the brain, mainly the brainstem and cerebellum, and the neural pathways that process and integrate the sensory information received from the peripheral vestibular organs (Highstein & Holstein, 2012).

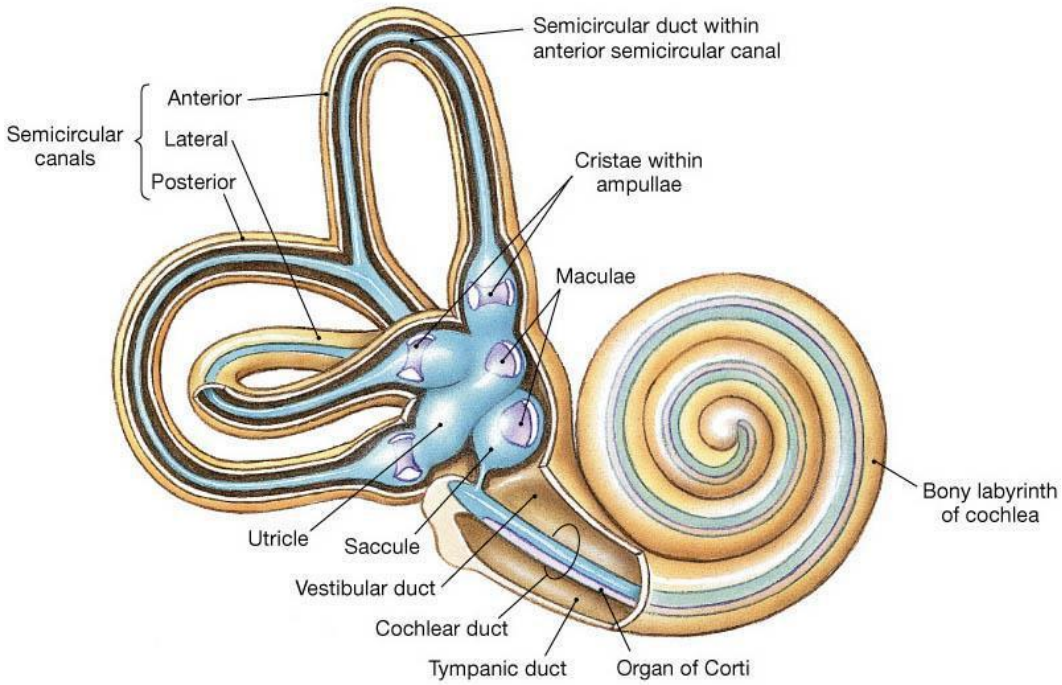

Figure 1.1: The structures of the peripheral vestibular system.

The membranous labyrinth is located within the bony labyrinth and contains tubes and sacs filled with endolymph, a fluid vital for hearing and balance. The membranous labyrinth is formed by two primary sacs: the utricle and the saccule. The utricle and saccule both detect linear accelerations and changes in head position relative to gravity (see Figures 1.2 and 1.3) (Jamali et al., 2008). Each of these sacs contains a sensory region called the macula, which has hair cells embedded in a gelatinous matrix with calcium carbonate crystals, known as otoliths, on its surface (Tilney et al., 1988). These otoliths add weight, allowing the gelatinous matrix to respond to gravity and head movements (Tascioglu, 2005).

Additionally, the membranous labyrinth includes the three semicircular canals, each ending in a region called the ampulla. Within each ampulla is the cupula, a gelatinous structure in which hair cells are embedded. These hair cells have bundles of hair-like structures: one longer kinocilium and several shorter stereocilia. The movement of the

endolymph fluid within the semicircular canals causes the cupula to shift, stimulating these hair cells and allowing the detection of angular (rotational) head movements in different planes (Angelaki, 2004; Angelaki & Hess, 2005; Angelaki & Cullen, 2008; Highstein & Holstein, 2012).

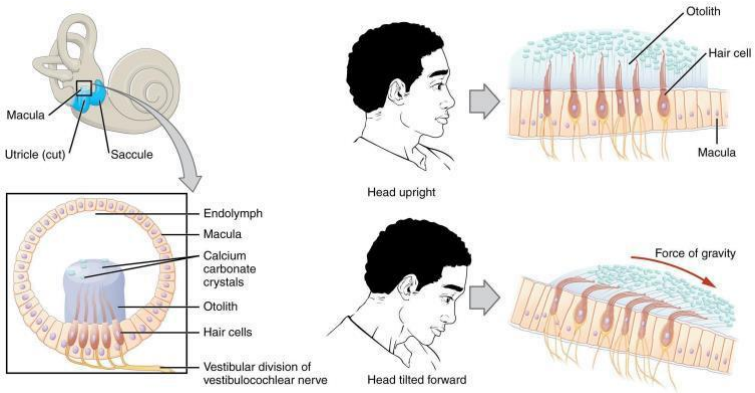

Figure 1.2: Diagram showing the sectional view of the ampulla, which contains the hair cells which make vestibular input to neuronal information.

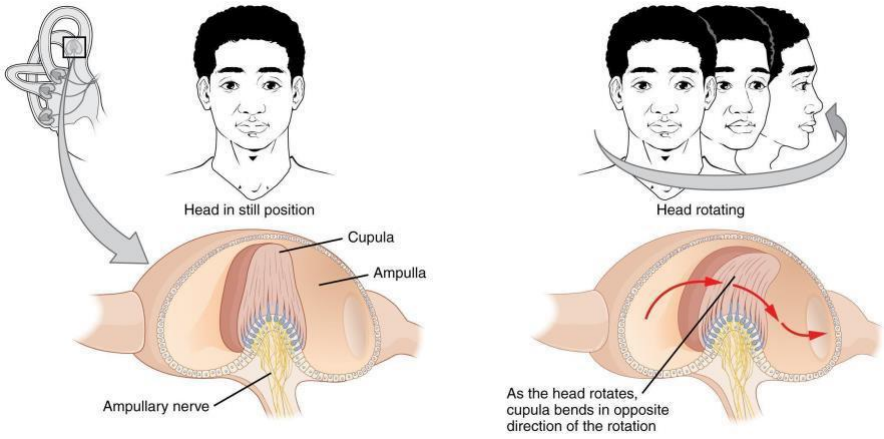

Figure 1.3: Diagram showing the vestibular hair cell in rotational acceleration.

Through these mechanisms, the vestibular system plays a pivotal role by converting mechanical stimuli into electrical signals. These are then transmitted to the brain via the vestibular nerve, a branch of the VIII cranial nerve, also known as the vestibulocochlear nerve (Korte & Mugnaini, 1979; Barmack, 2003; Highstein & Holstein, 2006). The impact of vestibular stimulation on the Central Nervous System (CNS) can be observed through the

integration of incoming signals from the semicircular canals and otolith organs at the secondary neuron level. This integration establishes connections with various regions of the CNS, with the initial processing taking place in the brainstem, specifically within the vestibular nuclei. This primary processing coordinates essential reflexes, like the vestibulo-ocular reflex (VOR) that stabilises gaze during head movements (Gurvich et al., 2013). After brainstem processing, these signals are transmitted to the cerebellum. At this time, the vestibular information integrates with several sensory systems: the visual system, aiding in the stabilisation of vision and the coordination of eye-head movements; the somatosensory system, related to tactile stimuli perception; and spinal inputs, which inform about body positioning, particularly of the lower half. When considering the peripheral vestibular responses, they influence the CNS through changes in eye movements, postural control, and the experience of dizziness or vertigo (Tarnutzer & Dieterich, 2019). This integration within the cerebellum ensures refined motor coordination and an accurate sense of spatial surroundings (Waespe & Henn, 1977; Kasper et al., 1988; Dickman & Angelaki, 2002; Barmack, 2003; Fitzpatrick & Day, 2004; Thaut et al., 2007; Shinder & Taube, 2010; Goldberg & Cullen, 2011; Cullen, 2012). Figure 1.4 (Duvernoy, 1999; Lopez & Blanke, 2011) shows several direct and indirect vestibular projections to cortical areas involved in cognitive processing (Lopez & Blanke, 2011).

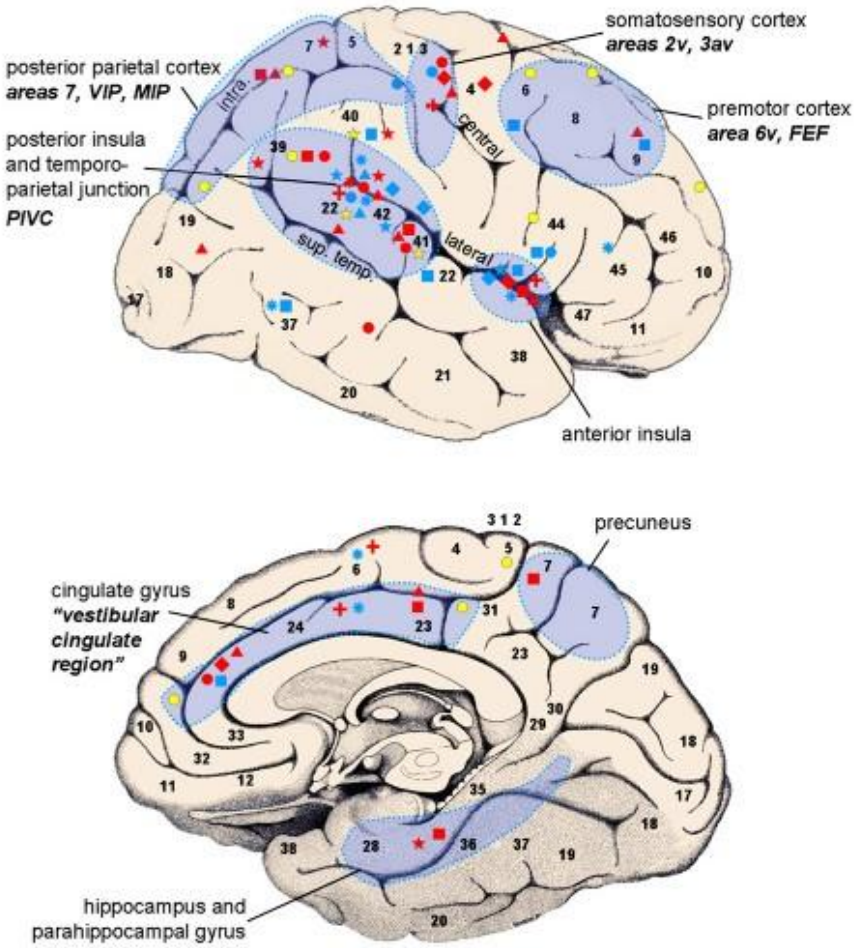

Figure 1.4: Vestibular areas in humans shown through neuroimagery during caloric (red symbols) and galvanic (blue symbols) vestibular stimulation, as well as during short auditory stimulation (yellow symbols). Right and left cerebral activations are displayed on a lateral view of the right hemisphere.

The vestibular system is linked to the central nervous system. The neuronal connections between the vestibular regions inside the brainstem and the cerebral and cerebellar cortex provide a neurophysiological basis for the relationship between vestibular and cognitive functions.

Vestibular stimulation (either naturally induced through head movement or via artificial thermal or galvanic stimulation) affects the endolymphatic fluid in the semicircular canals and otolith organs, leading to the modulation of firing rates in vestibular hair cells. Consequently, these alterations exert an impact on the activity of the vestibular nerve, an

integral part of the vestibulocochlear nerve (cranial nerve VIII), responsible for transmitting sensory information from the peripheral vestibular organs to the vestibular nuclei in the brainstem where it sends signals to the PIVC region which has crucial role in integrating and further processing sensory information, particularly vestibular information which then proceed to the thalamus and the cortical vestibular areas (Korte & Mugnaini, 1979; Barmack, 2003; Bense et al., 2003; Highstein & Holstein, 2006; Landau & Barner, 2009; Eggers & Benarroch, 2021).

Electrophysiological studies have further validated the presence of the PIVC in humans and its function as a core area of the vestibular network, receiving more than 50% of all vestibular inputs (Guldin & Grüsser, 1998). These findings underline the crucial role of the PIVC in vestibular function, and its diverse activation patterns - in memory, perception, attention, motor control, spatial orientation, navigation, mental representation of three-dimensional space, and other cognitive functions (Kotov et al., 2020).

Empirical evidence suggests that the PIVC region impacts blood flow across multiple cortical regions, with diverse activation patterns in response to varying configurations of GVS - a key method explored in this thesis. This influence is supported by observations made from lesion studies of infarctions within the middle cerebral artery territory (Brandt et al., 1994; Dieterich & Brandt, 1996; Fasold et al., 2002; Dieterich et al., 2003; Serrador et al., 2009; Wilkinson et al., 2013). Moreover, this phenomenon is endorsed by functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) studies, which have examined the effects of Caloric and Galvanic Vestibular Stimulations - modes of stimulation that are subject to variables such as type, intensity, individual health, and other physiological and environmental factors.

Caloric Vestibular Stimulation (CVS) and Galvanic Vestibular Stimulation (GVS) are two distinct methods used to assess the functionality of the vestibular system. CVS evaluates the horizontal semicircular canal and its associated neural pathways by applying thermal stimulation (Fitzgerald & Hallpike, 1942). In contrast, GVS involves the application of mild electrical currents to the mastoid processes, primarily stimulating the vestibular nerve and related structures in the inner ear, including the semicircular canals and otolith organs (Cohen & Yakushin, 2012; Ertl & Boegle, 2019;). Both CVS and GVS offer unique approaches to vestibular stimulation. GVS is non-invasive and precisely controllable, making it advantageous for research and potential clinical applications. However, discomfort and limited replication of natural sensations are challenges associated with GVS. On the other hand, CVS closely mimics natural vestibular stimuli through thermal stimulation, offering a more naturalistic experience and diagnostic value. Nevertheless, its invasiveness and variability in response pose limitations.

These techniques have validated the location of the PIVC, further showing that it is primarily activated by both whole vestibular nerve (GVS) and horizontal semicircular canal (CVS) stimulations. These stimulations cause changes in blood flow that correlate with improved repetition and comprehension in brain-injured patients (Muira et al., 1999; Heiss & Thiel, 2006; Hamilton et al., 2011). Neuroimaging findings have shown that various cortical and subcortical structures, including the Anterior Cingulate Cortex, temporoparietal cortex, insular cortex, and brain stem, are activated by vestibular stimulation (Lopez et al., 2012). It has been found that vestibular stimulation triggers the release of key neurotransmitters such as glutamate, noradrenaline, acetylcholine, and histamine (Horii et al., 1993; Horii et al., 1994; Ma et al., 2007; Samoudi, Nissbrandt, Dutia & Bergquist, 2012). These findings together suggest that vestibular stimulation could potentially modulate a wide range of sensory and higher-order functions, including cognitive function and recovery (Nishiike et

al., 2001; Klein & Albert, 2004; Miller et al., 2007; Holstein et al., 2012; Wilkinson et al., 2013; Black et al., 2016). This understanding of the PIVC region's impact on cognitive function sets the stage for exploring other brain regions involved in cognition.

The hippocampus uses a variety of sensory inputs to maintain cognitive function. One example is that the hippocampus is required for memory-processing tasks such as initial encoding, storage, and recall. It also has a role to play in spatial memory processes, working in conjunction with subcortical areas (Previc et al., 2014). This connection between sensory input and cognitive function mirrors the findings related to the PIVC region, further emphasising the complex interplay of different brain areas in maintaining and enhancing cognitive operations. Nonetheless, it is worth noting that within the scope of this thesis, only peripheral vestibular responses impacting the CNS will be considered. Further discussion of stimulation affecting the peripheral nervous system and musculoskeletal system will be excluded, as they are not relevant to the experimental outcome measures. In the forthcoming section, two methods of artificial vestibular stimulation will be elaborated on: Galvanic and Caloric methods. Elaborative focus will be directed towards the GVS as the primary method selected for examination within this thesis. However, for the purpose of facilitating comparison, a brief overview of the CVS will also be provided.

1.5 Galvanic Vestibular Stimulation (GVS)

Fitzpatrick and Day (2004) were two of the pioneers who utilised the Galvanic Vestibular Stimulation (GVS) as a method for evoking sensations of movement. GVS works by delivering low-amplitude electrical currents to the mastoid processes using self-adhesive electrodes as shown in Figure 1.5 (Ertl & Boegle, 2019), which primarily stimulates the vestibular nerve and associated structures within the inner ear, specifically the semicircular canals and otolith organs (Cohen & Yakushin, 2012). The inner ear contains sensory organs

known as cristae and maculae, responsible for detecting angular and linear accelerations, respectively. These organs are connected by primary afferent neurons, which convey information regarding head motion and position to the brainstem. Fitzpatrick and Day (2004) further indicated that the activity of these primary afferent neurons can be modified by the GVS current, thus altering the signals delivered to the brainstem. Research by Goldberg et al. (1984) demonstrated that both cathodal GVS in the perilymphatic space and anodal GVS on the afferent nerve fiber at a proximal point resulted in excitatory responses. This suggests that, in the presence of GVS, neurons might produce more action potentials than they would without such stimulation. The spike trigger zone of the primary afferent is where GVS acts, as both types of stimuli, cathodal and anodal, produce an outward depolarising current at this site. This depolarisation might result in an increased firing rate of the neuron (Fitzpatrick & Day, 2004). Interestingly, GVS seems to circumvent the transduction mechanism of the hair cells, the primary sensory cells in the vestibular organs, indicating that GVS might directly influence the activity of the primary afferent neurons without affecting the hair cells (Fitzpatrick & Day, 2004).

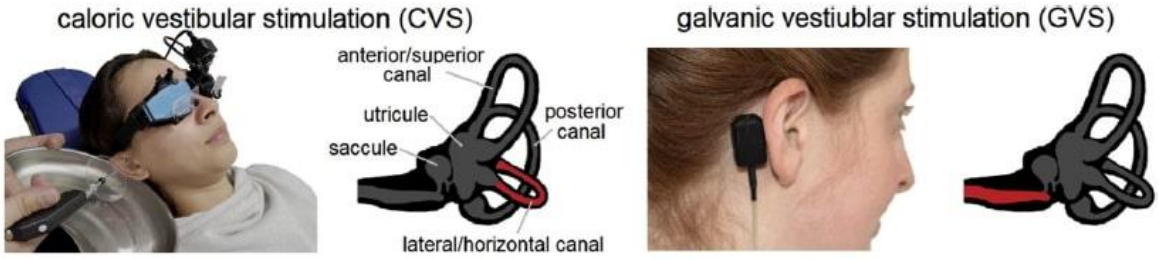

Figure 1.5. Illustration of two methods used to stimulate the vestibular system: CVS and GVS techniques. Permission has been requested from the authors for the inclusion of this figure.

Anode and cathode are terms used to refer to the two electrodes employed in GVS. During bilateral bipolar GVS, these electrodes are positioned on the mastoid processes, where the anode is placed on one side and the cathode on the other (Cohen & Yakushin, 2012). Current flows from the anode to the cathode, thereby generating an electrical field that

stimulates the vestibular nerve (Cohen & Yakushin, 2012). In the alternative configuration employed in this thesis, referred to as bilateral bipolar with positive Offset, the placement of the electrodes remained consistent, with the anode electrode positioned on the left mastoid and the cathode electrode placed on the right mastoid. However, a deliberate adjustment was executed on the GVS apparatus, manually configuring the current Offset to precisely half of the peak-to-peak amplitude. The Offset, serving as the reference point and representing the zero line, was positioned midway between the peak and trough of the AC waveform. This arrangement allowed the waveform to initiate from the Offset line, ascend to its peak amplitude, and subsequently return to the Offset line, all without crossing below the zero line. This distinctive pattern of oscillation would systematically repeat, maintaining a consistently positive Offset across all cycles during active GVS. The impact of GVS is dependent on several factors, including the polarity and intensity of the electrical current applied, as well as the individual's baseline vestibular function (Maitre & Paillard, 2016).

The forthcoming subsections will focus on an in-depth exploration of GVS, including physiological changes associated with stimulation, neuroimaging results, lateralisation results, postural effects, eye movement effects, as well as attentional and behavioural effects.

1.5.1 Vestibular System Network and Cortical Connections

Building upon its extensive network, the vestibular system establishes an expansive framework that extends to diverse brain regions through connections with the vestibular nuclei, effectively projecting its influence onto various higher level cortical centres (Lopez & Blanke, 2011). This network's operational effectiveness finds support in the diverse activation patterns evoked by GVS, as evidenced by studies conducted by Kim & Curthoys (2004), Ferrè et al. (2012), Wilkinson et al. (2014), Bressi et al. (2017), and Moossavi & Eshaghi (2022). These findings collectively imply that vestibular stimulation holds the potential to

engage thalamocortical mechanisms, thereby facilitating the restoration of dysfunctional cortical areas (Schiff & Pulver, 1999). The influence of GVS is far-reaching, extending to a range of brain regions including the limbic system, insula, cingulate gyrus, hippocampus, and parabrachial nucleus. This modulation is achieved through complex connections with cerebellar, brainstem, diencephalic centres, and amygdala cells (Lobel et al., 1998; Suzuki et al., 2001; Fasold et al., 2002; Stephan et al., 2005). The collective body of research emphases the profound implications of vestibular stimulation on the CNS.

1.5.2 GVS Influence on neurotransmission

Considering the impact of vestibular modulation on the CNS, it is expected to influence all regions receiving vestibular projections (Liu et al., 2023). The physiological changes associated with stimulation lead to the firing of GVS signals. These signals generate a time-dependent electric field that can modulate the signalling of Gamma-Aminobutyric Acid (GABA) receptors, (Farrant & Kaila, 2007; Rizzo-Sierra et al., 2014). As the primary inhibitory neurotransmitter in mammalian CNS, GABA plays a crucial role in regulating neuronal excitability. This is particularly evident in the vestibular system, where GABA controls the firing of vestibular afferent nerves (Rizzo-Sierra et al., 2014).

Building upon this understanding, research has highlighted the significant role of the GABAergic component within the olivocochlear system (auditory efferent system). This component is essential in maintaining the balance of structures within the inner ear, including hair cells and associated neurons (Maison et al., 2006, Rizzo-Sierra et al., 2014, Weech et al., 2018).

Stiles et al. (2018) marks a pivotal point in this exploration. Their study sheds light on how electrical stimulation of the vestibular system influences neurotransmitter activity in the

rat striatum, an fundamental part of the basal ganglia. This research not only enhances our understanding of the striatum's architecture and function, but also offers insights into neurological and behavioural mechanisms in rats, with potential implications for human studies. Stiles et al. (2018) further observed that electrical stimulation of the peripheral vestibular system alters the release of various neurotransmitters and neuroactive amino acids in the striatum. This includes changes in the extracellular levels of amino acids and monoamines, such as glutamate, GABA, glycine, dopamine, serine, threonine, and taurine, in response to vestibular stimulation. These findings align with earlier research by Ávila-Luna et al. (2015) and Khlebnikova et al. (2017). Furthermore, their study revealed a significant decrease in the release of serine and threonine, alongside a minor reduction in dopamine release within the striatum following vestibular stimulation (Kilb & Fukuda, 2017; Stiles et al., 2018). These outcomes emphasise the potential impact of vestibular stimulation on neurotransmission in the striatum.

These findings also contribute to our understanding of the role of the vestibular system in modulating neurotransmission within the basal ganglia. This is particularly relevant for conditions like Parkinson's Disease (Yamamoto et al. (2005); Pan et al. (2008); Ghazaleh Samoudi et al. (2012). The observed changes in neurotransmitter release in response to vestibular stimulation emphasise the complex relationship between the vestibular system and striatal neurochemistry. This opens new avenues for exploring the therapeutic potential of modulating vestibular input to improve neurotransmission and motor function (Pisani et al., 2005; Henneberger et al., 2010; Stiles et al., 2018).

1.5.3 Neuroimaging Insights into Vestibular Stimulation

Over the past few decades, considerable knowledge has been gained regarding the cortical processes and interactions of vestibular input through the comparative analysis of

results obtained from diverse imaging and stimulation techniques in human subjects using functional neuroimaging such as PET and fMRI, along with electroencephalography (EEG) and Event-Related Potentials (ERP) techniques, have been utilised to assess the effects of the stimulating site on cerebral blood flow and neuronal electrical activity (Ertl et al., 2019). For example, Bense et al. (2001) conducted a study utilising fMRI to examine the activation and deactivation patterns of specific brain regions during GVS. The study's notable activations of the blood-oxygen-level-dependent (BOLD) signal in various brain regions, including the anterior portions of the insula, paramedian and dorsolateral thalamus, putamen, inferior parietal lobule, precentral gyrus (frontal eye field), middle frontal gyrus (prefrontal cortex), middle temporal gyrus, superior temporal gyrus, and anterior cingulate gyrus, underscore the established involvement of these regions in diverse functions such as vestibular processing, attention, and motor control. In alignment with these findings, Philips, Ladoucer, and Drevets (2008) further suggest that GVS triggers activations in regions closely connected to the right parietal cortex. Particularly, the activation of the right dorsal anterior cingulate gyrus is associated with attention-generated goal-directed responses, supporting voluntary attentional control and temporal processes.

1.5.4 Lateralisation Effects of GVS

Lateralisation effects are described as the dominance of certain functions or processes in one hemisphere of the brain compared to the other (Bigelow et al., 2015). In the context of the vestibular system and spatial cognition, these effects are observed as differences in cognitive outcomes or behavioural responses, depending on the side of vestibular deficit or intervention (Dieterich et al., 2018). Understanding lateralisation effects is crucial in unravelling the complex interaction between the vestibular system and spatial cognition, shedding light on potential asymmetries in cognitive outcomes and the differential impact of interventions based on the side of vestibular deficit (Cross et al, 2020).

The physiological basis of these lateralised effects lies in the specialised organisation of brain functions across the hemispheres. Research by Vallar and Perani (1986) and Dieterich et al. (2003) highlights the hemispheric dominance for various cognitive and motor processes, explaining the complex relationship between specific brain regions and their associated functions. The left hemisphere predominantly controls functions such as receptive language, fine finger movements, and speech, while the right hemisphere is crucial for functions such as visuo-spatial orientation, attention, motion perception, saccadic and pursuit eye movements, and the processing of vestibular function (Dieterich et al., 2003).

Cross et al. (2020) further explored the lateralisation effects of GVS in the context of spatial cognition, focusing specifically on cases of unilateral vestibular deficits. The study highlighted the significance of applying GVS with the cathode on the lesion side, considering the varying effects depending on the side of vestibular deafferentation—a condition caused by the loss or dysfunction of the vestibular system, leading to reduced vestibular input to the brain. Cross et al. (2020) investigated the impacts of unilateral vestibular deafferentation (UVD) on spatial cognition and locomotion in mice. They observed the mice's movements in an open field task, noting that left-sided UVD caused more pronounced impairments in locomotion and spatial working memory compared to right-sided UVD. Interestingly, recovery in locomotion and spatial navigation was slower in mice with left-sided UVD. This results indicated that GVS intervention promoted vestibular compensation in both left and right GVS groups, evidenced by improvements in locomotion and spatial cognition. This led to the proposition that GVS, particularly when applied with the cathode on the lesion side, could be influential in managing spatial cognitive impairments due to unilateral peripheral vestibular damage (Borel et al., 2004).

The relevance of GVS extends to the study of lateralised effects in spatial attention, as documented in various studies (Karnath & Dieterich, 2005; Utz et al., 2011; Dieterich et al., 2018). For instance, in hemispatial neglect, the lateralised effects suggest a right hemispheric predominance in visuo-spatial processing and attention. This condition is further exemplified by the asymmetrical modulation of the left and right vestibular nerves in hemispatial neglect, where individuals often fail to acknowledge stimuli in contralesional space, mainly associated with right brain damage (Halligan & Robertson, 2014; Pellatt-Higgins, 2014). The study, supported by Wilkinson et al. (2014), suggested that GVS might induce cortical changes preferentially lateralised to the lesioned hemisphere, thereby rebalancing the attentional systems which are often chronically under or over activated. GVS has been instrumental in studying these lateralised effects as it can influence spatial cognition and attentional mechanisms, particularly in the context of vestibular deficits. Karnath & Dieterich (2005) and Utz et al. (2011) have documented the ability of GVS to shift attentional borders, influencing the perception of spatial information.

The effects of GVS extend to task performance, especially tasks that require balance or spatial awareness. GVS-induced lateralisation effects can pose challenges. During GVS, perceptual and postural shifts may lean towards the opposite side, potentially affecting task performance (Ferrè et al., 2013). Fink et al. (2003) highlighted that left-anodal and right-cathodal GVS predominantly activated the right hemisphere's vestibular projections, while right-anodal and left-cathodal GVS activated both hemispheres. Expanding on this, Ferrè et al. (2013) and Patel et al. (2015) noted a shift of spatial attention to the left with left-anodal GVS. In contrast, while Ferrè et al. (2013) observed a shift to the right with right-anodal GVS, Patel et al. (2015) found no noticeable effect. This suggests that GVS might overstimulate spatial attention networks in the hemisphere opposite the anode, leading to an attention bias on the converse side (Ferrè et al., 2013).

Transitioning from spatial cognition and attention, GVS has also been found to significantly alter an individual's body perception and task performance. Studies, such as those by Fitzpatrick et al. (2002) and Ferrè et al. (2013), show that GVS can induce sensations of movement or rotation even when stationary. Furthermore, GVS can alter perceptions of body size and shape (Ertl et al., 2018), who found that individuals under GVS influence perceived their bodies to be larger or smaller than actual, likely due to altered sensory information processing in the brain. This alteration in perception and sensory processing extends to behavioural domains as well (De Maio et al., 2021).

De Maio et al. (2021) demonstrated lateralised effects GVS on behavioural outcomes, particularly regarding risk-taking behaviour. The study found that left-anodal and right-cathodal GVS (L-GVS), predominantly stimulating the right hemisphere's vestibular projections, reduced risk-taking tendencies in the Balloon Analogue Risk Task (BART) compared to right-anodal and left-cathodal GVS (R-GVS), which activates the left hemisphere. This finding suggests a polarity-specific lateralised influence of GVS on behavioural outcomes. Additionally, neuroimaging findings have shown varying effects due to the activation of different hemispheric networks involved in behavioural control (Suzuki et al., 2001; Bense et al., 2001; Dieterich et al., 2003; Janzen et al., 2008; De Maio et al., 2021). These insights emphasise the role of the vestibular system in modulating risk-taking behaviour and highlight the lateralised impact of GVS on behavioural outcomes.

Lastly, it is vital to recognise that while general trends exist in brain lateralisation, there is considerable individual variation. Brain function lateralisation is not universally consistent and may vary among individuals. Evolutionary and developmental factors play a role in the emergence of lateralised functions. For instance, the maturation of certain sensory and motor systems, such as the vestibular system, may result in lateralised effects in specific

brain regions (Rogers, et al., 2021). Neuroanatomical connectivity is also crucial. Variations in the connectivity and organisation of neural pathways within the brain contribute to lateralised effects (Tomasi & Volkow, 2011). Differential connectivity of cortical and subcortical areas involved in sensorimotor control, spatial orientation, and attention can lead to lateralised processing of these functions (Dieterich & Brandt, 2023). Finally, genetic and environmental factors during brain development significantly influence the lateralisation of cognitive functions and sensorimotor processes, shaping an individual's unique neural architecture and capabilities (Duboc et al., 2015).

1.5.5 Posture and GVS

The complex anatomical, physiological, and neurochemical elements that make up the vestibular system render it essential for the control of movement and posture; it facilitates critical reflexes such as the vestibulo-ocular and vestibulo-spinal reflexes, essential for balance and spatial orientation (Bent et al., 2004; Chi & Crowson, 2022; Xie et al., 2023). The efferent component of the vestibular system, which regulates incoming sensory signals, plays a vital role in maintaining balance and spatial orientation (Bent et al., 2004; Straka et al., 2023). Postural control is greatly reliant on the vestibular system, which delivers continual feedback to the CNS about the body's position and movement (Cullen, 2023). This feedback is instrumental in real-time adjustments of muscle tone and activity, crucial for maintaining stable posture and balance (Markham, 2016). The vestibular system, working in conjunction with visual and proprioceptive inputs, is key for spatial navigation and postural control. Its significance is particularly highlighted in conditions where other sensory inputs are diminished or unreliable (Gaerlan et al., 2012; Markham, 2016; Chaudhary et al., 2022; Chepisheva, 2023).

GVS has been found to significantly influence postural stability (Dlugaiczyk et al., 2019; Paula, et al., 2022). Postural responses are especially elicited by GVS when individuals are in a standing position (Wardman et al., 2003; Fitzpatrick & Day, 2004; Cathers et al., 2005). GVS impacts posture by eliciting distinct balance responses in the semi-circular canals and otolith organs. Cathers et al. (2005) indicate that GVS evokes separate canal and otolith reflexes by altering afferent firing rates on both cathodal and anodal sides, resulting in changes in body alignment and motor responses. This suggests independent control mechanisms for balance, likely via different neural pathways. The otolith organs are linked to short-latency reflexes and minor sway, while the semicircular canals correlate with medium-latency responses and greater sway, demonstrating the ability of GVS to selectively activate specific vestibular organs for postural shift and regulation (Cathers et al., 2005).

In recent studies, its impact on postural management has been further illuminated. For instance, Nooristani et al. (2019) observed that postural steadiness improved during GVS administration, with the enhancement lasting several hours post-stimulation. Additionally, research involving Parkinson's disease patients with balance issues indicated that using GVS strengthened balance and subsequently improved their overall well-being (Inukai et al., 2020; Oliveira et al., 2023).

For individuals recovering from strokes, the vestibular system often contributes to skewed vertical perception and balance disturbances. Tohyama et al. (2021) examined the effect of GVS on these issues post-stroke, finding that the outcomes varied based on the polarity of the stimulation and the side of the hemispheric lesion, and noted that supra-threshold GVS can lead to compromised balance (Sprenger et al., 2020).

Other studies further reveal the effectiveness of GVS in enhancing postural stability in both healthy individuals and those with vestibular disorders like bilateral vestibulopathy (BV). GVS is known to amplify the vestibulo-ocular and vestibulo-spinal reflexes, integral for balance and coordinating eye movements with head and body motion (Iwasaki et al., 2014; Iwasaki et al., 2017). Anthony et al. (2014) demonstrated that GVS significantly impacts sensory reweighting, a process where the CNS integrates various sensory inputs to maintain postural equilibrium. This study found that short-duration GVS can counteract excessive postural sway caused by visual and proprioceptive disturbances in younger individuals. However, this benefit was less noticeable in the elderly individuals, possibly due to an age-related decline in vestibular function, which limits their ability to counter multisensory perturbations.

GVS is observed to increase ground reaction force and mean centre of pressure displacement, leading to greater postural instability, particularly in older individuals (Xie et al., 2023). It induces larger body sway and impairs static and dynamic postural control, exacerbating upper body, head, and trunk rotation, and increasing body sway in various directions during standing and walking tasks. The effects of supra-threshold GVS are more pronounced in older individuals, indicating higher susceptibility to GVS-induced perturbations compared to younger individuals (Xie et al., 2023).

The observed results aligned with the stochastic resonance phenomenon, a concept where the capacity of the system to detect weak signals is enhanced by the introduction of an optimal level of noise or electrical stimulation (Battaglini et al., 2023). This seemingly paradoxical effect, where noise actually improves signal detection and processing efficiency, sheds light on how low-level electrical stimulation can enhance sensory perception. For instance, in the human vestibular system, where the application of stimulation methods such

as sub-sensory GVS or Vibration-based Vestibular Stimulation (VVS) can enhance the detection of weak vestibular inputs (McDonnell & Ward, 2011). This optimal level of stimulation is thought to enhance information processing in the vestibular system, thereby improving postural stability (McDonnell & Ward, 2011; Wuehr et al., 2018; Xie et al., 2023).

In bilateral vestibulopathy, GVS has also shown promise in reducing the high-frequency components of centre of pressure movement, offering sustained postural stability improvements post-stimulation (Fujimoto et al., 2018). Thus, GVS presents significant implications for postural control. This is especially evident in the crucial role of stimulation intensity, as highlighted by findings that higher intensities of GVS result in a larger postural shift compared to sub-sensory GVS (Wardman, Day, et al., 2003).

1.5.6 Eye Movement and GVS

Subsequent research explored how various elements, like stimulation type and the presence of visual cues, can modify eye movements during GVS. Such information is pivotal in understanding the vestibular system and its relationship with other sensory modalities. One key role of the vestibular system is overseeing the vestibulo-ocular reflex (VOR), ensuring the stabilisation of the visual field during head or body movements (Say et al., 2021). Depending on the specifics of the GVS, like its intensity or duration, the VOR may be affected in different ways.

For instance, a study indicates that GVS can optimise the responsiveness of the VOR, implying a more accurate and timely eye movement in relation to head motion. Shanidze et al. (2012) observed that specific types of GVS influenced the VOR, irrespective of the lighting conditions or if the head was restricted in movement. The underlying belief is that GVS stimulates the semicircular canals, primary sensors in the vestibular system, and can

thus alter reflexes like the VOR and the vestibulo-collic reflex (VCR), which manages head and neck stabilisation during bodily movements. In contrast, some studies noted a reduction in VOR efficiency during GVS, especially if the stimulation direction aligned with the direction of head movement (McGarvie et al., 2015). Findings included alterations in VOR with varying gaze angles or head speeds and the observation that age had minimal impact on VOR up until the late 80s (McGarvie et al., 2015). Anson et al. (2016) found that as the VOR efficiency declined in elderly participants, there was a rise in compensatory saccades during head impulse tests. As such, Kaur (2022) suggested that such observations stem from the interaction of natural vestibular signals generated by head movements with those induced by GVS.

In the context of eye movements, both saccades, characterised by rapid shifts of gaze between objects, and smooth pursuit, which involves the eyes smoothly tracking a moving object, can be influenced by GVS (Kim, 2013). The stimulation parameters of GVS play a vital role in influencing the magnitude and trajectory of these eye movements. Research has shown that near-threshold stimulation can initiate swift eye movements (Cauquil et al., 2002). Further exploration into the specific intensities and response patterns of GVS effects on conscious vestibular perception, and reflexive oculomotor nystagmus in healthy individuals is needed (Thanh et al., 2022). Key findings revealed sensations such as dizziness or a tendency to fall were more pronounced towards the cathode, particularly when the current surpassed the vestibular threshold. Mild tingling was also felt more around the cathode, either exclusively or combined with the anode, when it surpassed the sensory threshold. When the current exceeded the oculomotor threshold, there was a more prominent horizontal and torsional nystagmus towards the cathode compared to the anode (Thanh et al., 2022).

1.5.7 Attentional Modulation

The vestibular system significantly influences various cognitive domains, including spatial and non-spatial perception, memory, and executive functions, through its connections with key brain regions such as the parietal and prefrontal cortices (Chen et al., 2013; Ertl & Boegle, 2019). GVS, in particular, plays a dynamic role in modulating visual attention and spatial cognition (Mast, 2010; Volkening et al., 2014). This modulation extends to memory processes, affecting both short-term and long-term memory, and executive functions, indicating the system's capacity to modify attentional resources in cognitive tasks (Ertl & Boegle, 2019).

Spatial attention is particularly influenced by GVS, which affects vestibular afferents and directs attention towards the stimulated side, a mechanism likely rooted in the connection between the vestibular nuclei and the parietal cortex (Eulenburg et al., 2012; Ferrè et al., 2013). Additionally, vestibular inputs have been shown to affect spatial perception, for instance, by inducing shifts in the perception of horizontal space, as demonstrated in a study by Ferrè et al. (2013). Moreover, vestibular stimulation has implications for visual attention, particularly in tasks involving rotational perception. For example, Berger and Bülthoff (2009) found that vestibular stimulation modulates attention in visual tracking tasks, suggesting an influence on the integration of visual and inertial cues.

Memory enhancement is another area impacted by GVS. Kamali et al. (2023) demonstrated that Vestibular Rehabilitation combined with GVS significantly improves memory recall in patients with amnestic Mild Cognitive Impairment. A study by Lee et al. (2014) indicated that GVS may enhance visual memory recall, as evidenced by reduced errors and altered beta waves in the frontal cortex. This supports the findings of Wilkinson et al. (2010) and Utz et al. (2010) regarding GVS's impact on cognitive functions and memory. Additionally, recent animal model studies involving mice have shown that GVS significantly

enhances long-term spatial memory, particularly in addressing spatial navigation deficits due to vestibular impairments. Mice subjected to bilateral vestibular deafferentation or unilateral labyrinthectomy demonstrated significant improvements in spatial memory and navigation following a five-day GVS procedure. These results suggest the potential of GVS as a therapeutic tool for spatial cognition-related memory impairments, though further investigation is required for its application in humans (Thanh et al., 2022).

The influence of the vestibular system extends to somatosensory sensation as well. A study by Ferrè et al. (2013) revealed that GVS improved the detection of light tactile stimuli on the fingertips, suggesting an enhancement of somatosensory sensitivity. This influence also extends to clinical populations, with evidence indicating that GVS enhances visual and spatial attention in individuals with neurological conditions like Parkinson's disease, highlighting its role in modulating executive functions (Cai et al., 2018).

Overall, while the vestibular system's role in modulating attention is evident, the exact mechanisms remain elusive. Theories range from the direct amplification of sensory stimuli to more indirect influences, such as arousal or cognitive control modulation, which are key components of executive function (Ertl & Boegle, 2019).

1.6 Caloric Vestibular Stimulation (CVS)

Caloric vestibular stimulation (CVS) is a physiological thermal technique used to assess the functionality of the vestibular system, specifically targeting the horizontal semicircular canal and its associated neural pathways (Figure 5) (Fitzgerald & Hallpike, 1942). This technique involves the introduction of warm or cold water into the external ear canal, resulting in a change in temperature of the endolymph fluid that fills the semicircular canals. Consequently, the movement of fluids triggers stimulation of the sensitive hair cells

within the semicircular canal. This stimulation leads to an eye movement response called nystagmus and can also elicit sensations of motion or vertigo in the individual receiving this type of stimulation (Lidvall, 1961). In addition to its applications in neurology and audiology, CVS has found used in the field of cognitive research due to its impact on a range of brain functions, including cognition and mood (Utz et al., 2010).

Despite the valuable insights that can be gathered from CVS, its potential to induce participant discomfort such as temporary sensations of dizziness, tingling, itching, or warmth must be acknowledged. In the context of this thesis, the distinct advantage of GVS lies in its capacity to precisely manipulate key electrical stimulus parameters, including amplitude, frequency, and waveform and, most importantly, to set its Onset (beginning of the electric current delivered) and Offset (ending of the electric current) to coincide tightly with that of visual stimuli. This tailored approach is in alignment with the research hypothesis, as it would provide me with the opportunity to experimentally manipulate the interaction between vestibular signals and temporal attention processes, mirroring the success observed in studies addressing visuo-spatial cognitive impairments (Kerkhoff & Schenk, 2012; Schmidt-Kassow et al., 2016).

1.7 Psychology of Temporal Attention

Temporal attention refers to the ability to focus attention on specific sensory, visual, or auditory stimuli from our environment to enhance our capacity to predict upcoming events (Coull et al., 2000). One way to quantify temporal attention is through behavioural measures, such as discrimination and detection tasks. These yield data suggesting that temporal attention enhances early perceptual processing. Another approach involves physiological measures, like the ERP methodology, which offers high temporal resolution. This is ideal for investigating the dynamic effects of temporal attention on real-time processing. This method

has provided insights into the modulation of P300 latency during early visual processing (Doherty et al., 2005; Correa et al., 2006).

ERP experiments use demanding perceptual tasks, such as letter discrimination, to detect modulations in early visual processing. A prior ERP study revealed that temporal attention affected the amplitude and latency of the P300 components. In the context of demanding perceptual tasks, the results suggest that directing temporal attention influences both late motor and early visual processing (Correa et al., 2006). Physiological investigations have pinpointed a network of brain regions responsible for directing visual attention to spatial locations (Corbetta & Shulman, 2002; Correa et al., 2006).

Studies on visuo-spatial attention have shown that responses to stimuli presented at specific locations increase cerebral blood flow and early electrophysiological activity in the contralateral extrastriate cortex concerning the attended location. Additionally, there is activity in the bilateral frontoparietal network, which, while not directly tied to visual attention, might overlap with visual processing areas (Heinze et al., 1994; Luck et al., 2000; Correa et al., 2006).

In comparison, the anatomy of visual temporal attention is less explored. Early fMRI studies by Coull and Nobre (1998) indicate that visual temporal attention activates the left premotor cortex more than spatial attention does. There is also activation in the superior colliculus and subcortical structures of the auditory pathway linked to temporal attention (Rinne et al., 2008). This implies that regulated motor processes are more commonly found in temporal attention compared to instinctive preparation processes (Correa et al., 2006). However, it is important to note that these observations were primarily evident in detection tasks requiring a quick motor response. The documented modulation of motor processes

might stem from the simplistic nature of the detection task, rather than the actual involvement of temporal attention orientation (Correa et al., 2006).

1.8 Vestibular information and Temporal Attention

The brain's capacity to integrate information from various modalities and develop robust sensory perceptions based on stimuli from our physical environment is known as multisensory integration (Ernst & Bülthoff, 2004; Chandrasekaran, 2017). Having multiple senses offers numerous advantages. Each sense excels in specific situations, and having multiple senses enhances the likelihood of perceiving and differentiating occurrences or objects of interest. Furthermore, the integrated output provides a more holistic understanding of external events than when considering its individual components (Stein & Stanford, 2008). Evaluating multisensory integration means comparing how effectively a combined stimulus from different sensory modes prompts a response in comparison to the singular stimuli forming that combination (Meredith & Stein, 1983; Stein & Stanford, 2008).

It is worth considering the difference in the strength or probability of a response to an event with both visual and auditory elements, as opposed to reactions to just the visual or auditory stimuli individually. Such multisensory integration can either amplify or diminish a neural response. In essence, the degree of multisensory integration mirrors the relative biological significance of an event (Stanford & Stein, 2007; Stein & Stanford, 2008).

Building upon this idea, multisensory integration principles suggest that temporally coincident sensory signals enhance signal processing in the brain. This integrated processing enhances our ability to differentiate between various sensory stimuli, directing effective action (Ernst & Bülthoff, 2004; Alais et al., 2010; Chandrasekaran, 2017). Temporal and spatial coincidence of these inputs is crucial for such integration. For instance, Talsma and

colleagues (2010) designed a demanding visual search experiment to demonstrate the impact of stimulus-driven multisensory integration on the process of attentional selection. The results of their study highlighted how the presence of auditory cues improved the visibility of a visual target in the midst of competing distractors.

Another study by Escoffier, Sheng, and Schirmer (2010) further explained auditory-visual cross-modal entrainment. They investigated how the alignment of visual attention Onset with the Onset of the musical creates a synergistic effect, where the combined interaction of these factors produces a result greater than the sum of their individual effects. The outcomes of both experiments confirm that multisensory interactions occur across different physiological stages within the processing hierarchy, highlighting the deep interconnected nature of brain networks (Klemen & Chambers, 2012).

Extending this line of thought to the vestibular system, one could propose that concurrent vestibular signals might also amplify temporal processing of attention. Schmidt-Kassow and colleagues (2016) explored the effects of GVS on auditory processing and target detection. They specifically explored GVS effects synchronised to the temporal characteristics of an auditory oddball task. Their findings suggest that synchronised vestibular signals can enhance auditory processing, potentially by entraining neural oscillations. Interestingly, while their study shed light on this neural activity, the behavioural consequences remain less explored. In this context, the DAT offers a compelling framework for further exploring the understanding of vestibular-visual temporal dynamics.

1.9 The Dynamic Attending Theory (DAT)

Patterns of the temporal oscillations within a metric framework are known as rhythm (Jones & Boltz, 1989). Rhythmic patterns are often characterised by unexpected temporal

highlights and attention-getting time variations, such as lengthened or shortened intervals (Jones & Boltz, 1989). Notably, the width of an attentional pulse is dependent on the temporal regularity of the stimulation. One might argue that there exists a significant phase coupling between the entraining process and the internal oscillation. This periodicity, driven by high rhythmic regularity, is crucial in guiding focused attentional pulses. However, an excessive unpredictability related to a rhythm of a pulse can scatter attentional resources. This is relevant as the attentional pulse can be envisioned as a probability distribution; therefore, its width and length are inherently connected. As events become more frequent, heightened attentional energy is directed towards predicting the next potential stimulus (Fard & Maisel, 2012). It follows that the temporal arrangement of an event plays a role in determining perceptual accuracy (Henry & Herrmann, 2014).

According to the DAT, neural mechanisms of attention are modulated and entrained by external stimuli (Jones & Boltz, 1989). Predictive temporal cues can synchronise attention and motor functions at precise moments in time (Vossel et al., 2014). Regularly presented sensory stimuli, in line with a set rhythm, entrain attentional oscillations and boost the processing of sensory information that aligns with this rhythm (Bendixen et al., 2015). This model is a valuable tool for exploring the interaction between the vestibular system and temporal attention.

The DAT provides an important insight into the core fundamental of attentional oscillations, particularly in the auditory domain (Jones & Boltz, 1989). The theory suggests that attention is not a constant occurrence, but varies in harmony with time-based patterns, such as the rhythmic elements found in music. Essentially, this theory proposes that individuals naturally align their state of attention with external rhythms, which enhances their concentration on anticipated beats or specific moments in time (Jones & Boltz, 1989).

The theory of dynamic attending proposes a unique relationship between rhythmic patterns and attentional systems. Originally proposed by Jones, Boltz, and Kidd (1982) and subsequently explored by Large and Jones (1999), this theory suggests that the attentional system aligns itself with rhythmic patterns, leading to heightened attention during moments considered rhythmically significant. Essentially, based on the environmental structure, the brain formulates predictions about incoming information, employing these anticipations to optimise the processing of sequential information (Paquette et al., 2013).

Empirical support for the dynamic attending theory can be found from research conducted by Kunert and Jongman (2017). Their experiments demonstrated shorter response times from participants when visual letter strings were synchronised with auditory rhythm peaks compared to when they matched rhythm troughs. These findings are in parallel with previous studies on nonhuman animals, which have shown that auditory periodicities can coordinate motor behaviours with an underlying rhythmic beat (Schachner et al., 2009). Thus, it can be inferred that auditory rhythms can potentially enhance visual attention and unconscious perception, especially in immediate judgment tasks. This implies that alterations in the frequency of sensory stimuli within a particular domain can exert a substantial influence on perceptual responses in a different domain.

Building on this, Paquette et al. (2013) argued that the auditory system automatically utilises predictions to optimise sequential processing. Rooted in predictive coding theories, it is suggested that the brain distinguishes environmental regularities, actively anticipating subsequent events. This continuous scanning for patterns aids in formulating predictions about imminent occurrences (Friston, 2005). Within this theoretical framework, the brain operates on a hierarchical prediction model influenced by Bayesian inference. This means the brain's predictions, spanning various processing stages, are hierarchically structured in which

upper-level predictions guide those at lower levels. As such, the brain continually refines its predictions, based on the accuracy of the sensory data it receives (Friston, 2005; Paquette et al., 2013).

In light of the fact that the vestibular system continuously monitors head movement, it is intriguing to speculate about whether rhythmic head movement can direct spatial attention in a manner similar to rhythmic sound. The intuitive way in which humans nod their head to music could be taken as informal evidence that vestibular inputs inform attentionally-guided action, and gives further reason to determine if a recurrent vestibular signal sharpens attention to other forms of sensory stimuli that occur at the same time.

The utilisation of GVS stands out as a particularly promising avenue for investigating the complex relationship between temporal attention, DAT principles, and the vestibular system. The technique enables a user-determined signal frequency to be set and by means of experimental software to be tightly coupled to the frequency and Onset of other forms of sensory input. In this way, it becomes possible to determine if an underlying vestibular rhythm, as ordinarily induced by periodic head movement, affects the time course and accuracy of visual response.

1.10 Thesis Plan

Chapter 1 was to build upon existing literature to lay the foundation for subsequent empirical chapters. Within this context, the rationale employs GVS in concurrence with the Delayed Matching-to-Sample (DMTS) attentional paradigm, guided by the principles of the DAT. By merging the vestibular modulation capabilities of GVS with the temporal attention principles proposed by the DAT, a DMTS framework was formulated to examine the

relationship between rhythmic vestibular signals and its effect on entraining temporal attention.

Chapter 2 investigates the potential of entraining the visual domain through the application of Direct Current (DC) GVS in alignment with the principles of DAT. The preliminary findings are of particular interest as they reveal an inhibitory effect emerging from the point of synchronous Offset. This observation is noteworthy given the traditional association of DC stimulation with enhanced performance in sensory tasks. Additionally, the same DC stimulation demonstrates an overall facilitating impact on auditory tasks. However, it does not appear to exhibit time-locked improvements in attentional processing when rhythmic DC signal is aligned with the auditory stimuli. This discrepancy between the visual and auditory domains warrants further investigation. As such, the stimulation protocol transitions to Alternating Current (AC) stimulation to validate and further investigate these inhibitory effects in the visual domain. This decision to shift to AC is informed by literature suggesting that AC can have different, often more powerful, entraining effects on cognitive processes compared to DC (Moreno-Duarte et al., 2014; Dowsett & Herrmann, 2016; Cole & Voytek, 2017; Żebrowska et al., 2020). Once more, inhibitory effects are seen, initiating from the synchronous Offset onwards. The recurring inhibitory impact in visual tasks across both DC and AC modalities raises new questions about the modality-specificity and temporal characteristics of vestibular influence on temporal attention.

In Chapter 3, two primary objectives were addressed. The first objective was to determine whether the AC signal, as a more effective entrainer, could align with the overarching hypothesis by enhancing auditory performance when time-locked at the synchronous Offset. Contrary to the hypothesis, the results indicated an overall facilitatory effect, similar to that discussed in Chapter 2. Interestingly, the same effect did not hold within

the clinical population with known temporal deficits. The second objective was to investigate the inhibitory effect in the visual domain. A novel AC bilateral bipolar stimulation protocol with a positive Offset was introduced, hypothesising that this would modulate only the right hemisphere. Surprisingly, findings were similar across both stimulation protocols, with performance deteriorating from the synchronous Offset onwards.

Further experiments indicated that optimal integration between visual attention and the vestibular cortex is influenced by visual contrast and cognitive load, possibly affecting mechanisms such as the VOR and activity in the PIVC. The synchronous time point and subsequent Offsets lasting 800 ms appear to be critical temporal markers for this cross-modal interference effect, which can be further compromised under suboptimal conditions. This finding opens a new avenue for exploring more specific time points to understand the timescale required for the brain to return to baseline.

Chapter 4 transitioned to employing the Rapid Serial Visual Presentation (RSVP) paradigm to gain a deeper understanding of the time-course and nature of the interference effect previously observed in Chapters 2 and 3, targeting a 100-800 millisecond window for more precise temporal insights. Unexpectedly, the RSVP paradigm did not alleviate the Attentional Blink (AB) effect. The three experiments detailed in Chapter 4 did not provide evidence to support the notion that the interference effect observed in prior chapters originates from processes engaged during the RSVP task. Moreover, these experiments failed to demonstrate a consistent enhancement effect. Interestingly, variations in GVS frequency within the upper alpha band resulted in contrasting performance outcomes, implying a potential modulation within this frequency band. These findings suggest that improvements in visual attention can be highly time-sensitive and may require innovative phase-locking techniques for further validation.

Chapter 5 brought together key findings that enhance the understanding of how the vestibular system interacts with temporal attention across visual and auditory domains. While the rhythmic properties of the vestibular system do influence attention, the effects are not uniform across tasks, timings, or sensory modalities. Notably, unique negative interference occurs in the visual domain, unlike the beneficial effects seen in auditory. These findings suggest an optimal range for effective visual-vestibular integration. Overall, the research advances our knowledge of multisensory temporal attention and raises new questions about the role of the vestibular system in higher cognitive functions and paves the way for further investigations into how this age-old sensory system integrates with complexities of human cognition.

Chapter 2 – Vestibular Modulation of Visual and Auditory Dynamic Attending

As observed in Chapter 1, the Dynamic Attending Theory (DAT) paradigm can be used to show that intermittent visual stimuli presented at the same rhythm as a continuous auditory rhythm are processed more efficiently than when presented alone. The following chapter will explore whether the same occurs when visual stimuli are presented against a continuous vestibular rhythm. To assess the generality of any effect, auditory stimuli are also deployed in several of the studies.

One of the most extensively researched constructs in cognitive psychology is working memory (WM), described as the capacity to store information for a short period (Daniel et al., 2016). Delayed matching-to-sample (DMTS) experiments are among the most widely used to investigate the underlying psychological and biological mechanisms of WM (Toornstra et al., 2019). In this chapter, the DMTS task was combined with the principles of The Dynamic Attending Theory (DAT) to test whether individual vestibular signals can inform attentional judgements of stimuli that must first be held in WM. In particular, I tested whether visual responses were shortened or more accurate when the delayed matching-to-sample visual stimulus occurs at the same temporal rhythm as the background vestibular signal. Both visual detection and visual discrimination tasks were administered to manipulate the difficulty and cognitive contribution. The detection task looks to see whether the processes involved in simply detecting the presence or absence of visual stimuli are affected while the discrimination task looks to see whether higher-level processes that draw on visual memory are affected. If response times to the appearance of the sample are either shortened or more accurate when it coincides with the Onset of the vestibular signal, then, consistent with DAT, it can be concluded that the periodicity of the vestibular signal affects the moment-to-moment responsiveness of visual attentional processes.

Several studies have focused on the utilising Direct Current (DC) or Alternating Current (AC) to stimulate and modulate the vestibular system (Scinicariello et al., 2001; MacDougall et al., 2006; Dakin et al., 2007). In this chapter, I used two types of sub-sensory galvanic currents controlled by the GVS device, resulting in DC stimulation (used in Experiments 1, 2 and 3) and an AC stimulation (used in Experiments 4, 5 and 6). The choice of using sub-sensory GVS in both DC and subsequent AC stimulation was based on its documented capability to enhance vestibular responses while also eliminating transcutaneous sensations, paraesthesia, and movement perception (Cauquil & Day, 1998; Cauquil et al., 2002; Wilkinson et al., 2012; Schmidt-Kassow et al., 2016; Duncan et al., 2022). During the initial experiments of this thesis, I experimented with a DC signal because this provided a simple means of sending discrete, individualised signals that could be tightly locked to the Onset and Offset of visual stimuli. In later experiments, I experimented with AC signals that are less discrete, but may have more powerful entraining effects.

Empirical research consistently demonstrates that trans-mastoidal stimulus amplitudes lower than 0.8 mA are effective in eliciting reliable vestibular responses. For instance, a study by Cauquil et al. (2002) found that 0.1 mA of stimulus is adequate for inducing torsional slow phase eye movement, indicating effective stimulation of the vestibular labyrinth. Complementing this evidence, Cauquil and Day (1998) asserted that a 0.7 mA stimulus can provoke a significant upper body tilt without causing saturation in the upper body segments or substantial pelvis tilt, further reinforcing the idea that such stimulations are congruent with vestibular labyrinth activation. Moreover, Schmidt-Kassow et al. (2016) utilised sub-sensory GVS at a current intensity of 0.3 mA, a level below the threshold for evoking sensations of movement or discomfort. Notably, this application of synchronous sub-sensory GVS at 0.3 mA during an auditory oddball task led to an enhanced

P300 response to pitch deviants, compared to both asynchronous and sham stimulation conditions.

Furthermore, in an EEG investigation conducted by Wilkinson and colleagues in 2012, a sub-sensory Direct Current Galvanic Vestibular Stimulation (DC-GVS) of 0.4 mA was administered to participants while they were engaged in a visual discrimination task. The post-data processing steps included the application of band-pass filtering to the EEG data within the range of 0.3–30 Hz, aimed at eliminating the GVS artifact. The results indicated that a sub-sensory GVS of 0.4 mA was sufficient to evoke the N170 event-related potential (ERP) component and to assess power within the alpha and beta frequency ranges (Duncan et al., 2022). These collective findings highlight the efficacy and reliability of low-amplitude trans-mastoidal stimuli in activating the vestibular labyrinth. Furthermore, a more recent study by Duncan et al. (2022) utilised a low amplitude current, oscillating between 0.20 and 0.30 mA, for several reasons. First, observable physiological responses such as oculomotor torsion and body roll-tilt have been reported from currents as low as 0.1 mA. Second, a lower amplitude current minimises sensations like itching or tingling at the stimulation site, which is crucial for maintaining effective blinding of participants between active and no stimulation conditions. Third, frequencies within the 0.01 Hz range, employed in this study, are known to alleviate motor symptoms in Parkinson's disease. Lastly, the choice of a low amplitude current was also driven by the need to ensure safety and tolerability for participants, in light of minor adverse effects reported in previous GVS studies. As such, I strategically selected a low amplitude current to balance the necessity of measurable physiological responses with the safety and comfort of the participants.

2.1 AC/DC reimagined

In this section, I will examine the differences between Direct Current Galvanic Vestibular Stimulation (DC-GVS) and Alternating Current Galvanic Vestibular Stimulation (AC-GVS) to provide an examination of their effects and a rationale for selecting each waveform in the following experiments.

DC-GVS displays a boxcar profile, with the current often elevated within the span of milliseconds to a constant plateau of intensity. Subsequently, it is deactivated after a specified duration. DC-GVS is the application of a small electrical current to the mastoid process behind the ear. This process can induce a sensation of movement or rotation in the body (Stephan et al., 2009). During the application of DC stimulation, it has been reported that the perception of rotation may not remain consistent throughout the entire duration of the stimulation (Stephan et al., 2009). This inconsistency appears to originate from the abrupt on and off states of stimulation, which correspond with the observable effects of GVS on behaviour, however these effects are weaker during periods of continuous DC stimulation (Stephan et al., 2009). The initiation and termination of the current results in pronounced vestibular sensations that persist until the stimulation is turned off. As a result, a significant portion of the Blood-Oxygen-Level-Dependent (BOLD) responses observed in fMRI, are triggered by DC-GVS, which are linked to the Onset and Offset of stimulation (Stephan et al., 2009). DC-GVS is commonly utilised in research to explore the involvement of the vestibular system in diverse cognitive and motor functions. According to Ertl and Rainer Boegle (2019), investigations employing DC-GVS have primarily observed whole body oscillations in the frontal/roll plane. In contrast, their findings indicate that ultra-short DC-stimuli lasting 3ms failed to elicit a sensation of body tilting.

AC-GVS smoothly transitions in its cycle and is visualised as a sine wave. Using AC to activate the vestibular system results in robust vestibular sensations, thus inducing movement sensations (Stephan et al., 2009; Cohen & Yakushin, 2012). Despite being less studied than DC-GVS, AC-GVS demonstrates potential for clinical applications in managing balance disorders and rehabilitating neurological conditions (Cohen & Yakushin, 2012). fMRI studies have revealed that the activation patterns elicited by AC-GVS are comparable to those seen with DC-GVS, involving multisensory vestibular projection areas (Stephan et al., 2009). The influence of AC or DC GVS on the vestibular system may differ depending on the brain hemisphere predominantly engaged in vestibular processing (Ertl & Rainer Boegle, 2019). Stephan et al. (2005) indicated that AC-GVS, whilst similar to DC-GVS, activates multisensory areas with some stimulation-specific differences, albeit relatively subtle for stimulation frequency or cortical location. Stephan et al. (2009) further highlighting that AC-GVS uniquely alters the perceived movement direction, an effect not observed with DC-GVS, thereby demonstrating distinct impacts on the vestibular system. AC-GVS significantly influences postural control by activating both canal and otolith afferent populations in the vestibulospinal tract, as demonstrated in animal studies (Nakazono et al., 2022). This emphasises the vestibular system's key role in postural control. However, the effect of AC-GVS is multifaceted, and depends on factors such as the frequency and intensity of the stimulation. For instance, frequencies above 1 Hz can enhance the phase lead of GVS-evoked spike discharges from vestibular afferents (Nakazono et al., 2022). In contrast, low-frequency AC-GVS (below 2 Hz) induces a mild rocking sensation and sinusoidal-patterned postural sways that are proportional to the current intensity until a saturation point is reached (Hammam et al., 2011). These effects tend to reduce or disappear at higher frequencies. As such, AC-GVS has proven to be a valuable tool for investigating postural responses (Lee et al., 2021).

To investigate the objectives of this thesis, I employed three distinct GVS configurations as illustrated in Table 2.1 (Day & Fitzpatrick, 2004). The first configuration used a traditional bilateral bipolar DC montage described by Day and Fitzpatrick (2004). In this setup, electrodes are positioned on both mastoid processes with a constant current passed between an anodal electrode on the left mastoid and a cathodal electrode on the right. In the other configurations, an AC signal was passed between the electrodes, with polarity constantly switching between the electrodes in one of these configurations, but remaining the same in the other.

In the other setup, the bilateral bipolar with positive Offset (explored in Chapter 3), a deliberate adjustment was made on the GVS device to manually set the current Offset to half of the peak-to-peak amplitude. This ensured that the waveform remained positive throughout its oscillation. To verify the desired effect, an oscilloscope was used during the pilot phase. The aim was to create a unique pattern of unilateral periodic excitation, based on traditional unilateral stimulation, where one electrode is placed on the mastoid and another non-stimulating electrode on areas like the forehead, neck, or arm. This modified setup intended to stimulate only one ear, mirroring Fitzpatrick and Day's (2004) approach. Such stimulation could potentially affect neural activity in specific areas of the right cerebral hemisphere, influencing spatial awareness, balance, and other brain functions.

In the initial experiments of this thesis, the DC bilateral bipolar waveform was chosen because it resembled the brief Onset/Offset of the auditory stimuli, based on the principles of the DAT by Jones and Boltz (1989). After initial experiments indicated that the DC waveform did not modulate temporal responses or induce temporal entrainment, variations in the AC waveform were introduced. However, it is essential to understand that waveform

selection was primarily for mirroring the structure of auditory stimuli or to provoke the psychological phenomenon of entrainment, not for their physiological impacts.

The primary objectives of this study were to investigate the temporal properties of the vestibular system by examining different electric charge flows (AC or DC) and polarities (zero Offset or positive Offset), aiming to enhance vestibular system temporal characteristics and improve performance in attention-based tasks reliant on WM.

2.2 General Method

2.3 Participants

A total of 144 participants were recruited across 6 experiments in this chapter with identical designs and procedures. Following Cohen's (1992) established guidelines, which form the foundational framework proposing a necessary statistical power of at least 0.80 for reasonably detecting an existing effect, a statistical power of 0.80 (as detailed in Section 2.11) was deemed suitable for this experimental paradigm, indicating a balanced approach that considers both statistical validity and practical factors such as time, resources, and participant recruitment logistics. The stopping rule for Chapters 2 and 3 was based upon maintaining a statistical power in excess of 0.8, resulting in a minimum sample size of n = 22.

All participants in this chapter were undergraduate students at local universities recruited by local and online advertisements. Participants received either partial course credit or payment equivalent to minimum wage. Individuals with neurodevelopmental conditions (e.g., ADHD or dyslexia) or neurological conditions (e.g., motor neurone disease or epilepsy), head injury with loss of consciousness, metallic or electronic implants, balance or hearing problems, or pregnancy were rejected in the initial screening session and therefore

were not part of the study. The screening process involved the completion of a self-administered questionnaire, which is detailed in Appendix A. The University of Kent School of Psychology ethics committee approved all studies. All participants signed written informed consent before taking part in any experiment.

2.4 Stimuli and apparatus

Visual and auditory stimuli were presented using PsychoPy, version 1.85.3 (Peirce et al., 2019). Visual stimuli consisted of 16 unique Gabor patches generated using a free website designed by Mathôt (2020). Gabor patches were presented on a 20-inch Dell monitor (1,024 x 768 pixels, 60 Hz refresh rate). Gabor patches were presented for a duration of 0.2 seconds at a size of 10 cm x 10 cm on a black background (standard RGB colour-space: 0, 0, 0, equivalent to PsychoPy's custom RGB scale: -1, -1, -1).

Gabor patches were presented at two screen locations per trial randomly chosen out of four, as shown in Figure 2.1. Presentation locations were the corners of an imaginary square, with its origin at the centre of the monitor. Distances to presentation locations were 15 % of both screen width and screen height from the centre. Screen coordinates for locations on a standard scale (x = 0, y = 0 being top left and x= 1, y = 1 being bottom right) were [0.35, 0.35], [0.65, 0.35], [0.35, 0.65], and [0.65, 0.65]. On PsychoPy's custom screen co-ordinate scale (x = -1, y = 1 being top left and x = 1, y = -1 being bottom right) locations were [-0.3, 0.3], [0.3, 0.3], [-0.3, -0.3], and [0.3, -0.3].

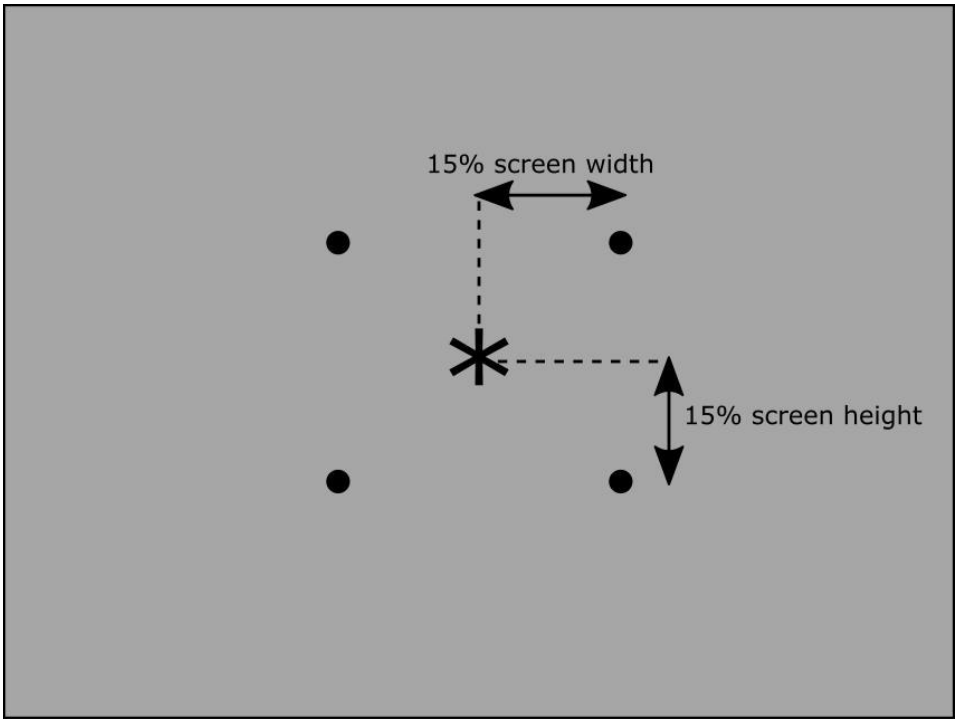

Figure 2.1: Possible on-screen presentation locations (dots) for Gabor patches in visual modality experiments (2 locations per trial). Distances are relative to the screen's centre (*), where the fixation asterisk is presented during the experimental task.

Auditory stimuli consisted of 16 unique tones with a 600–700 Hz frequency range in 6.25 Hz increments. These tonal frequencies fall outside the range associated with the induction of vestibular evoked myogenic potentials (Todd et al., 2014; Schmidt-Kassow et al., 2016). Tones were presented through Sony headphones (model number: MDR-ZX310/ZX310AP) at a volume of 75 decibels (dB) for 0.2 seconds.

GVS was delivered using a NeuroConn DC-Stimulator (model number: 0021) in combination with a pair of 5.1 x 10.2 cm carbon rubber, self-adhesive, disposable electrodes (Covidien, Uni-Patch Inc. product ID: EC89260). Three different GVS types employed are illustrated in Figure 2.2: DC bilateral bipolar pulse, AC bilateral bipolar and AC bilateral bipolar with positive Offset. In Chapters 2 and 3, all GVS configurations, the peak current was 0.05 mA below each participant's sensory threshold, the frequency was set to 0.5 Hz, and duty cycles were 2 seconds long. For DC bilateral bipolar the duty cycle was set to 50%. For

AC stimulation, the phase was 90 degrees (see Appendix C). The Offset for AC bilateral bipolar was 0 mA. The Offset for AC bilateral bipolar with positive Offset was equal to half the peak-to-peak amplitude.

To synchronise the timing of the experimental stimuli with the current stimulation, PsychoPy was employed as the experiment control system for administering the experimental protocol. The specifications to determine the suitable settings for parameters such as amplitude, frequency, duty cycles, and phase for each experimental setup were reviewed, as described in the neuroConn DC-Stimulator Plus manual (model number: 0021). This ensured an accurate setup and triggering of stimuli at the intended time points specified in the PsychoPy script. The current was transmitted via a parallel-to-coaxial cable to establish communication between the PsychoPy script and the GVS device. Within the PsychoPy code, a port address specification was included to enable interaction between the computer and the GVS device, thus facilitating control over stimulus presentation and timing. GVS cycles were delivered at a frequency of 0.5 Hz, signifying that each cycle lasted for 2 seconds, identical to the duration of each experimental stimulus. For synchronised trials, the instruction to deliver a GVS pulse from the neuroConn box was initiated at exactly the same time as the instruction was given to present the visual/auditory stimulus, in turn creating two temporally coincident signals. For asynchronised trials, the instruction to present the visual/auditory stimulus occurred either slightly before or after the instruction to deliver the GVS pulse, in turn reducing the temporal co-incidence of the two signals. During the pilot testing phase, electrodes were linked to an oscilloscope to visually confirm the waveform's shape and the current's direction, and to monitor the alignment between the simultaneous activation of the current and the Onset of the experimental stimuli. More details about the characteristics of the GVS waveforms and its physiological impact within the CNS can be seen in Table 2.1.

GVS configuration	Electrode positioning	GVS waveform	Waveform characteristics	Physiological effects within the CNS
DC bilateral bipolar	Anode on left mastoid and cathode on the right mastoid	Square Wave	DC current flows from the anode on the left mastoid to the cathode on the right mastoid	This setup decreases firing rate of the left vestibular nerve while increasing the firing of the right vestibular nerve. The targeted areas include the dorsolateral thalamus, anterior parts of the insula, the superior temporal gyrus, the inferior parietal lobule, the precentral gyrus, the middle frontal gyrus, and both cerebellar hemispheres.
AC bilateral bipolar	Initial Anode on left mastoid and initial Cathode on the right mastoid	Sinusoidal	When the Offset is set to zero, the direction of anodal current continually reverses as the wave alternates between its maximum (i.e., peak) and minimum (i.e., trough)	This set up leads to a continuous switch in the excitation and inhibition of the left and right vestibular afferent neurons. This might lead to successive stimulation of both hemispheres. The targeted areas include the dorsolateral thalamus, anterior parts of the insula, the superior temporal gyrus, the inferior parietal lobule, the precentral gyrus, the middle frontal gyrus, and both cerebellar hemispheres.
AC bilateral bipolar with positive Offset	Active Anode on left mastoid, and Cathode on the right mastoid	Sinusoidal	When the Offset is set to midway between current minimum and	This setup induces a repeated cycle in which excitation of the left afferent nerve rises and then falls back to zero. This waveform may

	maximum, the polarity of each electrode remains constant	elicit a similar pattern of excitation in right hemisphere. The targeted areas include the right hemisphere's anterior cingulate cortex, temporal gyrus, and middle/superior frontal gyrus.

Table 2.1: Details about the GVS Waveform and its physiological impact within the CNS.

2.5 Procedure

Participants were tested individually in a dimly lit laboratory at the University of Kent. After completing eligibility screening and informed consent, participants were fitted with GVS electrodes. The GVS montage, shown in Figure 2.2, included bilateral mastoid set up. To minimise impedance, the skin was cleaned using isopropyl alcohol wipes and abrasive electrolyte gel before applying GVS electrodes. Impedance was checked at the beginning of thresholding and before each of the four experimental blocks and kept at or below 10 kΩ.

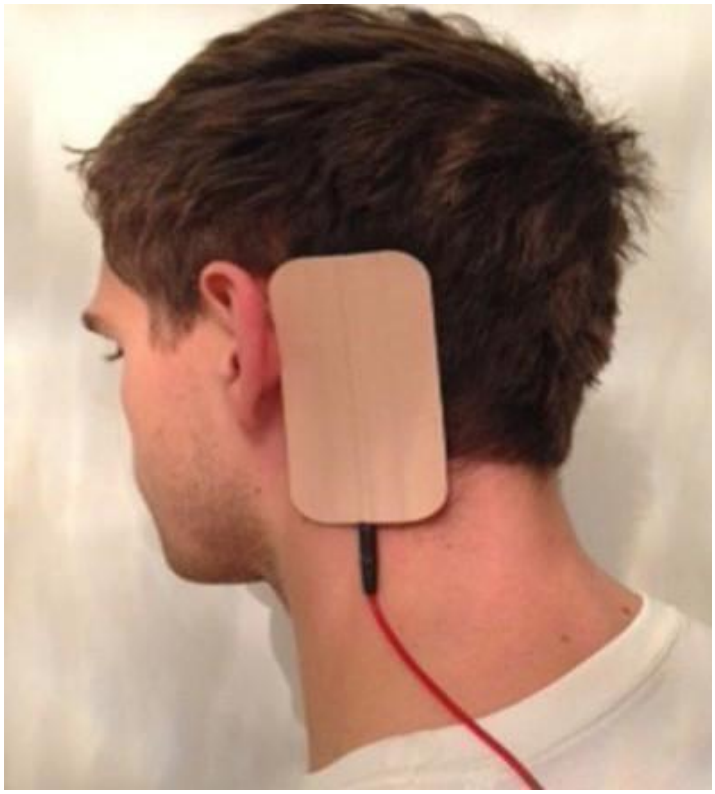

Figure 2.2: The montage for GVS used a pair of 5.1 x 10.2 cm carbon rubber, self-adhesive, disposal electrodes (Covidien, Uni-Patch Inc. product ID: EC89260) that covered bilateral mastoid. Photograph used with permission of the participant.

The choice of GVS electrode size is important, as it is a contributing factor to shaping cortical electric field patterns and should therefore be taken into consideration depending on the research objectives (Bikson et al., 2010). Small and large electrodes offer distinct advantages and limitations in terms of electrical current distribution, specificity, comfort, and impedance.

Small electrodes are an ideal choice for delivering targeted stimulation (Truong et al., 2023). These electrodes facilitate a focused delivery of current to the vestibular organs, especially to the anterior canals of the inner ear, which are vital for postural control, as demonstrated in Parkinson's disease studies (Nooristani et al., 2019). Multimodal Imaging-Based Detailed Anatomical Models show that with small electrodes, less current loss occurs at the scalp level (Truong et al., 2023). As such, the magnitude of the current entering the cerebellum and temporal regions is higher compared to larger electrodes, where more current

loss occurs at the scalp and results in more current flow in the brainstem regions (Truong et al., 2023). However, the reduced surface area of small electrodes tends to increase impedance, potentially compromising comfort during extended periods of use and, most importantly, reducing the sensory threshold at which the transcutaneous current can be felt (Truong et al., 2023).

In contrast, large electrodes spread current over a wider range of vestibular nerve and typically result in lower impedance, making them more suitable for extended use and enabling blinding at higher stimulus intensities. Additionally, the greater surface area facilitates easier placement and securement on the head. Furthermore, larger electrodes could take into account the position of the vestibular nerve underneath the mastoid which could be subject to inter-individual variability (Wyssen et al., 2023). However, on the downside, it may also contribute to non-specific influences on cortical excitability or arousal.

Importantly, both small and large electrodes will likely stimulate other sensory nerves (i.e., vagal, proprioceptive) within the region of the mastoid, making it very difficult to claim that GVS only stimulates the vestibular system. Accordingly, while my experimental set-up allows me to propose that the observed effects reflect vestibular stimulation, in the same fashion as every GVS experiment that has been published, I cannot make such a claim definitively and must accept the multi-sensory nature of GVS.

2.6 GVS sensory thresholding

The purpose of the thresholding procedure in this study was to establish the somatosensory threshold for GVS for each participant, thereby minimising their sensory responses to the stimulation. This was achieved by determining the sensory threshold for GVS using a modified Up-Down procedure (Dixon, 1965), which presumes a constant

sensory threshold. During this process, participants were seated, faced forward, and engaged in light conversation with the experimenter to distract them from the stimulation.

The initial GVS intensity was set at 0.3 mA for a duration of 10 seconds in the pilot test and extended to 30 seconds for the main experiment. This adjustment was made because participants could detect GVS with only 10 seconds of stimulation, compromising the integrity of the threshold determination.

To determine the somatosensory threshold, the intensity of GVS was gradually adjusted in increments of 0.05 mA, ranging from 0.3 mA to 0.6 mA, depending on the participant's perception of the stimulation. The final threshold was established at 0.05 mA below the lowest intensity that elicited a sensory response in each participant. This adjustment was to maintain blinding with respect to the conditions (active GVS or no stimulation) and to ensure that the stimulation did not produce a detectable sensory response. To confirm the GVS sensory threshold, the identified intensity was repeated across four additional trials.

In the pilot phase, the initial maximum stimulation intensity was 0.8 mA, later reduced to 0.7 mA after participants were able to identify active GVS blocks in a blinding questionnaire (Appendix A). To maintain the study's blinded design, the maximum intensity was further reduced to 0.6 mA. This adjustment ensured that participants could not detect the GVS during active blocks, thus preserving the blinding of experimental conditions.

Participants who reached the sensory threshold at the lowest intensity (0.2 mA) were excluded. Those who did not perceive the stimulation up to the maximum intensity of 0.6 mA were subjected to stimulation at this upper limit during the experiment. The effectiveness of

blinding was verified at the end of each session through a questionnaire (Appendix A), with participants reporting any sensations being excluded from the main study. Following thresholding, participants were positioned 57 cm from a computer monitor for subsequent tasks, with their dominant hand on designated keyboard response keys (N or M), arranged in a counterbalanced order across participants.

A benefit of employing sub-sensory GVS lies in its ability to minimise sensations such as itching or tingling at the stimulation site, vital for maintaining effective blinding of participants and ensuring their tolerability.

2.7 The role of no stimulation protocol

In GVS studies, the control of non-specific effects is crucial to the validity of a study. Non-specific effects include influences unrelated to the primary focus of the study, such as general arousal and tactile sensations from the electrodes or discomfort from the stimulation (Lopez et al., 2010). These can serve as distractors, altering participants' focus and thereby affecting the study's outcomes (Lopez et al., 2010). For example, if a participant is distracted by tingling sensations, their performance may be compromised, making it difficult to attribute observed changes specifically to GVS (Lopez et al., 2010).

There are some studies that support the use of 'no stimulation' as a control condition in GVS studies to differentiate between effects directly attributable to GVS and those induced by non-specific factors, as well as to minimise the placebo effect (Lenggenhager et al., 2007). The term 'no stimulation' has been used to describe the condition in which participants believe they are receiving stimulation when, in fact, they are not. In some studies, no stimulation is administered (e.g., Wilkinson et al., 2016). Other studies prefer an active sham stimulation, which involves an initial, brief period of super-sensory stimulation to deceive

participants into thinking they are receiving stimulation throughout the entire experiment (e.g., Sprenger et al., 2020). However, while this latter method controls for non-specific effects, it is likely to still produce unwanted physiological effects during the stimulation period. Accordingly, it may be best considered as a 'lower dose' rather than 'no dose' at all.

In the experimental design of this thesis, the no stimulation control group did not receive any active stimulation whatsoever. This 'no stimulation' method offers a cleaner interpretation of results (i.e. vestibular stimulation vs no stimulation at all).

2.8 Experimental Task

After the thresholding procedure, participants completed a practice block to familiarise themselves with the experimental task. The practice block consisted of 10 trials chosen at random from the main experimental block. Each experiment consisted of four blocks to counterbalance the ordering of GVS condition (active GVS and no stimulation) and response keys (N or M, depending on the task) in a Latin square (see Appendix D). Each block contained 64 trials (256 trials overall). Blocks were divided into 30-second break periods. Gabor patches were presented in visual modality experiments for 0.2 seconds at two randomly chosen screen locations out of four per trial. In auditory modality experiments, stimuli tones were presented via headphones. Detailed descriptions are provided in the Stimuli and Apparatus section.

At the beginning of each experimental block, a fixation asterisk (*) was presented in the centre of the monitor for 30 seconds. GVS was started at the Onset of the fixation asterisk in active conditions. Experimental trials began after this initial fixation period. A diagram of the trial sequence is shown in Figure 2.3. The first stimulus (S1, time 0) was presented for 0.2 seconds immediately after the initial fixation asterisk Onset. Two seconds

after S1 Onset, a second fixation asterisk was presented for 0.5 seconds. Stimulus 2 (S2) was presented at five different Offsets: 3.2, 3.6, 4, 4.4, and 4.8 seconds after S1 Onset (time 0).

In detection tasks, participants were instructed to respond as soon as they detected S2 by pressing the designated key (either M or N on the keyboard, depending on the block). In discrimination tasks, participants were instructed to indicate whether S2 matched or mismatched S1 as quickly and accurately as possible by pressing either M or N on the keyboard. Stimuli were chosen at random with the constraint that S1 and S2 matched on half the trials (on 128 out of 256 trials across the four blocks).

Participants' response times were calculated from S2 Onset. The waiting period for a participant's response was fixed to 3.5 seconds, after which a trial was marked as missing and excluded from analyses. Individual trials' duration was fixed to 8.3 seconds (latest Onset of S2 plus maximum wait for a response: 4.8 + 3.5 seconds). Including the initial fixation period, single block duration was approximately 9 minutes (30 sec fixation + [8.3 sec x 64 trials] = 561.2 seconds). Participants received a 30-second break after each of the four experimental blocks, during which they could move their heads freely while remaining seated. The overall experimental task duration including breaks was approximately 40 minutes ([561.2 seconds x 4 blocks] + [3 x 30 sec inter-block break] = 2334.8 seconds).

At the end of the experimental tasks, the GVS montage was removed. Participants filled in a blinding questionnaire (see Appendix A3), were debriefed (see Appendix B4), and received either course credit or payment.

2.9 Statistical Design

Demographics for eligible participants by experiment are reported in Table 2.2. Three participants were excluded. The chance level was 50% accuracy in this study; as per the exclusion criterion chosen by Knakker et al. (2021), the acceptable performance threshold was 60% accuracy averaged over no stimulation conditions.

All experiments in this chapter were identical in terms of statistical design and procedure but varied in modality (visual or auditory), task (detection or discrimination), and GVS type (DC bilateral bipolar pulse or AC bilateral bipolar).

ID	Modality	Task	GVS type	N	Male	Age (years)
E1	Visual	Detection	DC bilateral bipolar	23	8	M=20, SD=3 Min.=18, Max.= 32
E2	Visual	Discrimination	DC bilateral bipolar	22	9	M=22, SD=3 Min.=18, Max.= 29
E3	Auditory	Detection	DC bilateral bipolar	24	3	M=20, SD=2 Min.=18, Max.= 24
E4	Auditory	Discrimination	DC bilateral bipolar	24	10	M=21, SD=3 Min.=18, Max.= 29
E5	Visual	Detection	AC bilateral bipolar	24	8	M=23, SD=4 Min.=18, Max.= 33
E6	Visual	Discrimination	AC bilateral bipolar	24	5	M=21, SD=2 Min.=18, Max.= 25

Table 2.2: Demographics for analysed data by experiment.

In the Delayed Matching-to-Sample paradigm, the two main tasks—detection and discrimination—were distinguished by the cognitive demands they placed on participants. Detection tasks were simpler and involved the simple recognition of the presence of a stimulus. In these tasks, participants were instructed to press a key as quickly as possible when they perceived the second stimulus, irrespective of its attributes or its similarity to a prior sample. In contrast, discrimination tasks were more cognitively demanding, requiring not only detection, but also a comparative assessment between the initial sample stimulus and a second one. Participants had to press a key to indicate whether the second stimulus

was identical or different from the original, thereby engaging memory and decision-making processes. Therefore, while detection tasks were designed to measure the perceptual sensitivity of individuals to either auditory or visual stimuli, discrimination tasks went a step further by evaluating the participant's ability to differentiate between distinct stimuli.

As illustrated in Figure 2.3, the Offset variable indicates when S2 was presented relative to the Onset of the third intra-trial GVS cycle (counted from S1 Onset at the start [time 0] of each trial). S2 Onset occurred either before the Onset of the third GVS cycle (i.e., S2 was presented at an Offset of 3.2 or 3.6 seconds from S1 Onset), at the same time (i.e., S2 was presented at an Offset of 4 seconds from S1 Onset), or after (i.e., S2 was presented at an Offset of 4.4 or 4.8 seconds from S1 Onset). In other words, the timing of the Offset of the to-be-match stimulus in relation to the stimulation pulse Onset. These timings were manipulated and broken down into five conditions; four of them created asynchronous conditions, and one created a synchronous condition. It is worth mentioning that at time point 4, the Onset of the GVS and visual/auditory stimuli were presented in synchrony.

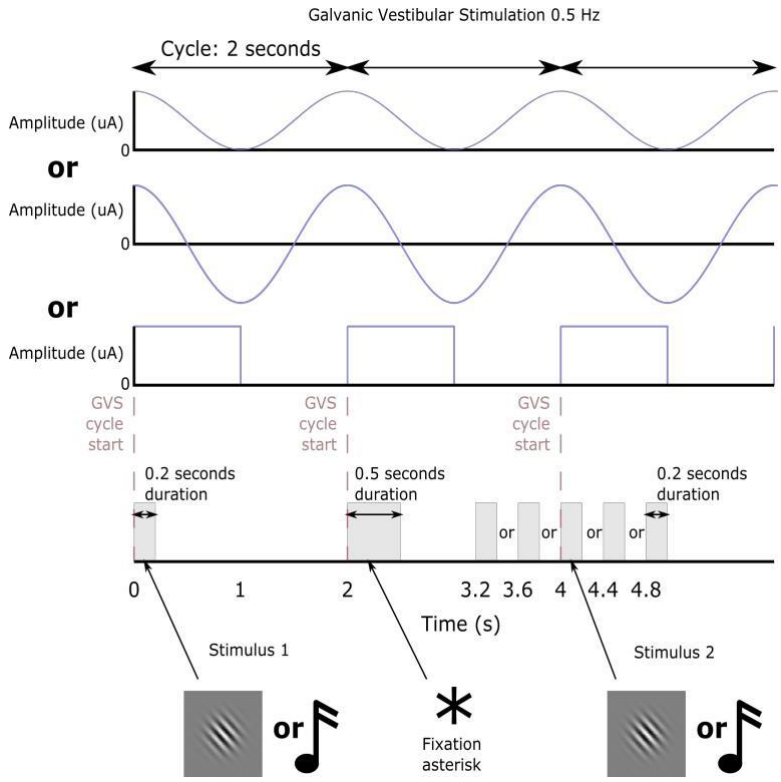

Figure 2.3: Trial sequence, including GVS for all 12 experiments. Stimuli in visual modality experiments were Gabor patches. Stimuli in auditory experiments were tones. GVS was either an AC bilateral bipolar with positive Offset (top), an AC bilateral bipolar (middle) or a DC bilateral bipolar pulse (bottom). Peak amplitude in all cases was 0.05 mA below the individualised GVS sensory threshold.

Understanding phase-locking characteristics is crucial to understand the synchronisation of neuronal action potentials within different brain regions, allowing them to fire simultaneously at a specific oscillatory timepoint. Magnetoencephalography (MEG) studies have revealed inter-area phase-locking target frontal, temporal, and parietal brain regions (Gross et al., 2004). Sampling different angles in a waveform cycle is crucial to understand if the driving effect is contributed to phase-locking, offering insight into how minor deviations in timing or phase alignment influence overall network dynamics. As such, five different Offsets were selected to investigate the aligning features of the rhythmic vestibular signals with the ongoing experimental stimuli, aligned with the principles of the DAT. By experimenting alignment at the point of highest synchronisation with the experimental target—and by contrasting this peak with positions slightly as well as

completely away from the peak, the experimental design could explore the level of synchronisation needed to drive any modulation.

2.10 The effect of temporally coincident vestibular signals on visual judgements

The current understanding of visuo-vestibular integration is built upon a traditional framework . This framework suggests that for optimal integration of visual and vestibular cues, the perception of a cohesive object—such as self-motion or heading direction—is essential (Ernst & Banks, 2002; Ernst & Bülthoff, 2004). In contrast, a modern approach utilises a Bayesian optimal integration framework to explore whether, by priming the visual processes with rhythmic vestibular signals, the brain can adaptively balance various sensory cues to minimise uncertainty, without the need for conscious perception. Within this context, one can argue that as the reliability of one cue declines, the weight allocated to the other cue increases (Gu et al., 2008; Angelaki et al., 2011; DeAngelis & Angelaki, 2012). The modern framework diverges from the traditional one in that it does not require bimodal conscious perception. In fact, protocols within this contemporary framework would actively exclude participants who report conscious perception of GVS signals. Nonetheless, the complex question is that whether subliminal perception of vestibular rhythm could find a place within the visuo-vestibular integration framework. As already discussed, if visual attention is sensitive to a periodic vestibular stimulus, regardless of whether the vestibular and visual stimuli form a unified percept, then one might expect to see either facilitation or inhibition in participants' performance.

The aim of the experiments about to be described was to investigate whether the visual system could benefit from temporally coincident vestibular signals presented at the

same temporal frequency. The DAT paradigm was adapted for this purpose, replacing the auditory signal with a vestibular one. To examine this hypothesis, a DC-GVS pulse was selected for its wave profile, which closely resembles the auditory stimuli used in the original DAT experiment by Jones and Boltz (1989). This wave profile has a sharp Onset/Offset and maintains a continuous intensity in between. The pulse was delivered using a bilateral bipolar arrangement with anodal stimulation applied to the left mastoid and cathodal stimulation to the right mastoid, a configuration shown to elicit a reliable central response according to Wilkinson et al. (2012).

In the experimental design, as illustrated in Figure 2.3, a visual sample stimulus was initially presented for each trial, followed by a matching stimulus either 2s later or at various other intervals such as 1.2s, 1.6s, 2.4s, or 2.8s. Alongside, a sub-sensory GVS pulse was delivered every 2s (i.e., 0.5 Hz). As such, the temporal spacing between successive visual and vestibular signals was matched when the interval was 2s (or multiples of 2), but unmatched at other intervals. It was hypothesised that delayed matching-to-sample responses would be more accurate or quicker when the temporal frequency of the visual and vestibular stimuli is the same (i.e., 2s) compared to when they are different (i.e., 1.2s, 1.6s, 2.4s, 2.8s).

2.11 Planned analysis

ANOVA was utilised to interrogate both the main effects and interactions. A Greenhouse-Gieser correction was applied where the assumption of sphericity was violated. Bonferroni-corrected pairwise comparisons were used via SPSS software (Version 25) to explore the interaction term.

The main effect of Offset was not subject to post hoc analysis because it did not address the hypothesis. The central hypothesis is to investigate whether attentional processes

can be enhanced by concurrent vestibular signals, specifically when the temporal frequency of the visual or auditory stimuli is synchronised with the Onset of the vestibular stimuli, as opposed to when they are asynchronous. Independent variables were GVS (2 levels: active GVS or no stimulation) and Offset (3.2, 3.6, 4, 4.4, 4.8. seconds from S1 Onset at the start of an experimental trial). Dependent variables were response accuracy, measured as the percentage of correct responses, with a minimum inclusion level of 60 % mean accuracy across no stimulation conditions, and median response times for correct trials calculated from S2 Onset reported in seconds. Response accuracies and response times were analysed separately.

An a priori sample size estimation was performed using the G*Power software package (version 3.1.9.3) during the planning and design of the trial. The input parameters were the following: statistical test = ANOVA: repeated measures, within factors; effect size f = 0.25; α err prob = 0.05; power (1 ß err prob) = 0.80; number of groups = 2; number of measures = 5; correlation among repeated measures = 0.5; non-sphericity correction e = 1. These conditions pre-determined a sample size of n = 22.

2.12 Experiment 1: Visual detection, response time

A 2 x 5 repeated measures ANOVA with Greenhouse-Geisser correction on median response time did not show a main effect of Stimulation [$F(1, 22)= 0.054$, $p= 0.818$, $\eta_p^2= 0.002$], or Offset [$F(2.113, 46.4992) = 1.759$, $p= 0.182$, $\eta_p^2= 0.074$]. The interaction [$F(2.103, 46.270) = 1.029$, $p= 0.369$, $\eta_p^2= 0.045$] also failed to reach statistical significance (Figure 2.4).

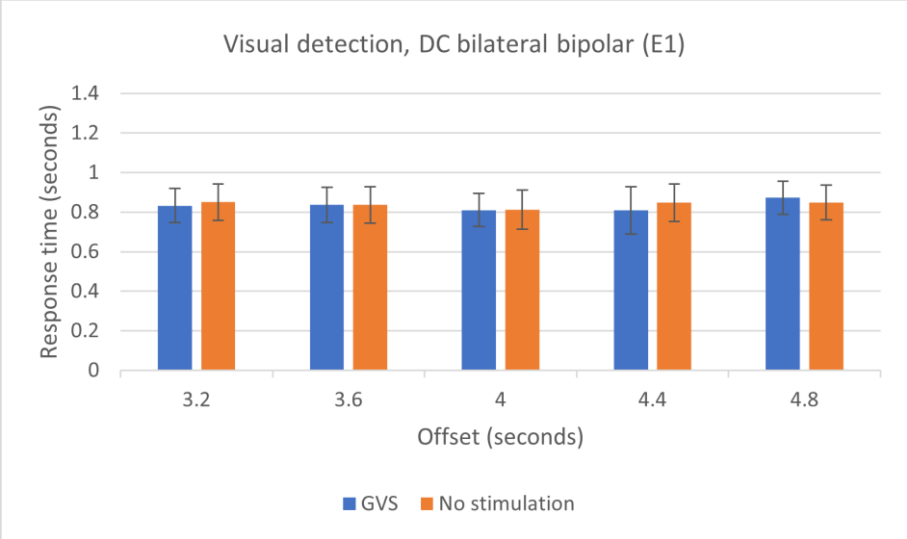

Figure 2.4: Median response time in Experiment 1 as a function of Stimulation x Offset.

2.13 Experiment 1: Visual detection, response accuracy

A 2 x 5 repeated measures ANOVA with Greenhouse-Geisser correction on response accuracy did not show a main effect of Stimulation [$F(1, 22)= 3.406$, $p= 0.078$, $\eta_p^2= 0.134$], or Offset [$F(3.449, 75.872) = 0.581$, $p= 0.653$, $\eta_p^2= 0.026$]. The interaction [$F(2.264, 49.799) = 1.724$, $p =0.185$, $\eta_p^2= 0.073$] also failed to reach statistical significance (Figure 2.5).

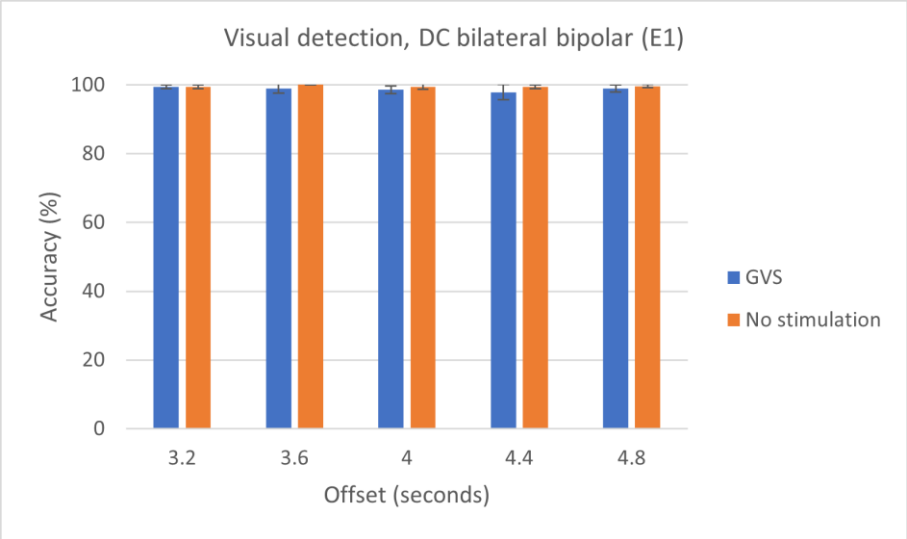

Figure 2.5: Response accuracy (%) in Experiment 1 as a function of Stimulation x Offset.

2.14 Experiment 2: Visual discrimination, response time

A 2 x 5 repeated measures ANOVA with Greenhouse-Geisser correction on median response time showed a main effect of Stimulation [$F(1, 21)= 5.140$, $p= 0.034$, $\eta_p^2= 0.197$],

whereby responses during GVS (*M*= 0.355; *SD*= 0.098) were generally longer compared to no stimulation (*M*= 0.334; *SD*= 0.07). There was also a main effect of Offset [*F*(1.032, 21.673)= 4.863, *p*= 0.037, ηp2= 0.188]. The interaction [*F*(1.241, 26.056)= 6.409, *p*= 0.013, η_p^2= 0.234] also reached statistical significance.

Pairwise comparisons between the Stimulation conditions within each level of Offset showed response time was longer during GVS (*M*= 0.370; *SD*= 0.098) versus no stimulation (*M*= 0.339; *SD*= 0.066) at Offset 4.4 [*t*(21)= 3.280, *p*<0.004] and in active GVS (*M*= 0.369; *SD*= 0.098) versus no stimulation (*M*= 0.338; *SD*= 0.066) at Offset 4.8 [*t*(21) = -3.374, *p*<0.004] (see Figure 2.6 and Table 2.3).

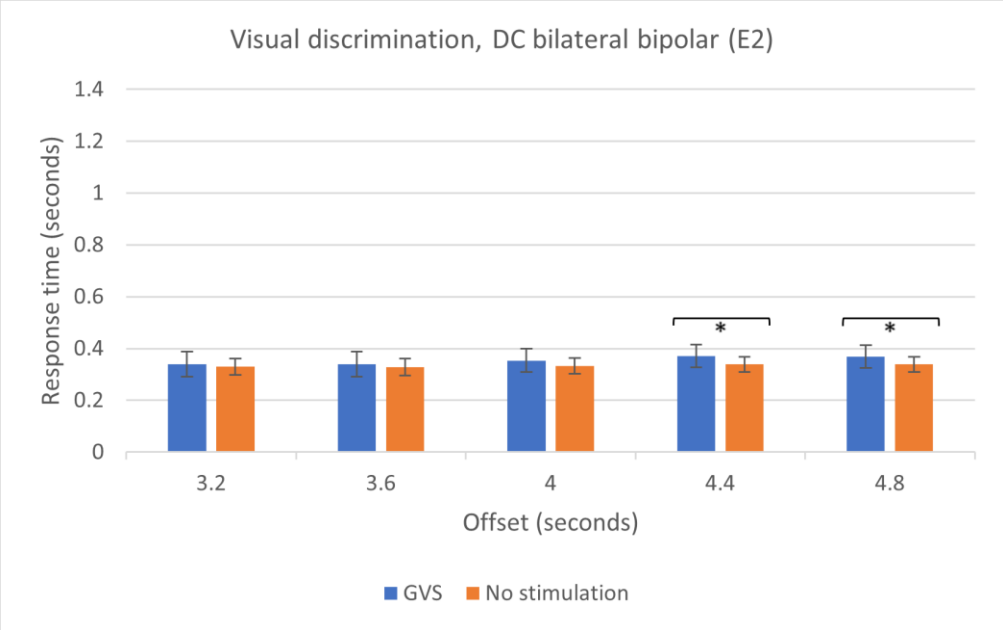

Figure 2.6: Median response time in Experiment 2 as a function of Stimulation x Offset. For ease of interpretation only significant post-hoc comparisons are marked (*).

Offset	**Stim.**		**t value**	**Sig.**	**95% CI**	
					Lower Bound	Upper Bound
3.2	GVS	No Stim	0.926	0.365	-0.012	0.032
3.6	GVS	No Stim	1.207	0.241	-0.009	0.032
4	GVS	No Stim	2.036	0.055	0.000	0.041
4.4	GVS	No Stim	3.280	0.004	0.012	0.052
4.8	GVS	No Stim	-3.374	0.004	0.011	0.051

Table 2.3: Post-hoc statistical analysis of pairwise comparisons showing stimulation conditions at each Offset. E2, response time

Pairwise comparisons also examined whether response time differed between Offset conditions within each Stimulation condition. No differences were revealed between any of the Offset conditions within each Stimulation condition (all *t*s<2.800, all *p*s>0.109, see Appendix B.2.1).

2.15 Experiment 2: Visual discrimination, response accuracy

A 2 x 5 repeated measures ANOVA with Greenhouse-Geisser correction on response accuracy did not show a main effect of Stimulation [$F(1, 21) = 2.808$, $p = 0.109$, $\eta_p^2 = 0.118$], or Offset [$F(2.092, 43.940) = 1.176$, $p = 0.320$, $\eta_p^2 = 0.053$]. The interaction [$F(2.651, 55.665) = 1.146$, $p = 0.335$, $\eta_p^2 = 0.052$] also failed to reach statistical significance (Figure 2.7).

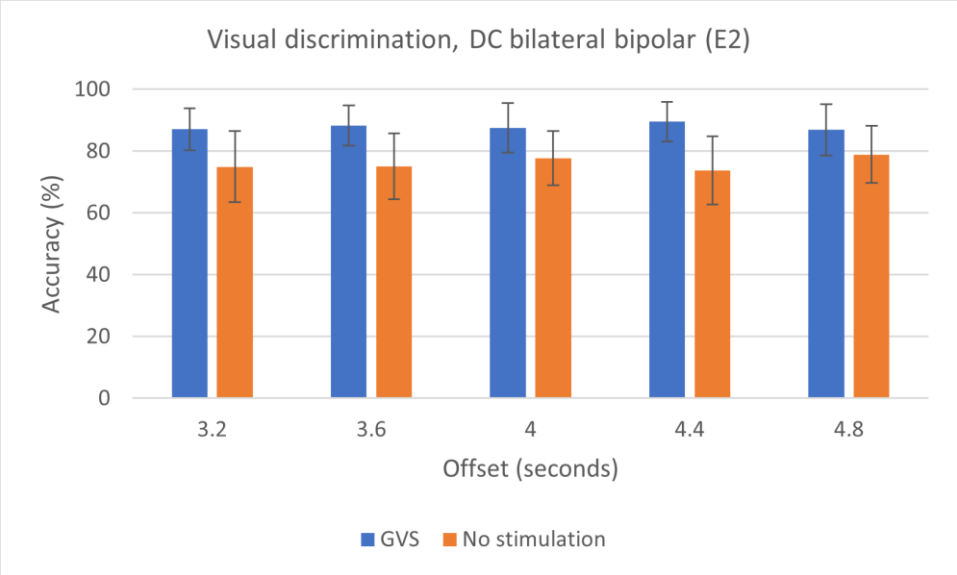

Figure 2.7: Response accuracy (%) in Experiment 2 as a function of Stimulation x Offset.

2.16 Discussion for Experiments 1 & 2

Experiment 1 utilised DC bilateral bipolar and was focused on visual detection. No significant main effects or interaction effects were observed for Stimulation or Offset.

Similarly, in E1, response accuracy was not significantly affected by Stimulation, Offset, or their interaction.

Experiment 2 utilised a DC bilateral bipolar waveform and assessed the effect of visuo-vestibular synchronicity on visual discrimination. The results showed a significant main effect of Stimulation, indicating that response times were generally longer during GVS compared to no stimulation. There was also a significant main effect of Offset, suggesting that response times varied depending on the Offset condition. The interaction between Stimulation and Offset was also significant. Further analysis revealed that response times during GVS were longer compared to no stimulation at Offset 4.4, and in active GVS versus no stimulation at Offset 4.8. However, when examining response accuracy in E2, no significant main effects or interaction effects were found for Stimulation or Offset.

The pattern of results from E1 did not provide any indication that the capacity to differentiate between the target and non-target stimuli was impacted by a non-specific GVS effect. However, the pattern of results from E2 give initial evidence of a late interference effect in response times following the synchronous timepoint in Offset 4.4 and Offset 4.8. This pattern demonstrates evidence of the anticipated visuo-vestibular interaction, albeit in a negative rather than positive manner, which is strongly influencing the post-synchronous Offsets. This observation implies that there could be differentiation in processing visual discrimination and detection stimuli when they coincide with the GVS signal.

Understanding the impact of vestibular stimulation on cognitive and behavioural responses requires an exploration of complex neural mechanisms. Vestibular stimulation leads to a complicated pattern of activation and deactivation in both the Parieto Insular Vestibular Cortex (PIVC) and the visual cortex (Brandt et al., 1998; Deutschländer et al.,

2002; Noohi et al., 2019). This may partially account for the behavioural interference observed in this study. This is achieved through a reciprocal inhibition mechanism which serves to reduce sensory conflicts and ensure coordinated responses by inhibiting unsuitable visual input during vestibular nystagmus. Vestibular nystagmus involves involuntary and repetitive eye movements triggered by disturbances in the vestibular system (Mast, 2009).

The deterioration of visual stability, which leads to nystagmus or oscillopsia, is an indirect outcome of usually supra-threshold GVS, leading to a decline in cognitive performance. Whilst supra-threshold GVS could not be a contributing factor to this effect given the low amplitudes applied, one must consider the potential of distracting effects and the application of multiple stimuli. Such circumstances could also lead to an increased cognitive load and the utilisation of attentional resources. This arises due to the brain's need to reconcile conflicting vestibular, visual, and proprioceptive sensory inputs to uphold orientation (Bigelow et al., 2015). However, some caution should be exercised when interpreting this outcome as the magnitude of response times change was small, and there was no allied effect in the accuracy data that reached ceiling levels of performance. The effect needs to be replicated to give confidence.

This inhibitory effect nevertheless raises the question of whether such effect is unique to the visual system or a general feature of how the vestibular system interacts with other sensory modalities in the delayed matching-to-sample tasks. Neuroimaging findings offer further insights into how GVS influences sensory processing. There are several brain regions targeted by GVS, including the inferior parietal lobule (IPL), crucial for visuo-spatial processing (Lidstone et al., 2021); the medial frontal cortex (MFC), involved in visual attention and working memory for visual stimuli (Reinhart et al., 2018); and the right inferior temporal cortex (rITC), which plays a vital role in object recognition (Lowe, 2001). While

all three regions are involved in both visual and auditory processing, the IPL and rITC seem to have a stronger connection with the visual system (Pfäffle et al., 2022; Uchiyama et al., 2023), whereas the MFC appears to have significant connections to both systems (Grimes et al., 2021; Kochar, 2024). As such, the anatomical connectivity patterns of these GVS-modulated regions suggest a bias towards visual processing. In contrast, auditory processing areas in the temporal lobe appear to have fewer direct anatomical connections with these GVS-modulated regions. Therefore because of the lower degree of integration with the primary and secondary auditory areas, it may be that the vestibular inhibition seen in E1 and E2 would subside when the visual stimuli are replaced with auditory stimuli. Other DAT experiments have shown that the auditory system is receptive to cross-modal facilitation, which may further increase the likelihood of attenuating the interference effect (Baier et al., 2006; James et al., 2022).

2.17 The effect of temporally coincident vestibular signals on auditory judgements

As substantiated above, the subsequent experiments aimed to determine whether the impact of vestibular stimulation on DMTS performance is also observed when visual stimuli are substituted by auditory stimuli, thereby suggesting that the previously observed effect is inhibitory within the visual domain. As before, if auditory processes can make use of coincident vestibular signals, then auditory detection and/or discrimination should improve when the Onset of the delayed matching-to-sample auditory stimulus coincides with the Onset of the DC-GVS pulse.

2.18 Experiment 3 Auditory detection, response time

A 2 x 5 repeated measures ANOVA with Greenhouse-Geisser correction on median response time did not show a main effect of Stimulation [$F(1, 23) = 0.285$, $p = 0.599$, $\eta_p^2 = 0.012$], or Offset [$F(1.654, 38.043) = 0.397$, $p = 0.636$, $\eta_p^2 = 0.017$]. The interaction [$F(1.976, 45.444) = 1.561$, $p = 0.221$, $\eta_p^2 = 0.064$] also failed to reach statistical significance (Figure 2.8).

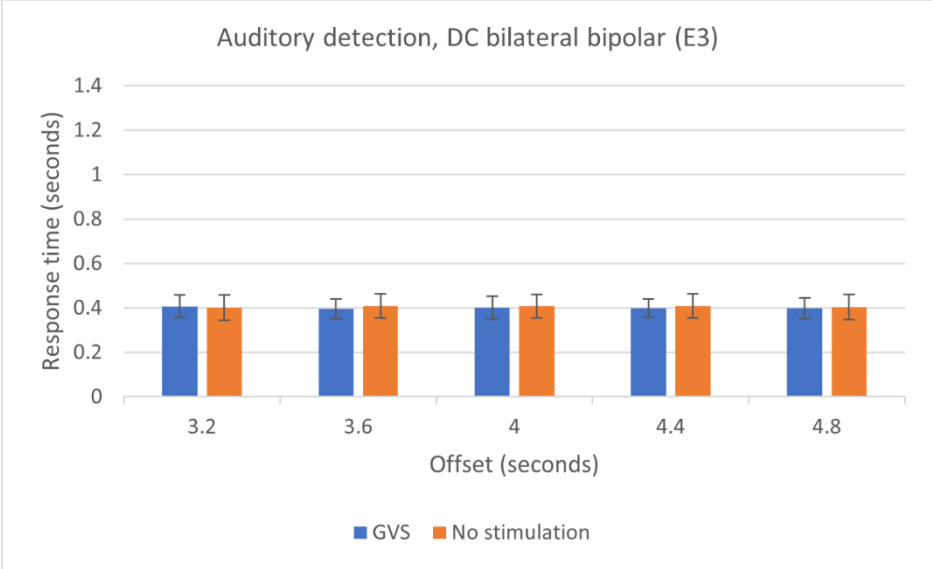

Figure 2.8: Median response time in Experiment 3 as a function of Stimulation x Offset.

2.19 Experiment 3 Auditory detection, response accuracy

A 2 x 5 repeated measures ANOVA with Greenhouse-Geisser correction on response accuracy did not show a main effect of Stimulation [$F(1, 23) = 2.010$, $p = 0.170$, $\eta_p^2 = 0.080$], or Offset [$F(3.076, 70.757) = 1.820$, $p = 0.150$, $\eta_p^2 = 0.073$] The interaction [$F(3.333, 76.664) = 0.400$, $p = 0.774$, $\eta_p^2 = 0.017$] also failed to reach statistical significance (Figure 2.9).

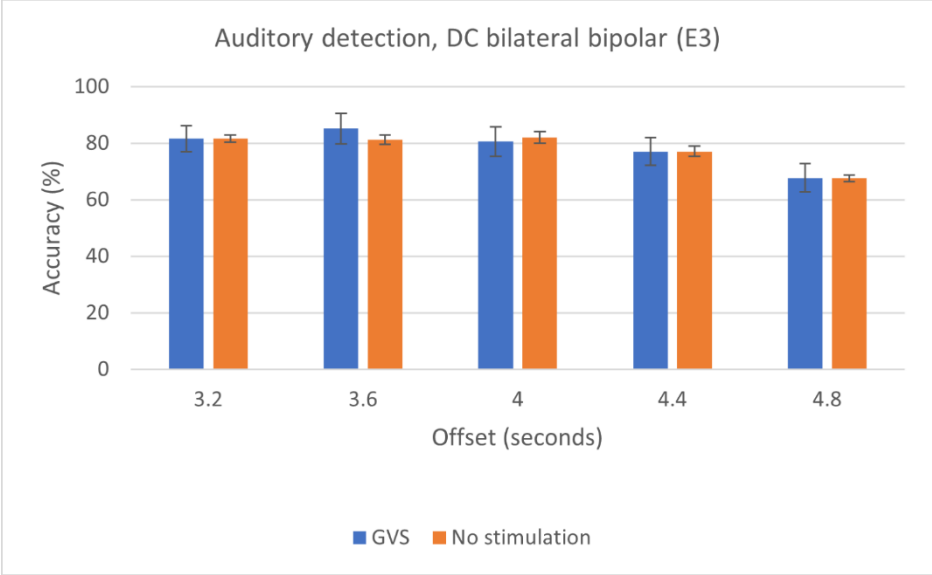

Figure 2.9: Response accuracy (%) in Experiment 3 as a function of Stimulation x Offset.

2.20 Experiment 4 Auditory discrimination, response time

A 2 x 5 repeated measures ANOVA with Greenhouse-Geisser correction on median response time showed a main effect of Stimulation, $F(1, 23) = 5.144$, $p = 0.033$, $\eta_p^2 = 0.183$, whereby responses during GVS ($M = 0.965$; $SD = 0.167$) were overall shorter compared to no stimulation ($M = 1.010$; $SD = 0.157$). The main effect of Offset [$F(2.191, 50.400) = 0.914$, $p = 0.415$, $\eta_p^2 = 0.038$] and the interaction term [$F(3.712, 85.387) = 2.171$, $p = 0.084$, $\eta_p^2 = 0.086$] failed to reach statistical significance (Figure 2.10).

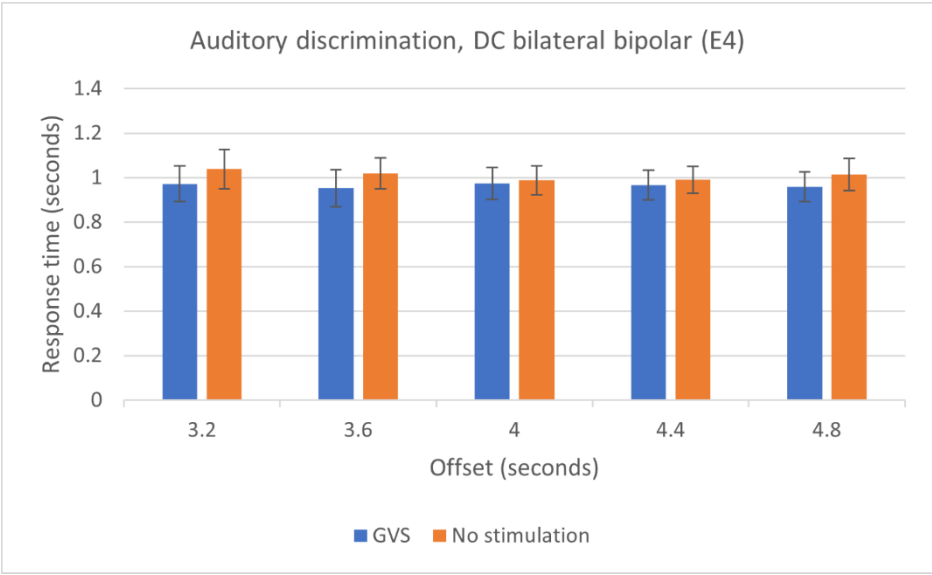

Figure 2.10: Median response time in Experiment 4 as a function of Stimulation x Offset.

2.21 Experiment 4 Auditory discrimination, response accuracy

A 2 x 5 repeated measures ANOVA with Greenhouse-Geisser correction on response accuracy did not show a main effect of Stimulation [$F(1, 23)= 0.240$ $p= 0.629$, $\eta_p^2= 0.010$], or interaction [$F(3.057, 70.315) = 0.817$, $p= 0.491$, $\eta_p^2= 0.034$]. The main effect of Offset [$F(1.384, 31.823) =10.500$, $p= 0.001$, $\eta_p^2= 0.313$] did however reach statistical significance (Figure 2.11). While post hoc analysis for the main effect of Offset was not conducted, the means and standard deviation for each Offset are presented in the table below. It seems that as the Offset increases, the accuracy tends to decrease (see Table 2.4).

	GVS		No Stimulation	
Offset	**Mean**	**SD**	**Mean**	**SD**
3.2	81.528	15.467	81.579	11.315
3.6	85.140	12.341	81.248	11.638
4	80.536	11.640	82.029	10.916
4.4	77.102	13.446	77.079	12.025
4.8	67.689	10.647	67.527	8.892

Table 2.4: Presenting means and SD for each Offset. E4, response accuracy

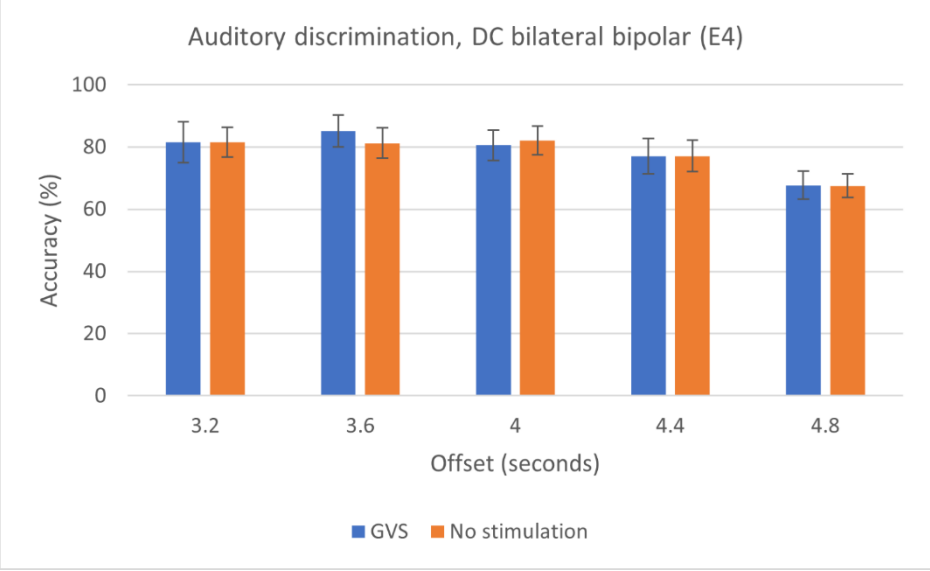

Figure 2.11: Response accuracy (%) in Experiment 4 as a function of Stimulation x Offset.

2.22 Discussion for Experiments 3 & 4:

Experiment 3 utilised a DC bilateral bipolar signal and assessed vestibular influences on auditory detection. No significant effects of Stimulation or Offset were observed on

median response time. The interaction between Stimulation and Offset also lacked statistical significance. Likewise, for response accuracy, no significant effects of Stimulation, Offset, or their interaction were found. By contrast, E4, which utilised the same signal, but assessed discrimination rather than detection, revealed a significant main effect of Stimulation on median response time. Specifically, responses during GVS were shorter compared to no stimulation irrespective of Offset.

In this experiment, the observed facilitation did not corroborate the hypothesised results regarding the DAT. However, it clearly indicates that GVS affects auditory match-to-sample judgments. Nonetheless, it is important to interpret these findings with caution. While non-specific effects may be at play, the effect will require replication before being deemed worthy of meaningful interpretation. Nevertheless, there were no significant effects of Offset or interaction. Regarding response accuracy in E4, there were no significant effects of Stimulation or the interaction between Stimulation and Offset. However, the main effect of Offset reached statistical significance. As mentioned, inferential analysis was not conducted on any main effect of Offset, that involved the Offset variable, as stated in the predictions and analysis plan. Nonetheless, the means and standard deviations for each Offset value were provided in Table 2.3, indicating that as the Offset increased, the accuracy tended to decrease.

In summary, the pattern of results suggests that Stimulation and Offset did not have a significant impact on response time or accuracy in E3, which focused on auditory detection. In E4, which examined auditory discrimination, Stimulation had an overall enhancing effect on response time, but Stimulation, Offset, and their interaction did not significantly influence response accuracy.

This experiment aimed to test if the negative interference seen in the response times of E2 could be replicated when the visual stimuli were replaced with auditory stimuli. As seen in E4 (response times of auditory discrimination) shown in Figure 2.7, responses to auditory stimuli were speeded during active GVS relative to no stimulation irrespective of Offset. The fact that this occurred at all Offsets does not fit with the predictions made by DAT and instead points to more general facilitation. The descriptive statistics suggest that the vestibular system may interact differently with the visual system compared to the auditory system. To date, there is no direct evidence of the positive impact of GVS on auditory processing, and this is the first time that behavioural facilitation has been shown.

The outcome of this study is aligned with findings reported by Schmidt-Kassow et al. (2013), which indicated that the P300, a component often observed in tasks that require the individual to detect infrequent or unexpected events among a series of more common stimuli, was enhanced during GVS, resulting in enhanced performance, when the sub-sensory stimulation's temporal frequency matched the rhythmic stimulus frequency.

Existing biological evidence from PET scans and fMRI studies further demonstrates that the brain's posterior parietal region is involved in auditory stimulation and is sensitive to auditory oddball (Abe et al., 1999; Janzen et al., 2008; Houston et al., 2012). This region is also involved during vestibular stimulation (Lobel et al., 1998; Fasold et al., 2002; Stephan et al., 2005). This integration suggests that the auditory system could use the vestibular system's temporal regularity and that the posterior parietal may be the site of this integration. These findings support the role of vestibular stimulation on the P300 component, which has a positive effect on auditory processes.

2.23 The effect of temporally coincident AC bilateral bipolar on visual judgements

The anticipation in the prior experiments was to observe a positive impact on response time or accuracy when the Onset of a visual stimulus aligned with the peak of a continuous vestibular rhythm marked by periodic, sub-sensory pulses. This anticipation was not fulfilled and, as such, in the subsequent experiments of this chapter, a different strategy was employed to manipulate the vestibular pulse in an effort to identify a signal that could achieve the expected outcome.

The approach was to change the stimulation waveform from one that was a DC bilateral bipolar to one that was an AC bilateral bipolar. This change in waveform was implemented based on reports that cross-frequency coupling and oscillatory entrainment are more powerfully evoked when sensory stimuli adopt an AC (sinewave) compared to the DC (boxcar pulse) pattern (Moreno-Duarte et al., 2014; Dowsett & Herrmann, 2016; Cole & Voytek, 2017; Żebrowska et al., 2020).

For example, Stephan et al. (2005) showed that neural responses evoked through AC-GVS and DC-GVS both activate the cerebral cortex. However, fMRI studies demonstrate that DC-GVS tends to be most effective at Onset and Offset timepoints with slight effectiveness throughout stimulation, whereas AC-GVS tends to have a more enduring and significant effect (Bense et al., 2001; Stephan et al., 2005).

Moreover, the frequency dependency of AC-GVS offers a more favourable clinical application over a DC-GVS as it can be designed to stimulate both cerebral hemispheres consecutively with the positive and negative current and can be set to match particular cerebral dynamics. As such, in the following experiment, significant alterations were made

to both the waveform shape and its hemispheric distribution. The stimulation was shifted from a DC bilateral bipolar configuration, characterised by a constant and unchanging level of vestibular nerve stimulation, to an AC bilateral bipolar configuration. The AC waveform, being sinusoidal, offers the advantage of fluctuating current levels, allowing for more complex interactions with neural structures and greater flexibility in matching specific cerebral dynamics. This change aims to benefit from on the documented benefits of AC waveforms for eliciting more enduring and significant physiological responses, as well as their potential for targeted applications through frequency dependency. All other methodological characteristics remained consistent with those employed in the DC-GVS experiment.

2.24 Experiment 5: Visual detection, response time

A 2 x 5 repeated measures ANOVA with Greenhouse-Geisser correction on median response time did not show a main effect of Stimulation [$F(1, 23) = 0.003$, $p = 0.954$, $\eta_p^2 = 0.000$], or Offset [$F(2.635, 60.616) = 0.665$, $p = 0.558$, $\eta_p^2 = 0.028$]. The interaction [$F(2.641, 60.753) = 0.434$, $p = 0.705$, $\eta_p^2 = 0.019$] also failed to reach statistical significance (Figure 2.12).

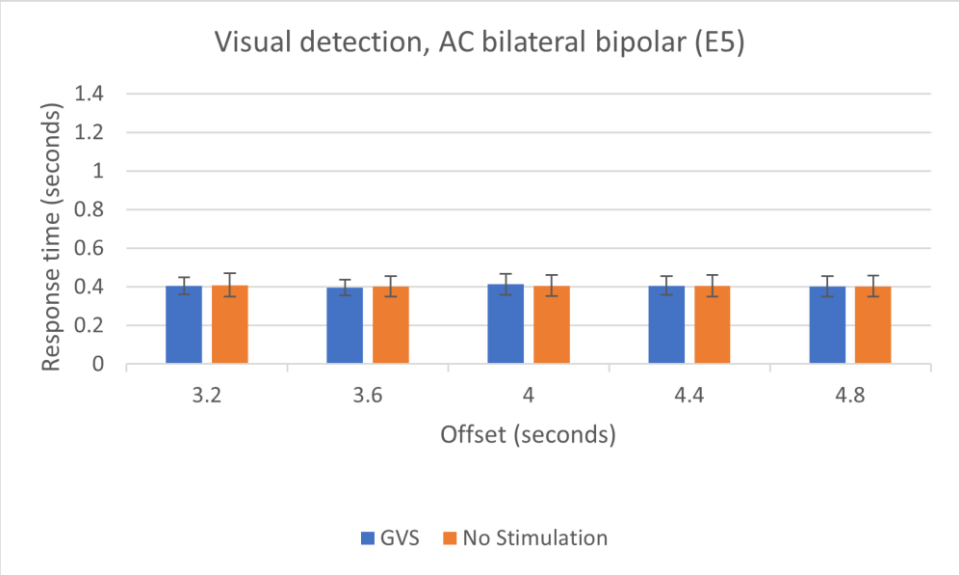

Figure 2.12: Median response time in Experiment 5 as a function of Stimulation x Offset.

2.25 Experiment 5: Visual detection, response accuracy

A 2 x 5 repeated measures ANOVA with Greenhouse-Geisser correction on response accuracy did not show a main effect of Stimulation [$F(1, 23) = 2.395$, $p = 0.135$, $\eta_p^2 = 0.094$], or Offset [$F(3.652, 83.987) = 0.656$, $p = 0.611$, $\eta_p^2 = 0.028$]. The interaction [$F(3.026, 69.594) = 0.954$, $p = 0.420$, $\eta_p^2 = 0.040$] also failed to reach statistical significance (Figure 2.13).

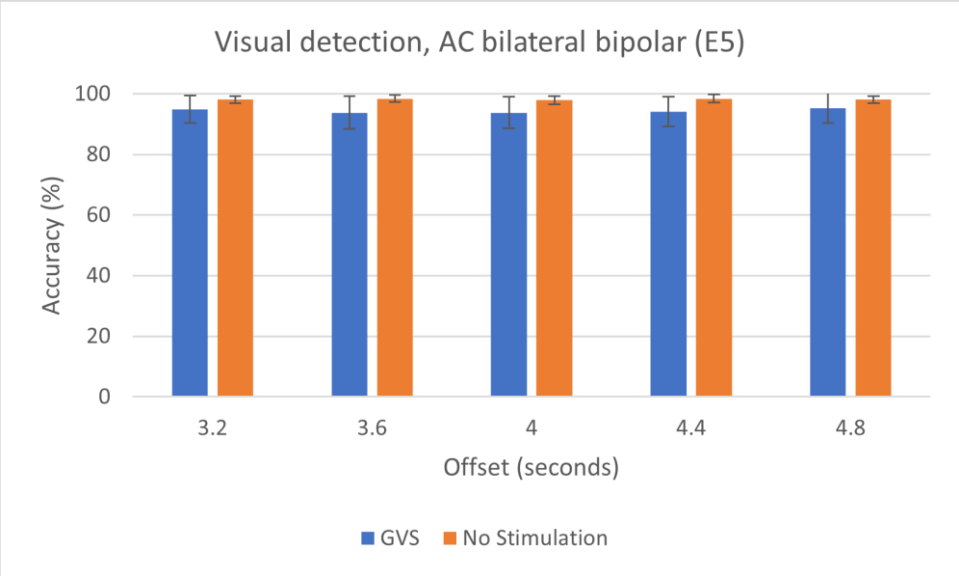

Figure 2.13: Response accuracy (%) in Experiment 5 as a function of Stimulation x Offset.

2.26 Experiment 6: Visual discrimination, response time

A 2 x 5 repeated measures ANOVA with Greenhouse-Geisser correction on median response time did not show a main effect of Stimulation [$F(1, 23) = 2.677$, $p = 0.115$, $\eta_p^2 = 0.104$]. However, the main effect of Offset [$F(1.873, 43.086) = 21.497$, $p = 0.001$, $\eta_p^2 = 0.483$], and the interaction [$F(3.447, 79.288) = 3.153$, $p = 0.024$, $\eta_p^2 = 0.121$] term reached statistical significance.

Pairwise comparisons between the Stimulation conditions within each level of Offset showed response times were shorter during GVS ($M = 0.567$; $SD = 0.191$) versus no

stimulation (*M*= 0.617; *SD*=0.191) at Offset 3.6 [*t*(23) = -2.531, *p*= 0.020] (Figure 2.14). All other comparisons failed to reach significance (all *t*s<2.004, all *p*s> 0.057; see Table 2.5).

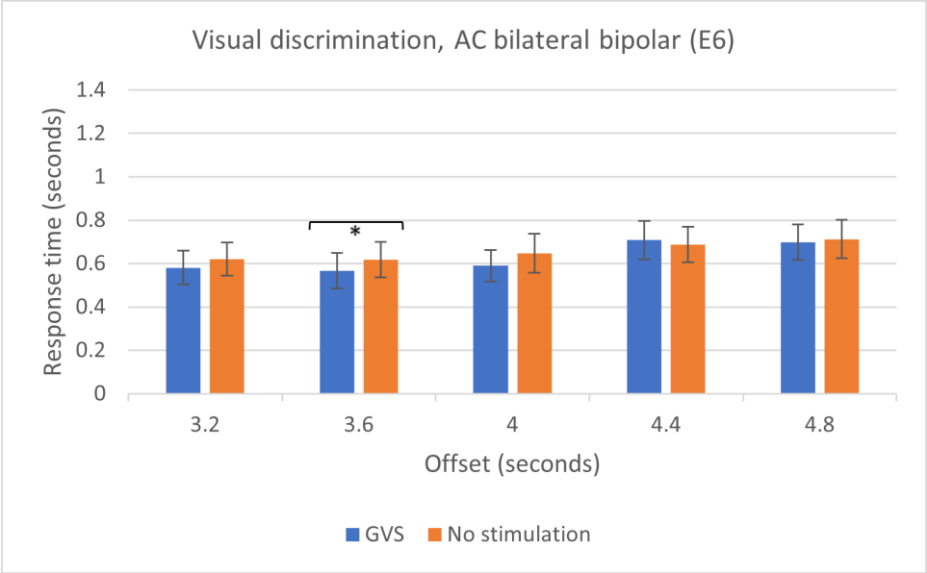

Figure 2.14: Median response time in Experiment 6 as a function of Stimulation x Offset. For ease of interpretation only significant post-hoc comparisons are marked (*).

Offset	Stim.		t value	Sig.	95% CI	
					Lower Bound	Upper Bound
3.2	GVS	No Stim	-2.004	0.057	-0.08	0.00
3.6	GVS	No Stim	-2.531	0.020	-0.09	-0.01
4	GVS	No Stim	-1.934	0.066	-0.12	0.00
4.4	GVS	No Stim	0.961	0.346	-0.02	0.06
4.8	GVS	No Stim	-0.569	0.575	-0.07	0.04

Table 2.5: Post-hoc statistical analysis of pairwise comparisons showing stimulation conditions at each Offset. E6, response time

Pairwise comparisons also examined whether response time differed between Offset conditions within each Stimulation condition. During GVS, Offset 3.2 (*M*= 0.581; *SD*=0.186) was significantly different to Offset 4.4 (*M*= 0.708; *SD*=0.211) [*t*(23)= -4.807, *p*<0.001] and Offset 4.8 (*M*= 0.698; *SD*=0.196) [*t*(23) = -5.579, *p*<0.001]. During GVS, Offset 3.6 (*M*= 0.567; *SD*=0.191) was significantly different to Offset 4.4 (*M*= 0.708; *SD*=0.211) [*t*(23) = -4.143, *p*<0.004] and Offset 4.8 (*M*= 0.698; *SD*=0.196) [*t*(23) = -4.267, *p*<0.003]. During GVS, Offset 4 (*M*= 0.590; *SD*=0.171) was significantly different to Offset 4.4 (*M*= 0.708;

SD=0.211) [*t*(23)= -4.959, *p*<0.001] and Offset 4.8 (*M*= 0.698; *SD*=0.196) [*t*(23) = -5.917, *p*<0.001] (Figure 2.15).

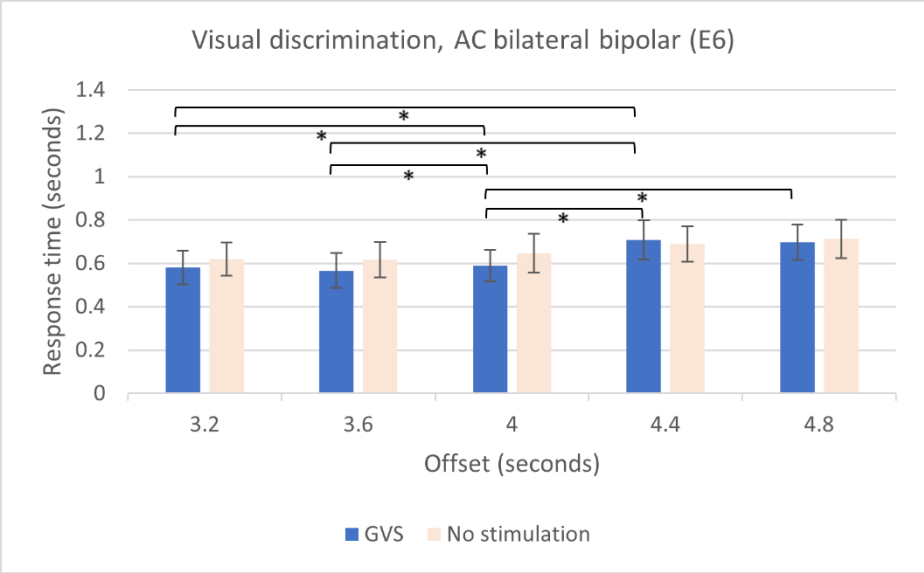

Figure 2.15: Response time difference between the Offset conditions within the GVS condition for Experiment 6. For ease of interpretation only significant post-hoc comparisons of association are marked (*).

During no stimulation, Offset 3.2 (*M* = 0.620; *SD*=0.181) was significantly different to Offset 4.4 (*M* = 0.689; *SD*=0.196) [*t*(23)= -3.865, *p*<0.008] and Offset 4.8 (*M* = 0.713; *SD*=0.211) [*t*(23)= -4.222, *p*<0.003]. During no stimulation, Offset 3.6 (*M* = 0.620; *SD*=0.181) was significantly different to Offset 4.4 (*M* = 0.689; *SD*=0.196) [*t*(23)= -4.348, *p*<0.002] and Offset 4.8 (*M* = 0.713; *SD*=0.211) [*t*(23)= -4.206, *p*<0.003]. During no stimulation, Offset 4 (*M* = 0.647; *SD*=0.211) was significantly different to Offset 4.8 (*M* = 0.713; *SD*=0.211) [*t*(23)= -3.983, *p*<0.006] (see Figure 2.16 and Appendix B.2.2)

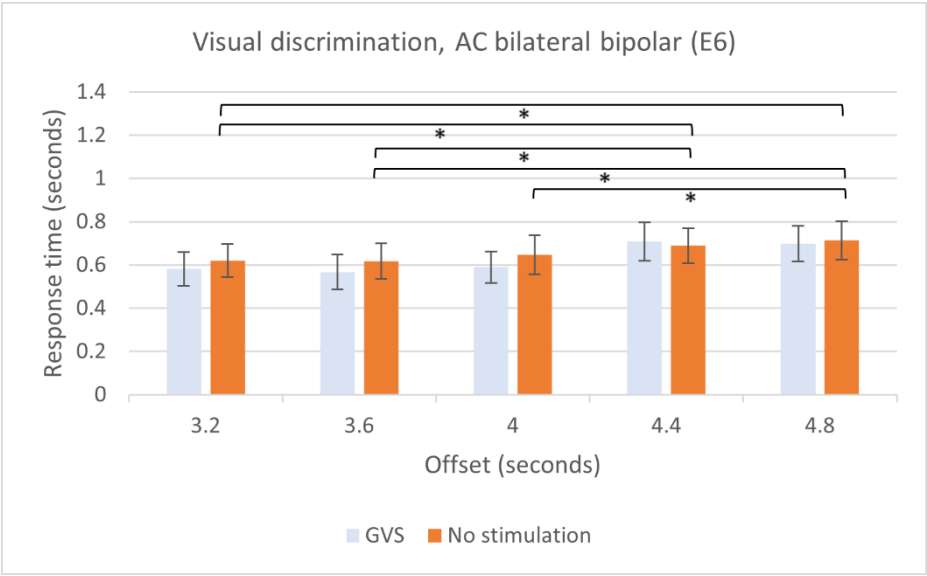

Figure 2.16: Response time difference between the Offset conditions within the no stimulation condition for Experiment 6. For ease of interpretation only significant post-hoc comparisons of association are marked (*).

2.27 Experiment 6: Visual discrimination, response accuracy

A 2 x 5 repeated measures ANOVA with Greenhouse-Geisser correction on response accuracy showed a main effect of Stimulation [F (1, 23) = 20.332, p = 0.001, η_p^2 = 0.469], whereby responses during GVS (M= 78.068; SD=9.298) were generally less accurate compared to no stimulation (M= 86.07; SD=5.653). There was also a main effect of Offset [F (1.489, 34.239) = 25.610, p = 0.001, η_p^2 = 0.527]. The interaction [F (1.757, 40.408) = 12.225, p = 0.001, η_p^2 = 0.347] also reached statistical significance.

Pairwise comparisons between the Stimulation conditions within each level of Offset showed response accuracy was lower during GVS (M = 79.737; SD=10.190) versus no stimulation (M = 85.704; SD= 7.579) at Offset 4 [t(23)= -3.660, p<0.001], also lower during GVS (M = 66.056; SD=21.487) versus no stimulation (M = 84.650; SD=9.489) at Offset 4.4 [t(23)= -4.143, p<0.001]. Similarly, the response accuracy was lower during GVS (M = 62.558; SD=19.126) versus no stimulation (M = 80.178; SD=8.255) at Offset 4.8 [t(23)= -4.513, p<0.001] (Figure 2.17 and Table 2.6).

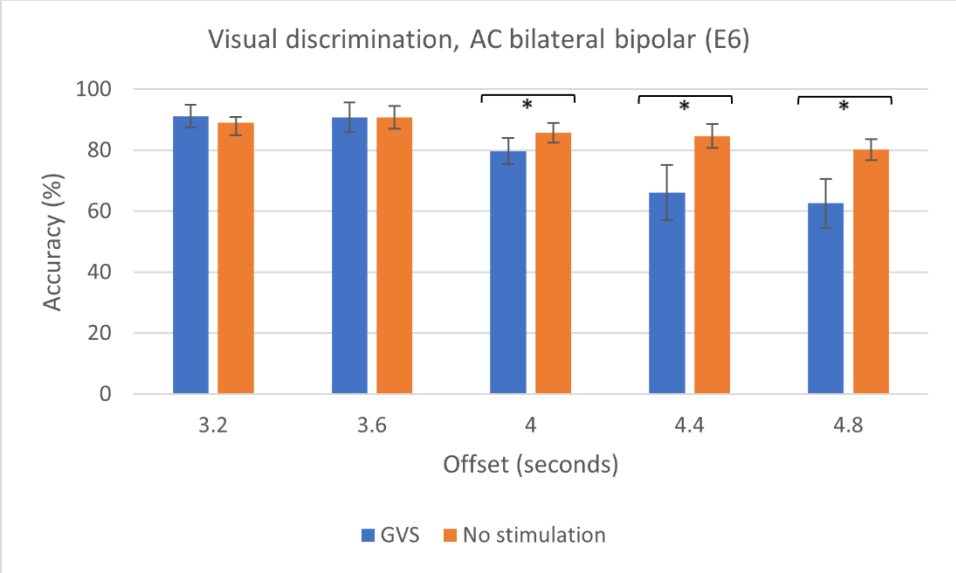

Figure 2.17: Response accuracy (%) in Experiment 6 as a function of Stimulation x Offset. For ease of interpretation only significant post-hoc comparisons are marked (*).

Offset	Stim.		t value	Sig.	95% CI	
					Lower Bound	Upper Bound
3.2	GVS	No Stim	1.072	0.295	-2.011	6.338
3.6	GVS	No Stim	0.003	0.997	-4.339	4.353
4	GVS	No Stim	-3.660	0.001	-9.339	-2.594
4.4	GVS	No Stim	-4.143	<.001	-27.878	-9.309
4.8	GVS	No Stim	-4.513	<.001	-25.696	-9.544

Table 2.6: Post-hoc statistical analysis of pairwise comparisons showing stimulation conditions at each Offset. E6, response accuracy

Pairwise comparisons also examined whether response time differed between Offset conditions within each Stimulation condition. During GVS, Offset 3.2 (*M*= 91.160; *SD*=8.740) was significantly different to Offset 4 (*M*= 79.737; *SD*=10.190) [*t*(23)= 5.267, *p*<0.001], Offset 4.4 (*M*= 66.056; *SD*=21.487) [*t*(23)= 4.946, *p*<0.001] and Offset 4.8 (*M*= 62.558; *SD*=19.126) [*t*(23)= 5.992, *p*<0.001]. During GVS, Offset 3.6 (*M*= 90.827; *SD*=11.606) was significantly different to Offset 4 (*M*= 79.737; *SD*=10.190) [*t*(23)= 4.528, *p*<0.002], Offset 4.4 (*M*= 66.056; *SD*=21.487) [*t*(23)= 4.523, *p*<0.002] and Offset 4.8 (*M*= 62.558; *SD*=19.126) [*t*(23)= 5.580, *p*<0.001]. During GVS, Offset 4 (*M*= 79.737;

SD=10.190) was significantly different to Offset 4.4 (*M*= 66.056; *SD*=21.487) [*t*(23)= 3.694, *p*<0.012] and Offset 4.8 (*M*= 62.558; *SD*=19.126) [*t*(23)= 4.832, *p*<0.001] (Figure 2.18).

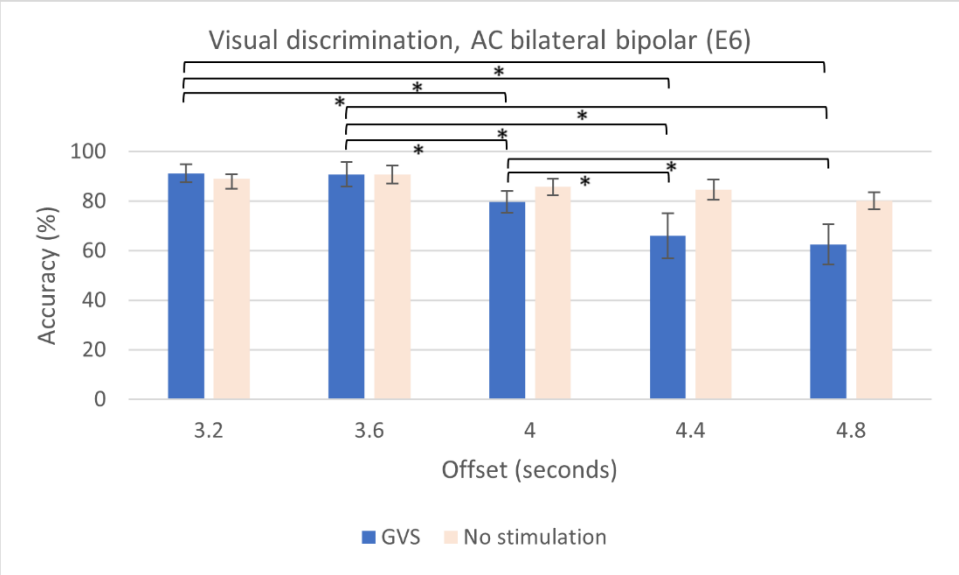

Figure 2.18: Response accuracy (%) difference between the Offset conditions within the GVS condition for Experiment 6. For ease of interpretation only significant post-hoc comparisons of association are marked (*).

During no stimulation, Offset 3.2 (*M*= 88.997; *SD*=8.740) was significantly different to Offset 4.8 (*M*= 80.178; *SD*=8.255) [*t*(23)= 4.860, *p*<0.001]. During no stimulation, Offset 3.6 (*M*= 90.820; *SD*=8.735) was significantly different to Offset 4.8 (*M*= 80.178; *SD*=8.255) [*t*(23)= 5.580, *p*<0.001]. During no stimulation, Offset 4 (*M*= 85.704; *SD*=7.579) was significantly different to Offset 4.8 (*M*= 80.178; *SD*=8.255) [*t*(23)= 3.098, *p*<0.051]. During no stimulation, Offset 4.4 (*M*= 84.650; *SD*=9.489) was significantly different to Offset 4.8 (*M*= 80.178; *SD*=8.255) [*t*(23)= 3.483, *p*<0.020] (Figure 2.19 and Appendix B.2.3).

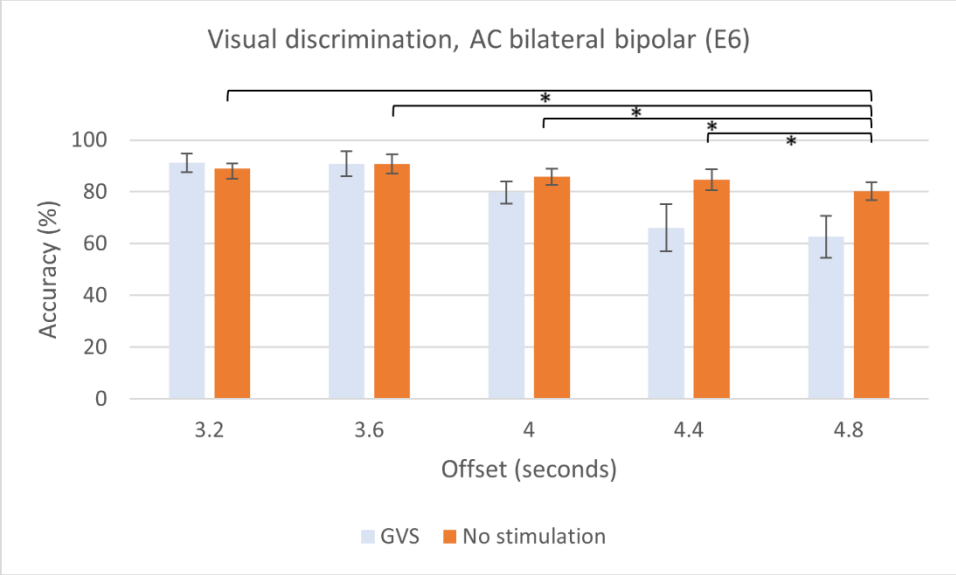

Figure 2.19: Response accuracy (%) difference between the Offset conditions within the no stimulation condition for Experiment 6. For ease of interpretation only significant post-hoc comparisons of association are marked (*).

2.28 Discussion for Experiments 5 & 6

The key findings from the experiments described above reveal an interference effect beginning at the Onset of the visuo-vestibular synchronisation point. This effect is broadly consistent with the predictions of the DAT, although it is more detrimental than beneficial. A similar inhibitory pattern observed in E6 was also noted in E2.

Experiment 5 utilised AC bilateral bipolar and was focused on visual detection and response time, the results showed that neither Stimulation nor Offset had a significant main effect on median response time or response accuracy. The interaction between Stimulation and Offset was likewise not significant in both cases. As such indicating a lack of substantial influence between these factors in both response time and accuracy.

Experiment 6 utilised AC bilateral bipolar and was focused on visual discrimination and response time, the results showed that Stimulation had no significant main effect on response time. The interaction between Stimulation and Offset was significant, suggesting

their combined influence on response time. Further analysis within each Offset level revealed that response time was shorter during GVS compared to no stimulation only at Offset 3.6. Comparisons between Offset conditions within each Stimulation condition revealed that during GVS, post-synchronous Offsets (4.4 and 4.8) exhibited longer response times compared to pre-stimulus Offsets (3.2 and 3.6) and the synchronous Offset (4). A similar pattern emerged in the no stimulation condition. Overall, the difference in performance between pre and post synchronous Offsets was larger during GVS (M=0.127) than no stimulation (M=0.069). Therefore, it suggests a greater interference effect from the synchronous Offset onwards when GVS is applied.

Experiment 6 utilised AC bilateral bipolar and was focusing on visual discrimination and response accuracy, significant effects of Stimulation and Offset were found. Stimulation led to less accurate responses during GVS compared to no stimulation. Different Offset levels also influenced response accuracy. The interaction between Stimulation and Offset was statistically significant. Specifically, when comparing Stimulation conditions within each Offset level, lower accuracy was observed during GVS at Offset 4, 4.4, and 4.8. When comparing the Offset conditions within each stimulation condition, during GVS, performance appears to be better in pre-synchronous Offsets (3.2 and 3.6) than in the synchronous Offset (4) and post-synchronous Offsets (4.4 and 4.8). Similarly, during periods of no stimulation, the results also favour pre-synchronous Offsets (3.2 and 3.6), but the difference between synchronous and post-synchronous Offsets is less pronounced. Overall, the difference in performance between pre and post synchronous Offsets was more pronounced during GVS (M= 28.602) than during no stimulation (M= 8.819). Therefore, this suggests a more marked inhibitory effect from the synchronous Offset onwards when GVS is applied.

In summary, during visual experiments, E5 found no significant effects of Stimulation or Offset on response time or accuracy. In contrast, E6 indicated that interaction between GVS and Offset significantly impacted response time, particularly at Offset 3.6, where responses were shorter during GVS. In terms of accuracy, lower accuracy was observed during GVS at Offsets 4, 4.4, and 4.8. The GVS condition also showed more significant differences between Offsets than the no stimulation condition. As such, while E5 showed no impact of Stimulation or Offset, E6 emphasised their individual and interactive effects, with specific Offsets showing significant influence.

To recap, there is a distinct interference effect from the synchronous Offset onwards. The timing of this effect fits with a visual sensitivity to the frequency of the vestibular signal. This outcome is in line with the DAT hypothesis as the effect occurs at and post synchronous Offsets, that is, when the delay between the visual match and sample mirrors the frequency of the background vestibular stimulus. This entrainment effect is less noticeable in the detection tasks as most participants performed at the ceiling. This effect, therefore, suggests that the visual attentional processes are sensitive to coincident vestibular signals when they are at the same temporal frequency as the incoming visual information. In the next chapter, I try to understand the inhibitory nature of this effect and reproduce it.

2.29 General Discussion

This study aimed to investigate whether a 0.5 Hz background vestibular signal could improve the accuracy and speed at which delayed matching-to-sample judgments were made to visual stimuli that appeared at the same temporal frequency. If this were found to be the case, then it would have been shown for the first time that, consistent with the DAT, visual detection and/or discrimination processes can utilise coincident (i.e., frequency-matched) vestibular signals.

The descriptive statistics revealed a coherent pattern of performance. Overall, the detection tasks (E1, E3 and E5) showed near-perfect performance at 95% accuracy or above, which may have limited the extent of the effect. Few visual effects of interest were found when the GVS signal was delivered in DC bilateral bipolar format. Nevertheless, most interestingly, there were lower accuracy rates in the visual discrimination task when the Offset of the delayed matching-to-sample of the task was in synchrony with the AC bilateral bipolar vestibular signal (E6). This result confirms that visual processing can indeed be affected by the temporal synchronicity of vestibular signals, albeit in an unfavourable manner.

By contrast, responses in the auditory discrimination task were generally enhanced – regardless of when the auditory stimuli appeared relative to the GVS signal is accompanied by a DC bilateral bipolar pulse (E4). It may be of note here that GVS was administered at a frequency of 0.5 Hz, which may have tapped into endogenous cortical rhythms associated with central auditory processing (Wilsch et al., 2015). Interestingly, in line with theoretical and empirical evidence, Busse et al. (2005) proposed a cross-modal phase reset operating within the delta frequency band in which attended stimuli in one sensory modality impact the processing of inputs in another modality. Brain imaging studies have shown that this neural alignment reconstitutes auditory cortical oscillations to a position of high excitability (Schroeder & Lakatos, 2009; Zaehle et al., 2011; Hauthal et al., 2013; Kranczioch & Thorne, 2013; Wilsch et al., 2015). Together these findings strengthen the outcome of this study, suggesting that processing auditory stimuli can improve when the ongoing neural oscillatory activity becomes realigned where the listeners develop temporal expectations (Rimmele et al., 2011; Wilsch et al., 2015).

The conclusions drawn in this chapter need to be understood in the context of its limitations. One of these limitations concerns to the nature of the detection task. The natural characteristics of the detection task, characterised by relatively low complexity, facilitated nearly widespread ceiling-level performance among the participants across multiple instances of the detection tasks. The minimal cognitive load necessitated by the test hindered the need for substantial attentional resources, and there was little opportunity for their performance to improve further, given that the ceiling effect might have obscured any potential effects that could have been observed at lower levels of accuracy. Future research could consider employing a different metric such as d-prime to provide a more comprehensive analysis that would be less influenced by saturation effects and offer valuable insights into how an individual's ability to detect experimental stimuli is influenced by attentional dynamics, especially when conventional performance measures are unable to reveal subtle differences due to the ceiling effects. However, the reason the experimental design of this chapter did not incorporate d prime was based on precedent set by earlier DAT experiments, specifically the original study conducted by Jones and Boltz (1989). As such, due to the saturation effect observed, the detection task was eliminated in the following chapter.

In conclusion, the findings from this chapter indicate a general facilitation effect in the auditory domain and a distinct interference effect in the visual domain. In the subsequent chapter, I will investigate the potential extension of the auditory processes affected by substituting the DC signal with an AC signal. Additionally, I will further explore the characteristics of the visual interference effect, specifically evaluating the extent to which the interference effect relies on an AC bilateral bipolar. Furthermore, I will examine whether the specific viewing conditions could mitigate the inhibitory effect.

Chapter 3 – The Effects of Stimulus Factors, Language Impairment and Hemispheric Involvement on Vestibular Modulation

Chapter 2 uncovered conditions in which visual discrimination was impacted by vestibular stimulation while auditory discrimination, albeit via a differently shaped waveform, showed an overall facilitatory effect irrespective of Offset. This chapter aimed to understand more about these visual interferences and auditory facilitation effects. I aimed to explore whether the overall auditory facilitatory effect observed in E4, using a DC signal can be enhanced, perhaps most of all at the synchronous Offset, when using a stronger entrainer like the AC signal. As explained later, this exploration holds potential implications for advancing therapeutic interventions for individuals with Auditory Processing Disorder (APD). A second aim of this chapter was to further understand the interference effect reported in the last chapter. In particular, I sought to understand if it might have a hemispheric basis and whether it is partly conditional on viewing conditions which are known to constrain multi-sensory facilitation.

For the auditory experiment (E7), the stimulation protocol transitioned from a DC bilateral bipolar configuration to an AC bilateral bipolar configuration. With an AC signal the electrical polarity switches repeatedly between the two electrodes. This set up leads to a continuous switch in the excitation and inhibition of the left and right vestibular afferent neurons which in turn might lead to successive, preferential stimulation of either cerebral hemisphere. Partly for this reason, AC is documented as a more powerful entrainer, providing further customisation in neural interactions and heightened adaptability in aligning with cerebral dynamics (Dennis, 2016; Pei & Shinn-Cunningham, 2022). The AC enables frequency-specific modulations that can be fine-tuned by adjusting frequency, amplitude, and phase during stimulation which in turn can modulate neural oscillation frequencies (Violante et al., 2017). These frequency-dependent attributes of AC-GVS heighten its clinical relevance

in comparison to DC-GVS, inducing a more distinct blood oxygenation level-dependent (BOLD) response (Gloviczki et al., 2011). This raises the question of whether stronger auditory facilitation will be seen following AC compared to DC stimulation.

As mentioned, another aim of this chapter was to understand if the visual interference induced by an AC current relied on bilateral hemispheric stimulation or whether unilateral stimulation was sufficient. To test this, I created a unique configuration in which the AC signal was discharged with a positive Offset set to midway between the minimum and maximum current. Accordingly the polarity of each electrode remained constant, with the right electrode remaining cathodal and the left electrode anodal. This set-up aimed to induce a repetitive cycle in which the excitation of the left afferent nerve would rise and then fall back to zero, eliciting a similar pattern of preferential (but not exclusive) excitation in the right hemisphere alone. Targeted areas included the anterior cingulate cortex, temporal gyrus, and middle/superior frontal gyrus of the right hemisphere (see Section 2.1 and Section 2.3 for further explanation).

The emphasis was on the right hemisphere as opposed to the left hemisphere because preceding research has often shown pronounced behavioural effects particularly with left-anodal and right-cathodal configurations (Wilkinson et al., 2005, 2008, 2010, 2014; Wilkinson, 2021). This finding highlights a distinct vestibular influence contingent upon GVS polarity. These findings hint at a potentially greater involvement of the right hemisphere in vestibular information processing and behavioural responses to GVS. Nonetheless, it is worth noting that fMRI studies with healthy controls receiving GVS has revealed more distinct activation patterns in the right hemisphere, regardless of the side of stimulation (Tohyama et al., 2021).

A final aim in this chapter was to examine the effects of reducing the contrast of previously presented visual stimuli to a level barely visible to participants (E11 and E12). In prior experiments, the visual stimuli were clearly detectable, potentially diminishing the sensory weight that the brain gave to the coincident vestibular stimuli to make accurate judgments. This hypothesis aligns with the principles of the maximum-likelihood estimator (Helbig & Ernst, 2004). These principles propose that the importance of a particular sensory channel shifts when its reliability reduced due to increased signal noise. Within the scope of this thesis, it may be that the brain makes more use of coincident vestibular signals when the visual stimuli are weak and ambiguous.

The integration of diverse sensory modalities, such as visual, auditory, and somatosensory inputs, within the superior colliculus (SC) forms the physiological basis for multisensory integration. This phenomenon has been extensively researched and documented in various studies (Stein and Meredith, 1993; Naumer and Kaiser, 2010; Murray and Wallace, 2012; Stein, 2012; Stein & Rowland, 2020). Neurons in this region integrate and intensify different sensory inputs, enhancing the physiological projection of the initial event and increasing the probability of triggering detection, localisation, and orientation behaviours (Stein, 2012; Stein & Rowland, 2020). Additionally, the cortex, particularly the anterior ectosylvian cortex, plays a vital role in supporting these midbrain processes. The absence of corticotectal influences impairs the ability of multisensory SC neurons to integrate sensory cues and mediate overt multisensory behaviours (Stein et al., 1983). This integrative process is driven by both excitatory and inhibitory inputs from various sensory sources. When multiple sensory inputs are concurrent, an enhanced response is often observed (Stein et al., 1989; Wilkinson et al., 1996; Burnett et al., 2004; Gingras et al., 2009; Stein & Rowland, 2020).

In their 2020 study, Stein and Rowland explored the adaptability of multisensory neurons in the SC. They found that repeated exposure to congruent visual-auditory stimuli can heighten sensitivity to individual sensory inputs. They noted that this approach can restore visual responsiveness in neurons that were previously impaired by unilateral visual cortex lesions. This finding supports the principle of inverse effectiveness, suggesting that integrating weak visual inputs with auditory stimuli can revive visual functions, potentially offering therapeutic benefits for conditions like hemianopia, a neurological disorder characterised by the loss of vision in half of the visual field, commonly resulting from cerebral injury.

The principle of inverse effectiveness suggests that multisensory integration is most influential when individual unisensory stimuli are weak or ineffective on their own, a theory that informed my experimental paradigms in reducing visual contrast. The inverse effectiveness rule is central to this thesis on multisensory integration. It suggests that combining multiple sensory stimuli results in a greater neural response than individual stimuli alone. This emphasises an organism's heightened sensitivity to events when multiple sources of information are accessible, emphasising the synergistic effects on neural processing and behavioural responses (Meredith & Stein, 1987).

Holmes and Spence (2005) provided a comprehensive overview of multisensory integration in the SC. This midbrain structure is crucial in orchestrating eye and head movements and is fundamental for overt attention and orientation behaviours (Stein, 1998). Integration in this context involves the synthesis of visual, auditory, and somatosensory information by neurons in the SC to generate motor commands (Sparks, 1986; Stein et al., 2004). They also highlighted the three primary theoretical frameworks for multisensory integration identified by Stein et al. (1989). These include the spatial and temporal rules of

multisensory integration, involving the alignment of spatial maps across different sensory modalities (Knudsen & Brainard, 1991) and the integration of nearly simultaneous signals (Irini Skaliora et al., 2004). For instance, when watching a video of a person speaking, the brain integrates slightly asynchronous visual and auditory signals to create a coherent perception.

The significance of timing in multisensory integration within neurons was emphasised by Meredith and Stein (1987) and Stein and Meredith (1993). Despite varying processing speeds across sensory modalities, a 'temporal window' of several hundred milliseconds allows for effective integration, which is crucial for detecting relevant environmental stimuli. This allows stimuli from different modalities to interact despite their varying input latencies. An example is the "McGurk effect" (McGurk and MacDonald, 1976), where the brain forms a unified perception from incongruent auditory and visual speech components. This shows that multisensory neurons not only combine, but also transform information into an integrated output distinct from individual unimodal inputs (Stein, 1998), often leading to heightened activity in multisensory SC neurons and influencing associated behaviours (King & Palmer, 1985; Meredith & Stein, 1986; Wallace et al., 1996; Stein, 1998; Stein et al., 1989; Frens et al., 1995; Wilkinson et al., 1996).

Stanford et al. (2005) found that while timing variations did not change the overall pattern of results, namely “super additivity”, they did affect the relative proportions of interaction types. Super additivity, where the combined response to multisensory stimuli surpasses the sum of responses to individual stimuli (Stanford & Stein, 2007; Rowland et al., 2007), is most evident with near-threshold stimulus efficacies and minimal modality-specific influences. This suggests that weak inputs can elicit a strong multisensory response (Stanford and Stein, 2007; Miller et al., 2017).

The inverse effectiveness rule, which is central to this thesis on multisensory integration, suggests that combining multiple sensory stimuli results in a greater neural response than individual stimuli alone. This thesis aims to determine if this magnification of response extends to functions (e.g., visual and auditory discrimination) that lie outside the SC and can be driven by vestibular inputs. This emphasises an organism's heightened sensitivity to events when multiple sources of information are accessible, underlining the synergistic effects on neural processing and behavioural responses (Meredith & Stein, 1987).

3.1 General Method

3.2 Participants

A total of 144 participants were recruited across 6 experiments in this chapter (see Table 3.1). Following Cohen's (1992) established guidelines, which form the foundational framework proposing a necessary statistical power of at least 0.80 for reasonably detecting an existing effect, a statistical power of 0.80 (as detailed in Section 2.11) was deemed suitable for this experimental paradigm, indicating a balanced approach that considers both statistical validity and practical factors such as time, resources, and participant recruitment logistics. The stopping rule for Chapters 2 and 3 was based upon maintaining a statistical power in excess of 0.8, resulting in a minimum sample size of n = 22.

Participants in all but Experiment 9 were students at local universities (majority undergraduate level) recruited by local and online advertisements. Participants received either partial course credit or payment equivalent to minimum wage. Participants were screened against eligibility criteria to rule out underlying neurological conditions, metallic or electronic implants, balance or hearing problems, physical abrasions or inflammation in the electrode montage area, and potential pregnancy. However, Experiment 9 additionally

required a formal, confirmed diagnosis of either ADHD or dyslexia or both obtained from a qualified healthcare professional. All studies were approved by the University of Kent's Psychology research ethics committee. Participants were treated in line with the Code of Conduct guidelines provided by the British Psychological Society (BPS).

ID	Modality	Task	GVS type	n	Male	Age (years)	Population
E7	Auditory	Discrimination	AC bilateral bipolar	23	7	*M*=22, *SD*=4 Min.=18, Max.= 32	Normative group
E8	Auditory	Discrimination	AC bilateral bipolar with positive Offset	Invalid data			Normative group
E9	Auditory	Discrimination	AC bilateral bipolar with positive Offset	24	7	*M* = 24, *SD*=7 Min.=18, Max.= 47	Clinical group, ADHD: *n* = 6 Dyslexia: *n* = 16 ADHD & Dyslexia: *n* = 2
E10	Visual	Discrimination	AC bilateral bipolar with positive Offset	22	7	*M*=26, *SD*=4 Min.=18, Max.= 33	Normative group
E11	Visual	Detection	AC bilateral bipolar	24	9	*M*=20, *SD*=2 Min.=18, Max.= 25	Normative group
E12	Visual	Discrimination	AC bilateral bipolar	22	7	*M*=22, *SD*=3 Min.=18, Max.= 27	Normative group

Table 3.1: Demographics for analysed data by experiment.

3.3 Stimuli and apparatus

Visual and auditory stimuli used for Experiments 7, 8, 9 and 10 were identical to stimuli presented in Chapter 2 using PsychoPy, version 1.85.3 (Peirce et al., 2019). In Experiments 11 and 12, stimuli were presented on a 24.5-inch BenQ monitor (1920 x 1080 pixels, 100 Hz refresh rate).

Gabor patches were presented for duration of 0.2 seconds at a size of 10 cm x 10 cm on a grey background in Experiments 11 and 12 (standard RGB colour-space: 0.5, 0.5, 0.5; equivalent to PsychoPy's custom-RGB scale: 0, 0, 0). In Experiments 11 and 12, the screen

background colour was changed from black to grey, and Gabor-patch contrast (i.e., the luminance difference between light and dark gratings) was adjusted to each participant's contrast sensitivity threshold. These changes were made to eliminate the problem with ceiling effects in visual detection experiments presented in Chapter 2 (near-perfect performance at or above 95% accuracy in E2 and E6). Gabor patch contrast was adjusted such that performance fell within 60–70 % detection accuracy (chance performance was 50 % accuracy).

3.4 Methods

The procedure, experimental tasks, and statistical design were all identical to the experiments presented in Chapter 2.

3.5 Auditory discrimination AC bilateral bipolar

The auditory discrimination task using DC bilateral bipolar (E4) showed a main effect of GVS and proved to be facilitatory irrespective of Offset. In this experiment (E7), I was interested in seeing if the same facilitatory results can be obtained and further aligned with the central hypothesis that the enhancement would occur at Offset 4 where the peak of the GVS pulse would align with the Onset of the synchronised stimuli by using an AC bilateral bipolar. If this is true, then it demonstrates that the DC-GVS is not necessary for vestibular-auditory enhancement, and that may be, instead, any shape of the waveform is sufficient. Alternatively, it may be that the AC-GVS has a more profound effect, as was the case in the previous Chapter.

3.6 Planned analysis

ANOVA was utilised to interrogate both the main effects and interactions. A Greenhouse-Gieser correction was applied where the assumption of sphericity was violated.

Bonferroni-corrected pairwise comparisons were used via SPSS software (Version 25) to explore the interaction term.

The main effect of Offset was not subject to post hoc analysis because it did not address the hypothesis. The central hypothesis is to investigate whether attentional processes can be enhanced by concurrent vestibular signals, specifically when the temporal frequency of the visual or auditory stimuli is synchronised with the Onset of the vestibular stimuli, as opposed to when they are asynchronous. Independent variables were GVS (2 levels: active GVS or no stimulation) and Offset (3.2, 3.6, 4, 4.4, 4.8. seconds from S1 Onset at the start of an experimental trial). Dependent variables were response accuracy, measured as the percentage of correct responses, with a minimum inclusion level of 60 % mean accuracy across no stimulation conditions, and median response times for correct trials calculated from S2 Onset reported in seconds. Response accuracies and response times were analysed separately.

An a priori sample size estimation was performed using the G*Power software package (version 3.1.9.3) during the planning and design of the trial. The input parameters were the following: statistical test = ANOVA: repeated measures, within factors; effect size f = 0.25; α err prob = 0.05; power (1 ß err prob) = 0.80; number of groups = 2; number of measures = 5; correlation among repeated measures = 0.5; non-sphericity correction e = 1. These conditions pre-determined a sample size of n = 22.

3.7 Experiment 7: Auditory discrimination (AC bilateral bipolar)

A 2 x 5 repeated measures ANOVA with Greenhouse-Geisser correction on median response time did not show a main effect of Stimulation [F (1, 22) = 0.145, p = 0.707, η_p^2 = 0.007], or Offset [F (1.847, 40.642) = 1.292 p = 0.284, η_p^2 = 0.055]. The interaction [F

(3.129, 68.830) = .086, p = 0.971, η_p^2 = 0.004] also failed to reach statistical significance (Figure 3.1).

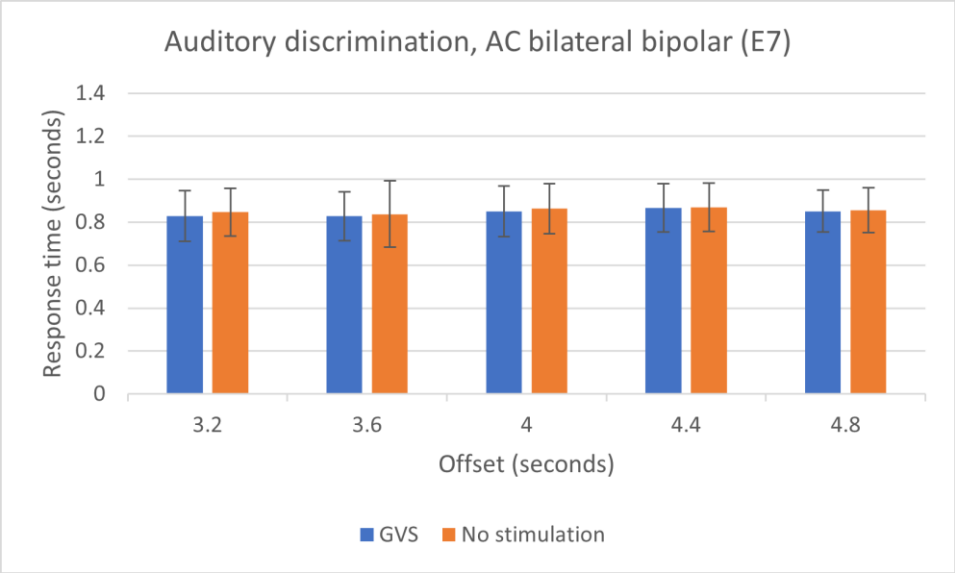

Figure 3.1: Median response times in Experiment 7 as a function of Stimulation x Offset.

A 2 x 5 repeated measures ANOVA with Greenhouse-Geisser correction on response accuracy showed a main effect of Stimulation [F (1, 22) = 8.853, p = 0.007, η_p^2 = 0.287], whereby responses during GVS (M = 76.581; SD=7.755) were generally more accurate compared to no stimulation (M = 68.956; SD=14.699). There was also a main effect of Offset [F (1.947, 42.844) = 6.500, p = 0.004, η_p^2 = 0.228]. While post hoc analysis for the main effect of Offset was not conducted, the means and standard deviation for each Offset are presented in Table 3.2. It seems that as the Offset increases, the accuracy tends to decrease. However, the interaction term [F (1.857, 40.855) = 0.740, p = 0.474, η_p^2 = 0.033] failed to reach statistical significance (see Figure 3.2 and Appendix B.3.1).

	GVS		**No Stimulation**	
Offset	Mean	SD	Mean	SD
3.2	84.261	11.97	73.816	28.692
3.6	83.19	10.774	73.476	26.763
4	78.575	11.024	67.093	21.764
4.4	71.662	16.508	67.392	21.221
4.8	65.217	12.676	63.004	16.064

Table 3.2: Presenting means and SD for each Offset. E7, response accuracy

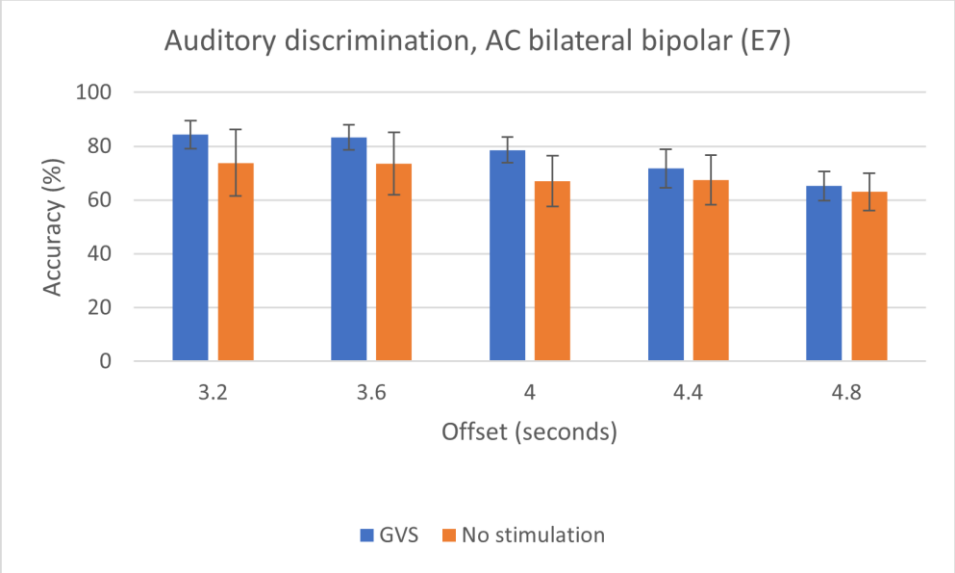

Figure 3.2: Response accuracy (%) in Experiment 7 as a function of Stimulation x Offset.

3.8 Discussion for Experiment 7

Experiment 7 utilised AC bilateral bipolar and was focused on auditory discrimination and response time. The results showed no significant differences in response times among the conditions of Stimulation, Offset, or the interaction between Stimulation and Offset. However, in terms of response accuracy, participants showed higher accuracy during GVS compared to the no stimulation condition. Nevertheless, the combined effect of Stimulation and Offset on accuracy was not found to be significant.

The accuracy data from E7 support the idea that the auditory system is more positively responsive to GVS compared to the visual system when the stimulation is conveyed in the form of an AC bilateral bipolar. This strengthens the evidence of shortened response time in auditory discrimination during DC bilateral bipolar stimulation (E4) presented in the previous chapter; however, the effects found in this experiment are much bolder, which supports the idea that the experimental paradigm has engaged a more robust form of facilitation through harnessing both hemispheres and neural entrainment mechanisms. A reason behind the more powerful effect is that the AC-GVS simulates gentle

rocking which is more periodic and naturalistic than a DC-GVS which signals sudden movement and may not have the same entraining effect (Aw et al., 2000).

3.9 Experiment 9: Auditory discrimination AC bilateral bipolar with positive Offset, Clinical group

The previous experiments investigated the role of GVS in modulating temporal attention in the normative group. Two of these experiments indicated that GVS could improve auditory matching-to-sample performance, albeit at all stimulus Onsets rather than those that coincide with the GVS pulse. In the present experiment, I tested whether this effect held in individuals with Auditory Processing Disorder (APD).

According to the British Society of Audiology (2011), APD is characterised as a neurological disorder rather than an auditory disorder and can coexist with other disorders such as Attention Deficit Hyperactivity Disorder (ADHD) (Nafi, 2013). This emphasises that the origins of APD lie in higher-order cognitive processes and are associated with impairments in recognising and processing auditory information (Moore et al., 2012; Bellis & Bellis, 2015). Notably, while individuals diagnosed with APD do not exhibit difficulty attributed to hearing sensitivity, they often face challenges in auditory discrimination, auditory pattern recognition, and temporal aspects of audition, including temporal resolution, masking, integration, and ordering (Putter-Katz et al., 2002; Veeranna et al., 2019; Lam et al., 2019).

The body of literature suggests overlapping manifestations among APD, ADHD, and dyslexia (Glennon & Kirby, 2018; Alanazi, 2023). Earlier study by Castellanos and Tannock (2002) proposed that temporal processing challenges might play a vital role in the performance of those with ADHD. Furthermore, corroborative studies have highlighted that

that individuals with ADHD may also experience auditory processing challenges (Gascon et al., 1986; Cook et al., 1993).

A number of studies have discussed abnormal multisensory integration in individuals with ADHD and dyslexia, emphasising their ability or inability to identify and recognise unisensory inputs (Dean et al., 1989; Dokka et al., 2015). Findings from an fMRI study revealed that the midbrain superior colliculus (SC) in individuals with ADHD and dyslexia is impaired, leading to disruptions in the temporal window of integration (Clements et al., 2014; Panagiotidi et al., 2017; Panagiotidi et al., 2018).

Studies suggest that ADHD is linked to deficits in temporal processing for both tones and consonant-vowel syllables (Chan et al., 2022). These deficits can influence an individual's capacity to estimate time, sustain attention, and complete tasks. In an online temporal processing assessment study, participants with ADHD exhibited less precision in tone tasks and demonstrated a higher ISI passing threshold for consonant-vowel tasks than the healthy controls (Chan et al., 2022). Similarly, Suarez et al. (2020) noted that individuals with ADHD displayed greater variability in auditory and visual temporal tasks and tended to overestimate time durations during experiments. The authors suggested that these temporal processing challenges could stem from a dysfunction in switch mechanisms and/or memory impairments (Suarez et al., 2020). Similarly, individuals with dyslexia frequently experience challenges in auditory and visual temporal processing. This hinders their ability to recognise and process speech sounds, leading to reading and spelling difficulties (Casini et al., 2017; Wang & Bi, 2021; Wang & Yang, 2020). Further, those with dyslexia often have difficulty discerning rapid successive stimuli sequences, and they show atypical neural synchronisation. Notably, these challenges are observed in both verbal and non-verbal stimulus processing, indicating that they are not exclusive to speech processing (Wang & Bi, 2021). Overy (2000)

suggested that music training, particularly when it necessitates precise timing skills, has the potential to facilitate the development and enhancement of temporal processing abilities. As a result, it may represent a valuable supplementary rehabilitation approach for individuals with dyslexia.

Given the substantial body of evidence from studies, it has been established that individuals with neurodevelopmental disorders, such as ADHD or dyslexia, exhibit deficiencies in temporal processing (Brown et al., 2020). These deficiencies impede their capacity to accurately perceive and process time intervals. Such impairments stem from dysfunction within the cerebral regions responsible for supporting the internal clock mechanism. Consequently, the present experiment aimed to assess whether individuals within this specific demographic could derive advantages from rhythmic vestibular signals in the auditory domain, when engaged in the DMTS paradigm.

Prior to conducting the experiment on the clinical group, I first administered it to a control group (originally designated as Experiment 8) using a set-up in which the right hemisphere was preferentially activated by means of a half-width positive Offset applied to an anodal left-cathode right configuration. The preliminary analyses revealed a significant main effect of stimulation which prompted me to use the same configuration in the clinical group. However, during the review of my findings in the final stages of writing the thesis, I observed anomalies in the data patterns. These deviations from the expected results raised concerns about the accuracy of the results. Upon thorough examination of both the raw data and the PsychoPy script, I identified an oversight. Specifically, during the third block of the experiment, only partial data were recorded, thus compromising the validity and reliability of the entire experiment. This unfortunate oversight emphasises a vital lesson for me on the importance of continuous data verification throughout the data collection process. By

analysing data on a per-participant basis, one could promptly identify and rectify potential discrepancies, ensuring both the efficient use of resources and the respect for participants' time and effort. Guided by this newfound understanding, I attentively incorporated regular data checks in subsequent experiments reported in this thesis. This proactive approach ensured that similar discrepancies were proactively identified and addressed, affirming the reliability of the subsequent experiments. In the present context, however, I chose not to report this experiment given that it did not produce interpretable data.

3.10 Methods

3.11 Pure-tone Audiometry

In Experiment 9, participants' hearing was first assessed through the Pure-tone Audiometry, which determined if their hearing fell within the normal range. Pure-tone audiometry administers noises above the normal threshold, which can recruit and register even the most basic sensory encodings (Sams et al., 1991; Bellis & Bellis, 2015). If participants reported they could hear the tone, the intensity would be reduced by 10-dB levels until they were unable to report hearing a tone. Afterwards, the intensity was increased to 5-dB levels until their lowest hearing threshold was established. The range of frequency tested runs was between 250 to 8000Hz. All participants performed within the average hearing threshold (0.5, 1, 2 & 4 kHz) and performed within normal limits (≤20 dB HL). A reason for implementing this test was to rule out any hearing deficit.

3.12 SCAN-3:A

The next test conducted; the SCAN-3 (Lovett & Johnson, 2010) served as a baseline measure to exclude the presence of APD among the clinical population. Six sub-tests from SCAN-3: A were administered, which involved participants repeating speech sounds

presented through headphones in a sound-treated room. These sub-tests included the following conditions: 1) Filtered Words (FW), 2) Auditory Figure Ground: Monosyllabic words with eight-talker speech babble masking noise, where the speech signal was 8 dB louder than the masking noise. 3) Competing Words (CW): Simultaneous presentation of monosyllabic words, one in each ear. 4) Competing Sentences (CS): Simultaneous presentation of sentences, one in each ear. 5) Auditory Figure Ground (AFG 0): Monosyllabic words with eight-talker speech babble masking noise, where the loudness of speech and masking noise were equal. 6) Time Compressed Sentence (TCS): Sentences compressed at 60%, creating a fast-speaking effect.

A total of 28 participants diagnosed with ADHD and/or dyslexia completed the SCAN-3A as a baseline assessment to rule out the possibility of APD within this population. The raw scores of each participant were manually recorded and calculated, and then compared to the normative data provided in the test manuals. Among the participants, 24 scored within the normal range (Minimum mean: 7 and Maximum mean: 19, according to the Scaled Score Chart, Table 3.1). Four participants performed below the threshold (Minimum mean: 1 and Maximum mean: 6) and were consequently excluded from the main study (Table 3.3)

	FW	**AFG+8**	**CW**	**CS**	**AFG0**	**TCS**
Mean	12.29	12.54	12.33	12.13	11.46	13.04
SD	2.92	3.23	2.69	1.82	2.46	2.11

Table 3.3: The table presents the mean scores and standard deviations of a clinical population (n=24) at baseline in six subtests of the SCAN-3A test battery.

3.13 QuickSIN Auditory Assessment

In a preliminary pilot trial, I incorporated the QuickSIN Auditory Assessment (Elrefaey et al., 2018) to assess participants ability to discriminate speech in the presence of

background noise. The purpose of adding QuickSIN was primarily to further rule out potential cases of APD within our clinical group. However, when advancing to the main trial, I decided to omit QuickSIN. This decision stemmed from the observation that the SCAN-3 A components were sufficiently robust in evaluating potential APD diagnoses. Furthermore, including QuickSIN would have excessively lengthened the experiment duration for our target clinical group. As a result, QuickSIN was not included in the main trial's test battery.

The outcome of Pure-tone audiometry combined with SCAN-3: A demonstrated no signs of developmental hearing or language impairments in the clinical population.

3.14 Experiment 9: Auditory discrimination, Clinical group

A 2 x 5 repeated measures ANOVA with Greenhouse-Geisser correction on median response time did not show a main effect of Stimulation [F (1, 23) = 0.094, p = 0.762, η_p^2 = 0.004], or Offset [F (2.390, 54.964) = 1.549, p = 0.219, η_p^2 = 0.063]. The interaction [F (2.988, 68.727) = 0.335, p = 0.799, η_p^2 = 0014] also failed to reach statistical significance (Figure 3.3).

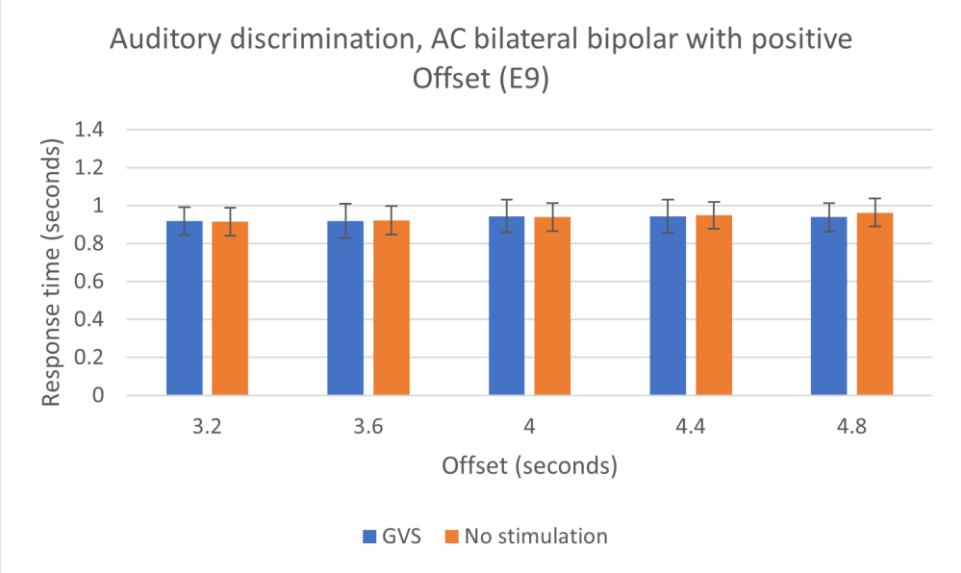

Figure 3.3: Median response time in Experiment 9 as a function of Stimulation x Offset.

A 2 x 5 repeated measures ANOVA with Greenhouse-Geisser correction on response accuracy did not show a main effect of Stimulation [F (1, 23) = 1.513, p = 0.231, η_p^2 = 0.062]. The main effect of Offset [F(2.189, 50.348) =132.075, p < 0.001, η_p^2= 0.852] did however reach statistical significance. While post hoc analysis for the main effect of Offset was not conducted, the means and standard deviation for each Offset are presented in the table below. It seems that as the Offset increases, the accuracy tends to decrease (see Table 3.4). The interaction [F (3.313, 76.204) = 4.622, p = 0.004, η_p^2 = 0.167] also reached statistical significance (Figure 3.4).

	GVS		**No Stimulation**	
Offset	Mean	SD	Mean	SD
3.2	88.782	13.174	88.942	7.020
3.6	87.019	14.338	94.070	6.611
4	82.532	15.088	85.096	8.953
4.4	67.147	12.002	66.987	10.139
4.8	57.692	11.841	63.782	8.250

Table 3.4: Presenting means and SD for each Offset. E7, response accuracy

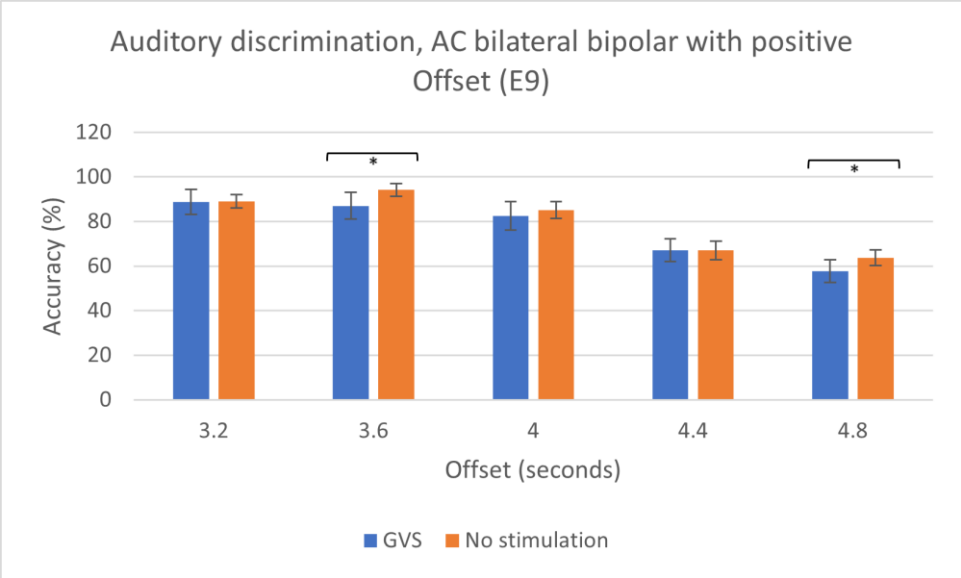

Figure 3.4: Response accuracy (%) in Experiment 9 as a function of Stimulation x Offset. For ease of interpretation only significant post-hoc comparisons are marked (*).

Pairwise comparisons between the Stimulation conditions within each level of Offset showed that response accuracy was significantly lower during GVS (M = 87.019; SD=14.339) compared to no stimulation (M = 94.07; SD=6.614) at Offset 3.6 [t(23)= 2.150,

p = 0.042]; and during GVS (M = 57.692; SD=11.841) compared to no stimulation (M = 63.782; SD=8.250) at Offset 4.8 [t(23)= 2.326, p = 0.029]; (see Figure 3.4 and Appendix Table B.3.1).

Pairwise comparisons also examined whether response accuracy differed between Offset conditions within each Stimulation condition. For ease of interpretation, the means and standard deviations for each Offset during each condition are presented in Table 3.5 below.

	GVS		**No Stimulation**	
Offset	Mean	SD	Mean	SD
3.2	88.782	13.173	88.942	7.020
3.6	87.019	14.339	94.070	6.614
4	82.532	15.089	85.096	8.955
4.4	67.147	12.002	66.987	10.141
4.8	57.692	11.841	63.782	8.250

Table 3.5: Presenting means and SD for each Offset during each condition. E9, response accuracy

The results revealed that during GVS, there were significant differences between Offset 3.2 (M=88.782; SD=13.173) and Offset 4 (M=82.532; SD=15.089) [t(23)= 3.787, p=0.01], Offset 3.2 (M=88.782; SD=13.173) and Offset 4.4 (M=67.147; SD=12.002) [t(23) = 10.396, p<0.001], Offset 3.2 (M=88.782; SD=13.173) and Offset 4.8 (M=57.692; SD=11.841) [t(23)= 14.322, p<0.001], Offset 3.6 (M=87.019; SD=14.339) and Offset 4.4 (M=67.147; SD=12.002) [t(23)= 8.965, p<0.001], Offset 3.6 (M=87.019; SD=14.339) and Offset 4.8 (M=57.692; SD=11.841) [t(23) = 10.752, p<0.001], Offset 4 (M=82.532; SD=15.089) and Offset 4.4 (M=67.147; SD=12.002) [t(23)= 9.592, p<0.001], Offset 4 (M=82.532; SD=15.089) and Offset 4.8 (M=57.692; SD=11.841) [t(23)= 15.490, p<0.001], as well as Offset 4.4 (M=67.147; SD=12.002) and Offset 4.8 (M=57.692; SD=11.841) [t(23)= 6.627, p<0.001] (see Figure 3.5 and Table 3.6).

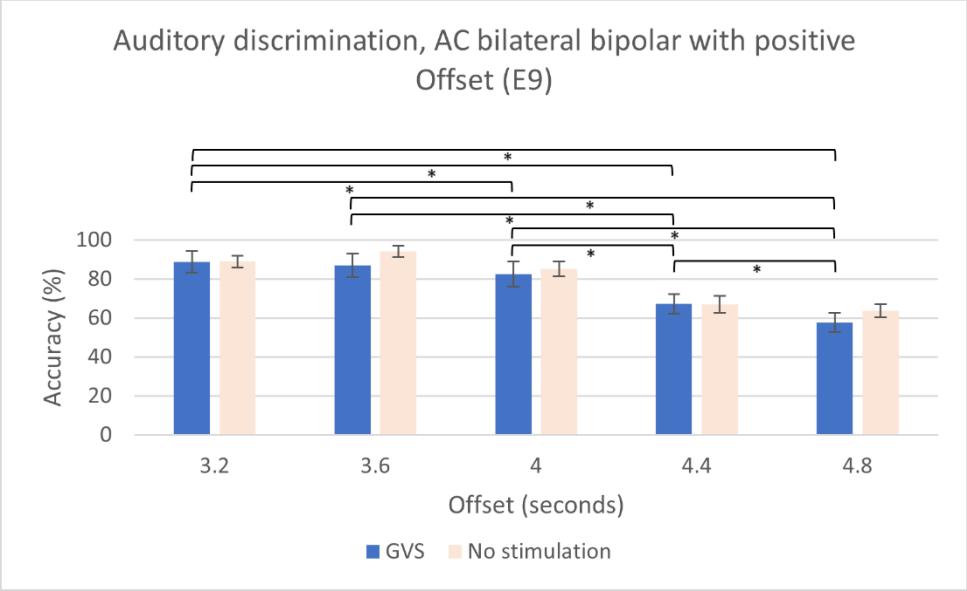

Figure 3.5: Response accuracy (%) difference between the Offset conditions within the GVS condition for Experiment 9. For ease of interpretation only significant post-hoc comparisons of association are marked (*).

Offset	**Stim.**		**t value**	**Sig.**	**95% CI**	
					Lower Bound	Upper Bound
3.2	GVS	No Stim	-0.057	0.955	-5.996	5.675
3.6	GVS	No Stim	-2.150	0.042	-13.835	-0.267
4	GVS	No Stim	-0.840	0.409	-8.875	3.747
4.4	GVS	No Stim	0.059	0.953	-5.414	5.735
4.8	GVS	No Stim	-2.326	0.029	-11.506	-0.673

Table 3.6*:* Post-hoc statistical analysis of pairwise comparisons showing stimulation conditions at each Offset. E9, response accuracy

During no stimulation there were significant difference between Offset 3.2 (*M*=88.942; *SD*=7.020) and Offset 4.4 (*M*=66.987; *SD*=10.141) [*t* (23) = 8.676, *p*<0.001], Offset 3.2 (*M*=88.942; *SD*=7.020) and Offset 4.8 (*M*=63.782; *SD*=8.250) [t (23) = 10.41, p<0.001], Offset 3.6 (*M*=94.070; *SD*=6.614) and Offset 3.2 (*M*=88.942; *SD*=7.020) [*t* (23) = 3.278, *p*<0.001], Offset 3.6 (*M*=94.070; *SD*=6.614) and Offset 4 (*M*=85.096; *SD*=8.955) [*t* (23) = 5.934, *p*<0.001], Offset 3.6 (*M*=94.070; *SD*=6.614) and Offset 4.4 (*M*=66.987; *SD*=10.141) [*t* (23) = 12.881, *p*<0.001], Offset 3.6 (*M*=94.070; *SD*=6.614) and Offset 4.8 (*M*=63.782; *SD*=8.250) [*t* (23) = 15.385, *p*<0.001], Offset 4 (*M*=85.096; *SD*=8.955) and Offset 4.4 (*M*=66.987; *SD*=10.141) [*t* (23) = 9.252, *p*<0.001], as well as Offset 4 (*M*=85.096;

SD=8.955) and Offset 4.8 (*M*=63.782; *SD*=8.250) [*t* (23) = 10.704, *p*<0.001] (Figure 3.6 and Appendix B.3.1).

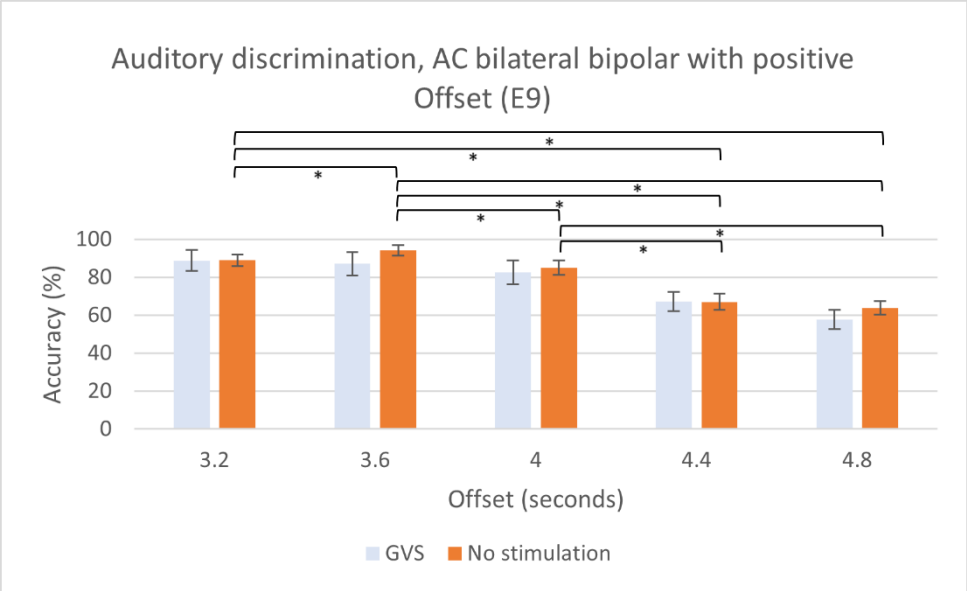

Figure 3.6: Response accuracy (%) difference between the Offset conditions within the condition for Experiment 9. For ease of interpretation only significant post-hoc comparisons of association are marked (*).

3.15 Discussion for Experiment 9

Experiment 9 utilised AC bilateral bipolar with positive Offset and was focused on auditory discrimination and response time. The results showed that effects of Stimulation and Offset and their interaction on response time, analysis of response accuracy showed a significant interaction between Stimulation and Offset. Specifically, the accuracy was notably lower during GVS than no stimulation condition at Offsets 3.6 and 4.8. Further analysis within the Stimulation conditions indicated that during GVS, performance declined significantly from Offset 3.2 to Offset 4 and continued to decrease at post-synchronous Offsets (4.4 and 4.8). Interestingly, during the no-stimulation condition, the performance decline was consistent across all Offsets. However, there was a more prominent decrease in performance following the synchronous condition at Offset 4.

As mentioned above, due to technical errors, I cannot conclude how the normative group (E8) would have behaved in this experimental setup. However, I can conclude that this setup does not appear to have any therapeutic benefit or engage with the DAT framework. It is plausible that one of the explanations for the inhibitory outcome of the current experiment is that individuals with ADHD have significant sensitivity impairment in all sensory response patterns (Shimizu et al., 2014), which could have been worsened during GVS. Atypical sensory sensitivity has also been documented in the ADHD population (Bijlenga et al., 2017). Adults with ADHD have more significant impairments in filtering out irrelevant auditory stimuli, which could be characterised as auditory hypersensitivity (Micoulaud-Franchi et al., 2015). They also reported that abnormal sensory sensitivity was related to an increased likelihood of a missed or incorrect response; suggesting that hypersensitivity in the ADHD population could be associated with a defective dopaminergic system (Romanos et al., 2008; Treister et al., 2013). The previous findings go in line with the outcome of E9, which demonstrates overly responsive behaviours in some ADHD groups while under-responsivity in others. Another explanation could be that although the GVS threshold was adjusted at a sub-sensory level for each participant, it is notable that as accuracy declines across Offset, the effect of stimulation does not change. The auditory sensory processing, as defined by DSM-IV, indicates that a low sensory threshold may lead to distractibility in response accuracy during an auditory task, while a high threshold may lead to inattentive responses during the task (Gioia et al., 2000).

The results of E9 are nevertheless broadly aligned with the minimal available literature on the impact of vestibular stimulation on neurodevelopmental disorders. Other cross-modal studies in individuals with ADHD have also reported minor detrimental effects. Mazaheri et al. (2009) conducted a cross-modal study between typically developed children and those with diagnosed ADHD. They employed a cross-modal attentional cueing paradigm

where the cues indicated the modality of upcoming stimuli, comparing attentional origination between the two groups and evaluating functional connectivity. They concentrated on oscillatory activity in the theta and alpha frequency bands, as earlier studies have closely connected these bands to different elements of attentional orienting and cognitive processing (Thut, 2006; Klimesch et al., 2007; Zhang et al., 2008). They reported that frontal theta activity is found to be negatively correlated with posterior alpha activity during directed attention (Mazaheri et al., 2009). Furthermore, undertaking a task requiring cross-modal attention, where participants expected an upcoming target, lead to a reduction in posterior alpha activity, which is linked to behavioural advantages in the normative group, but not in the ADHD population (Mazaheri et al., 2010). These findings suggest a physiological disconnection between the frontal and occipital cortex of individuals with ADHD compared to the normative group.

3.16 Visual discrimination AC bilateral bipolar with positive Offset

In Chapter 2, the effects of AC bilateral bipolar GVS on visual responses were investigated. The outcome of the visual discrimination task (E6) indicated that visual processing had been negatively affected by the temporal synchronicity of vestibular signals, and the performance worsened from the synchronous Offset onwards. The following experiment explored whether, by means of discharging an AC bilateral bipolar with positive Offset, this interference effect might in some way be hemispheric specific. The setup in E6 produced consecutive activation of both hemispheres, aiming to test whether this bilateral activation is necessary, or if unilateral hemispheric stimulation alone is sufficient.

3.17 Experiment 10: Visual discrimination AC bilateral bipolar with positive Offset

A 2 x 5 repeated measures ANOVA with Greenhouse-Geisser correction on median response time did not show a main effect of Stimulation [F (1, 21) = .227, p = 0.639, η_p^2 = .011], or interaction [F (3.141, 65.966) = 1.080, p = 0.366, η_p^2 = 0.049]. The main effect of Offset [F (2.605, 54.706) = 20.149, p = 0.001, η_p^2 = 0.490] did however reach statistical significance. While post hoc analysis for the main effect of Offset was not conducted, the means and standard deviation for each Offset are presented in Table 3.7 below. It seems that as the Offset increases, the response time tends to get longer (see Figure 3.7).

	GVS		**No Stimulation**	
Offset	Mean	SD	Mean	SD
3.2	0.656	0.144	0.671	0.173
3.6	0.661	0.111	0.651	0.163
4	0.688	0.137	0.673	0.162
4.4	0.75	0.168	0.721	0.155
4.8	0.75	0.156	0.737	0.181

Table 3.7: Presenting means and SD for each Offset. E10, response time

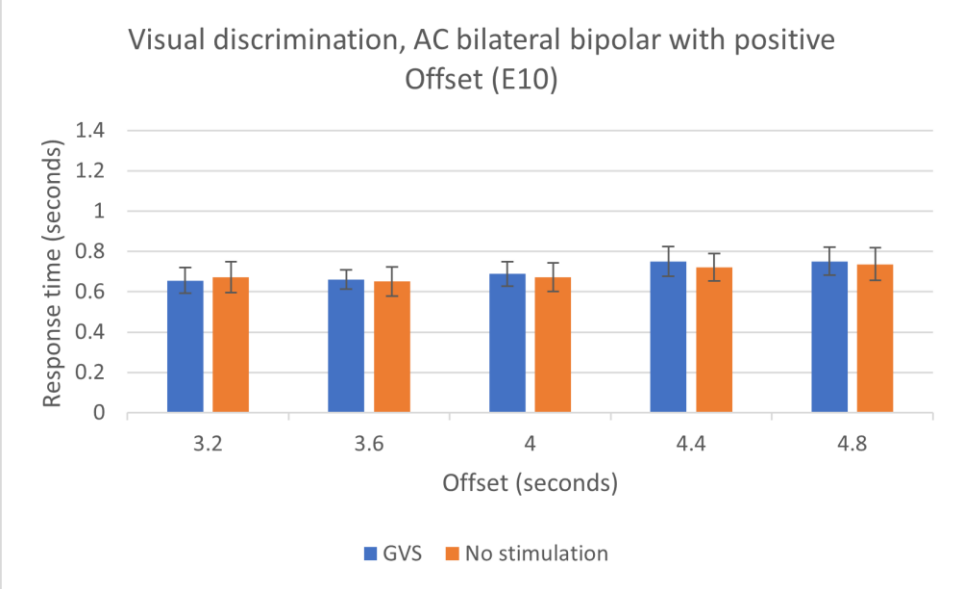

Figure 3.7: Median response times in Experiment 10 as a function of Stimulation x Offset.

A 2 x 5 repeated measures ANOVA with Greenhouse-Geisser correction on response accuracy showed a main effect of Stimulation [F (1, 21) = 11.476, p = 0.003, η_p^2 = 0.353],

whereby responses during active GVS (*M* = 81.581; *SD*=9.864) were generally less accurate compared to no stimulation (*M* = 89.247; *SD*=5.394). There was also a main effect of Offset [*F* (1.392, 29.236) = 31.055, *p* = 0.001, η_p^2 = 0.597]. The interaction [*F* (1.688, 35.439) = 10.745, *p* = 0.001, η_p^2 = 0.338] also reached statistical significance.

Pairwise comparisons between the Stimulation conditions within each level of Offset showed response accuracy was lower during GVS (*M* = 81.668; *SD*=9.601) versus no stimulation (*M* = 87.480; *SD*= 7.083) at Offset 4 [*t* (21) = -2.656, *p* = 0.015], also lower during GVS (*M* = 70.901; *SD*=21.069) versus no stimulation (*M* = 88.691; *SD*=8.311) at Offset 4.4 [*t*(21)= -3.628, *p* = 0.002]. Similarly, the response accuracy was lower during GVS (*M* = 67.494; *SD*=20.91) versus no stimulation (*M* = 82.910; *SD*=7.341) at Offset 4.8 [*t*(21)= -3.576, *p*= 0.002] (see Figure 3.8 and Table 3.8).

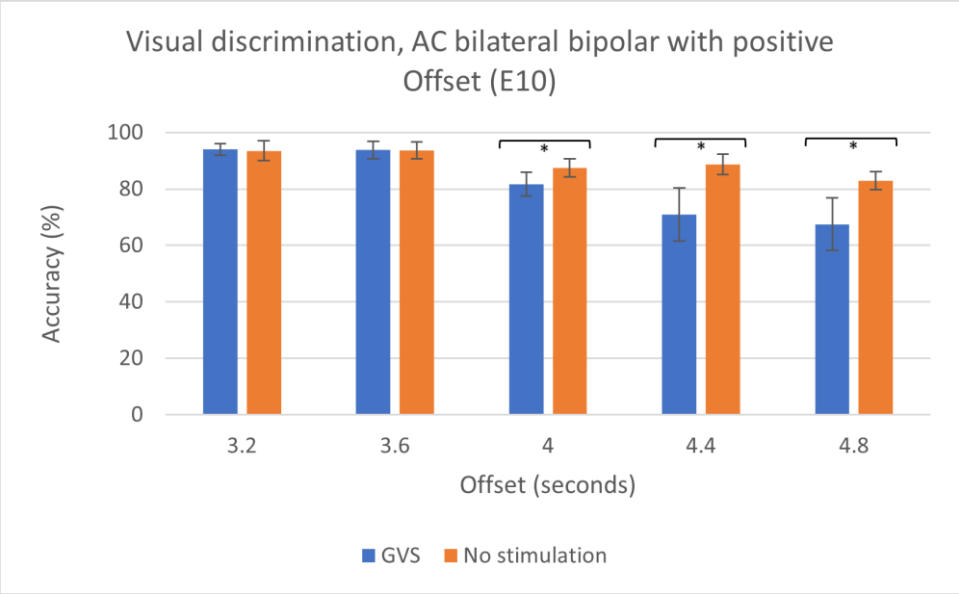

Figure 3.8: Response accuracy (%) in Experiment 10 as a function of Stimulation x Offset. For ease of interpretation only significant post-hoc comparisons are marked (*).

Offset	Stim.		t value	Sig.	95% CI	
					Lower Bound	Upper Bound
3.2	GVS	No Stim	0.312	0.758	-2.949	3.992
3.6	GVS	No Stim	0.100	0.921	-3.316	3.653
4	GVS	No Stim	-2.656	0.015	-10.362	-1.263
4.4	GVS	No Stim	-3.628	0.002	-27.986	-7.593
4.8	GVS	No Stim	-3.576	0.002	-24.381	-6.452

Table 3.8: Post-hoc statistical analysis of pairwise comparisons showing stimulation conditions at each Offset. E10, response accuracy

Pairwise comparisons also examined whether response time differed between Offset conditions within each Stimulation condition. For ease of interpretation, the means and standard deviations for each Offset during each condition are presented in Table 3.9 below.

	GVS		**No Stimulation**	
Offset	Mean	SD	Mean	SD
3.2	94.024	4.695	93.503	7.810
3.6	93.818	6.900	93.650	6.825
4	81.668	9.601	87.480	7.083
4.4	70.901	21.069	88.691	8.314
4.8	67.494	20.910	82.910	7.341

Table 3.9: Presenting means and SD for each Offset during each condition. E10, response accuracy

During GVS, Offset 3.2 (M = 94.024; SD=4.695) was significantly different to Offset 4 (M = 81.668; SD=9.601) [$t(21)$= 6.166, p<0.001], Offset 4.4 (M= 70.901; SD=21.069) [$t(21)$= 5.140, p<0.001] and Offset 4.8 (M= 67.494; SD=20.910) [$t(21)$= 5.983, p<0.001]. During GVS, Offset 3.6 (M= 93.818; SD=6.900) was significantly different to Offset 4 (M= 81.668; SD=9.601) [$t(21)$= 4.653, p=0.001], Offset 4.4 (M= 70.901; SD=21.069) [$t(21)$= 4.438, p=0.002] and Offset 4.8 (M= 67.494; SD=20.910) [$t(21)$= 5.302, p<0.001]. During GVS, Offset 4 (M= 81.668; SD=9.601) was significantly different to Offset 4.4 (M= 70.901; SD=21.069) [$t(21)$= 3.463, p=0.023] and Offset 4.8 (M= 67.494; SD=20.910) [$t(21)$= 4.644, p=0.001] (Figure 3.9).

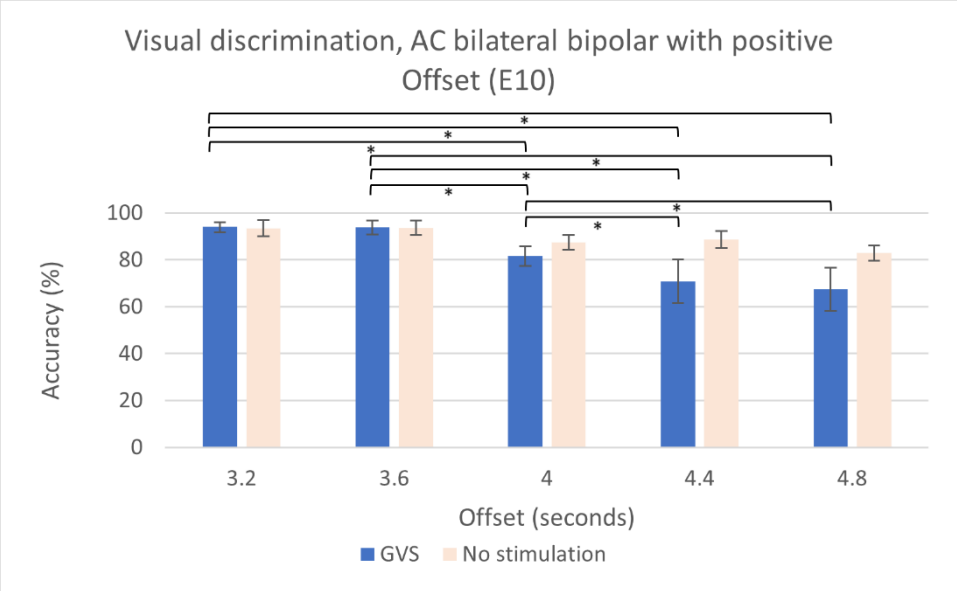

Figure 3.9: Response accuracy (%) difference between the Offset conditions within the GVS condition for Experiment 10. For ease of interpretation only significant post-hoc comparisons of association are marked (*).

During no stimulation, Offset 3.2 (*M* = 93.503; *SD*=7.810) was significantly different to Offset 4 (*M* = 87.480; *SD*=7.083) [*t*(21)= 4.208, *p*=0.004], and Offset 4.8 (*M*= 82.910; *SD*=7.341) [*t*(21)= 5.252, *p*<0.001]. During No Stimulation, Offset 3.6 (*M*= 93.650; *SD*=6.825) was significantly different to Offset 4 (*M*= 87.480; *SD*=7.083) [*t*(21)= 7.880, *p*<0.001], and Offset 4.8 (*M*= 82.910; *SD*=7.341) [*t*(21)= 5.480, *p*<0.001] (see Figure 3.10 and Appendix B.3.2).

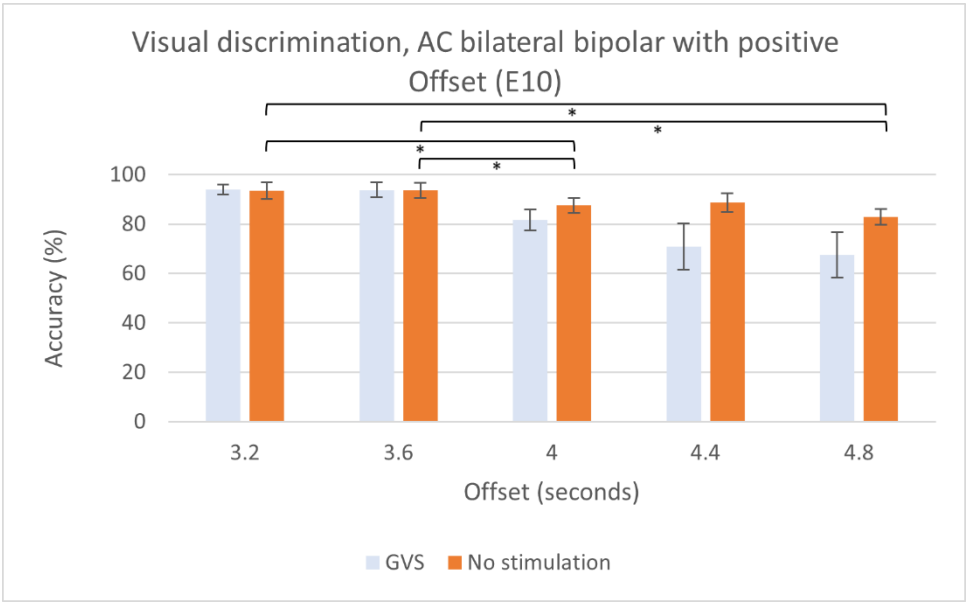

Figure 3.10: Response accuracy (%) difference between the Offset conditions within the no stimulation condition for Experiment 10. For ease of interpretation only significant post-hoc comparisons of association are marked (*).

3.18 Discussion for Experiment 10

Experiment 10 explored the effects of a AC bilateral bipolar signal on visual discrimination performance. The results showed no influence of stimulation on the median response time, and similarly, no significant interaction effect was detected. However, the presence of GVS resulted in significantly lower accuracy compared to the no stimulation condition. Specifically, the interaction between stimulation and Offset was significant, suggesting a relationship between stimulation and response accuracy depending on the level of Offset. As in my previous experiment that stimulated both hemispheres equally, at Offsets 4, 4.4, and 4.8, accuracy was lower during GVS than in the no stimulation condition. Further analysis within the stimulation conditions revealed that during GVS, performance at pre-synchronous Offsets (3.2 and 3.6) is consistently higher than at Offset 4. From Offset 4 onwards, there is a noticeable decline in performance, reaching its lowest at Offsets 4.4 and 4.8. Interestingly, the no stimulation condition exhibits a similar pattern, with the lowest performance occurring at Offset 4.8 with 83% accuracy. This parallels the lowest performance seen during active GVS, which also occurs at Offset 4.8, but with a lower 67% accuracy.

There are striking similarities between the outcomes of the current experiment (E10) and E6 of Chapter 2. Both experiments were visual discrimination tasks that utilised AC-GVS. However, the earlier experiment applied a bilateral bipolar configuration, while the current experiment used a bilateral bipolar configuration with a positive Offset. There was no change in response times; however, there was a statistically significant deterioration in response accuracy for both tasks. The outcome of the visual task, specifically when using an

AC bilateral bipolar configuration, resulted in higher error rates compared to the AC bilateral bipolar configuration with a positive Offset. Therefore, this implication suggests that this inhibition effect does not necessarily require bilateral involvement. Rather, preferential stimulation of the right hemisphere is sufficient to produce the interference effect. It remains inconclusive whether the observed effect is right hemisphere-specific until compared with a stimulation protocol that exclusively targets the left cerebral hemisphere. Nonetheless, at the very least, it can be concluded that the interference does not rely on the two cerebral hemispheres receiving the AC signal.

It is also possible that the high-contrast visual stimuli resulted in sensory overload, negatively impacting the processing and integration of sensory information. This gives rise to the question: are the effects of coincident vestibular signals more pronounced when visual stimuli are harder to distinguish from their background?

3.19 Experiment 11: Adjusted contrast, visual detection & discrimination

The following experiment aimed to understand further the unexpected visual interference effect observed previously. As mentioned, it is possible that the interference effect will be eliminated and perhaps even replaced with a facilitation effect if the visual stimuli are degraded, and judgments become more receptive to coincident sensory information such as that received from the vestibular system.

This hypothesis is derived from the principles of the multisensory integration, which suggest that different sensory modalities work together as a unit to gather information about an event which is then combined to facilitate responses (Murray & Wallace, 2011). This principle has been operationalised in three ways: spatial, temporal, and inverse effectiveness (IE) (Stein et al., 1993). The temporal underpins much of this thesis rationale, states that

sensory stimuli that relate to the same external event will occur at the same time and periodicity (Wallace et al., 1998; Holmes, 2009). The principle of IE in multisensory integration may also be of particular relevance to the visual interference reported. The IE proposes that multisensory integration and unisensory response have an inverse association which in the literature often is simplified and referred to as stimulus effectiveness (Wallace et al., 1998; Holmes, 2009). In other words, the strength of multisensory integration increases as the receptivity to individual sensory inputs diminishes (Holmes, 2009). In the present context, this means that the reliance on vestibular inputs will increase as the visibility of the visual inputs decreases. The stimulus effectiveness has been identified in various brain regions (Alvarado et al., 2008). One region that has a role in modulating and integrating multisensory inputs to generate motor commands is the superior colliculus (SC) of the midbrain (Bauer et al., 2012). Feedback from the motor and sensory layers of the SC and maximum likelihood estimator are some methods that have been proven useful in modelling and interpreting multisensory biological integration in a wide range of experiences (Trommershauser et al., 2011). As a result, the physiological intensity of the triggering event is expected to increase.

To overcome the inverse stimulus effectiveness in my paradigm, I decreased the visual contrast between the stimuli and their background. To further meet the conditions for multisensory facilitation, efforts to achieve temporal synchronicity were put into practice through the verification of periodic trigger transmissions from the PsychoPy script to the DC-stimulator device. These transmissions were predicated on timings specified in the Excel trial sheet, enabling the configuration of four asynchronous conditions (Offsets: 3.2, 3.6, 4.4, and 4.8) and one synchronous condition (Offset: 4) relative to the Onset of the trigger signal. In the subsequent experiment, a pilot test was conducted first to confirm that the stimulus contrast was reduced to a level where judgments were challenging, yet still above the baseline.

3.20 Stimuli and apparatus

In Experiments 11 and 12, Gabor patch contrast (i.e., the luminance difference between light and dark gratings) was adjusted to each participant's contrast sensitivity threshold to ensure that the stimuli were degraded. Gabor patch contrast was adjusted such that detection accuracy fell within 60–70 %. The contrast sensitivity threshold was determined across a sequence of 32 trials, starting with a contrast of 5% implemented on a greyscale (RGB: 0 to 1, PsychoPy custom RGB: -1 to 1). Gabor patches were presented in random screen locations for a duration of 0.2 seconds. Participants were instructed to respond as soon as they detected a Gabor patch. The maximum wait time for a response was 3.5 seconds, after which a trial was marked as incorrect. If performance was outside the acceptable range (60–70 % detection accuracy), the process was repeated with a 5% change in Gabor-patch contrast (increase if performance was too high, decrease if performance was too low). No GVS was administered during Gabor patch contrast sensitivity thresholding. A cut-off point of between 60–70 % accuracy during contrast sensitivity thresholding was selected, where participants responded to 260 experimental stimuli. Any participant with a performance of below 60% accuracy was excluded to ensure above-chance performance.

3.21 Experiment 11: Adjusted contrast, visual detection

A 2 x 5 repeated measures ANOVA with Greenhouse-Geisser correction on median response time did not show a main effect of Stimulation [F (1, 23) = 0.100, p = 0.755, η_p^2 = 0.004], or Offset [F (1.428, 32.855) = 0.394, p = 0.608, η_p^2 = 0.017]. The interaction [F (1.528, 35.137) = 1.101, p = 0.329, η_p^2 = 0.046] also failed to reach statistical significance (Figure 3.11).

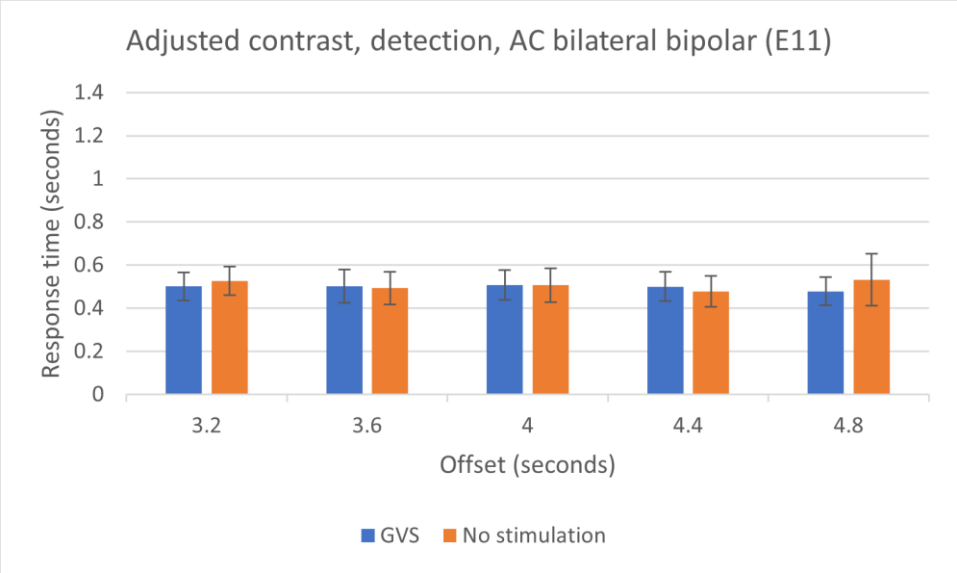

Figure 3.11: Median response times in Experiment 11 as a function of Stimulation x Offset.

A 2 x 5 repeated measures ANOVA with Greenhouse-Geisser correction on response accuracy showed a main effect of Stimulation [F (1, 23) = 5.336, p = 0.030, η_p^2 = 0.188], whereby responses during active GVS (M = 68.269; SD=21.556) were generally more accurate compared to no stimulation (M = 61.417; SD=19.498). There was also a main effect of Offset [F (3.083, 70.898) = 5.064, p = 0.003, η_p^2 = 0.180]. However, the interaction term [F (2.338, 53.780) = 0.465, p = 0.661, η_p^2 = 0.020] failed to reach statistical significance. While post hoc analysis for the main effect of Offset was not conducted, the means and standard deviation for each Offset are presented in Table 3.10 below. The result does not follow a consistent pattern. There is no clear trend between the Offset level and mean (Figure 3.12).

	GVS		**No Stimulation**	
Offset	Mean	SD	Mean	SD
3.2	70.833	23.761	66.346	21.135
3.6	65.385	24.536	56.25	24.399
4	68.429	21.874	59.071	21.835
4.4	66.186	23.844	60.545	21.615
4.8	70.513	22.759	64.872	20.494

Table 3.10: Presenting means and SD for each Offset. E11, response accuracy

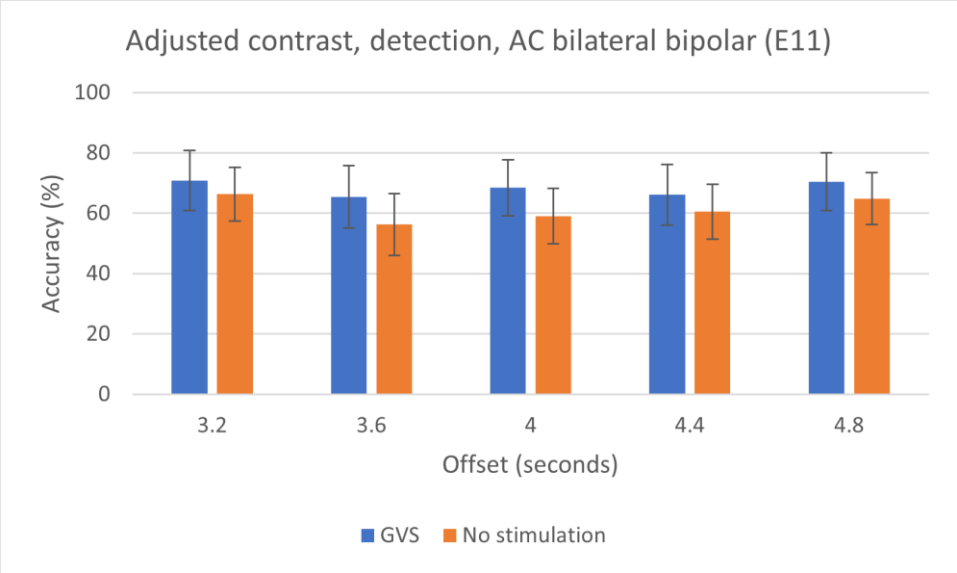

Figure 3.12: Response accuracy (%) in Experiment 11 as a function of Stimulation x Offset.

3.22 Experiment 12: Adjusted contrast, visual discrimination

A 2 x 5 repeated measures ANOVA with Greenhouse-Geisser correction on median response time did not show a main effect of Stimulation [F (1, 21) = 0.593, p = 0.450, η_p^2 = 0.027], or interaction [F (2.911, 61.127) = 1.832, p = 0.152, η_p^2 = 0.080]. The main effect of Offset [F (2.978, 62.528) = 5.835, p = 0.001, η_p^2 = 0.217] did however reach statistical significance. While post hoc analysis for the main effect of Offset was not conducted, the means and standard deviation for each Offset are presented in Table 3.11 below. There is no consistent relationship between with the Offset levels and the direction (increase or decrease) of mean values. (Figure 3.13).

	GVS		**No Stimulation**	
Offset	Mean	SD	Mean	SD
3.2	1.006	0.29	1.005	0.281
3.6	1.072	0.4	1.053	0.311
4	0.998	0.3	0.929	0.256
4.4	1.144	0.385	1.011	0.234
4.8	0.986	0.276	0.983	0.278

Table 3.11: Presenting means and SD for each Offset. E12, response time

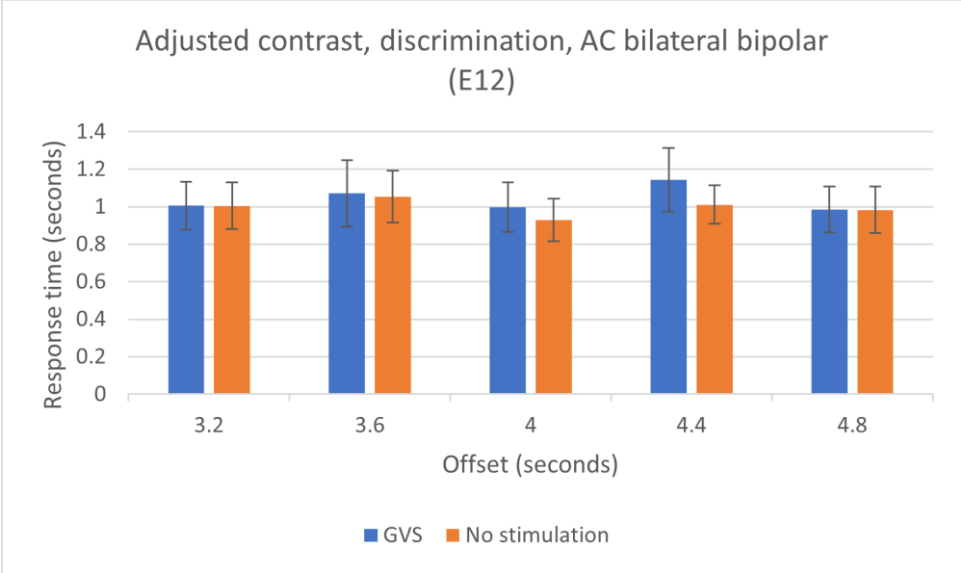

Figure 3.13: Median response times in Experiment 12 as a function of Stimulation x Offset.

A 2 x 5 repeated measures ANOVA with Greenhouse-Geisser correction on response accuracy did not show a main effect of Stimulation [F (1, 21) = 0.015, p = 0.903, η_p^2 = 0.001], or interaction [F (3.470, 72.869) = 0.799, p = 0.514, η_p^2 = 0.037]. The main effect of Offset [F (2.230, 46.820) = 6.552, p = 0.002, η_p^2 = 0.238] did however reach statistical significance. While post hoc analysis for the main effect of Offset was not conducted, the means and standard deviation for each Offset are presented in Table 3.12 below. It seems that as the Offset level increases, the accuracy tends to also increase (Figure 3.14).

	GVS		**No Stimulation**	
Offset	Mean	SD	Mean	SD
3.2	51.415	23.538	54.586	21.716
3.6	64.109	22.479	62.809	20.656
4	64.412	23.445	67.364	20.3
4.4	65.198	16.143	66.537	16.717
4.8	72.874	10.869	68.292	17.042

Table 3.12: Presenting means and SD for each Offset. E12, response accuracy

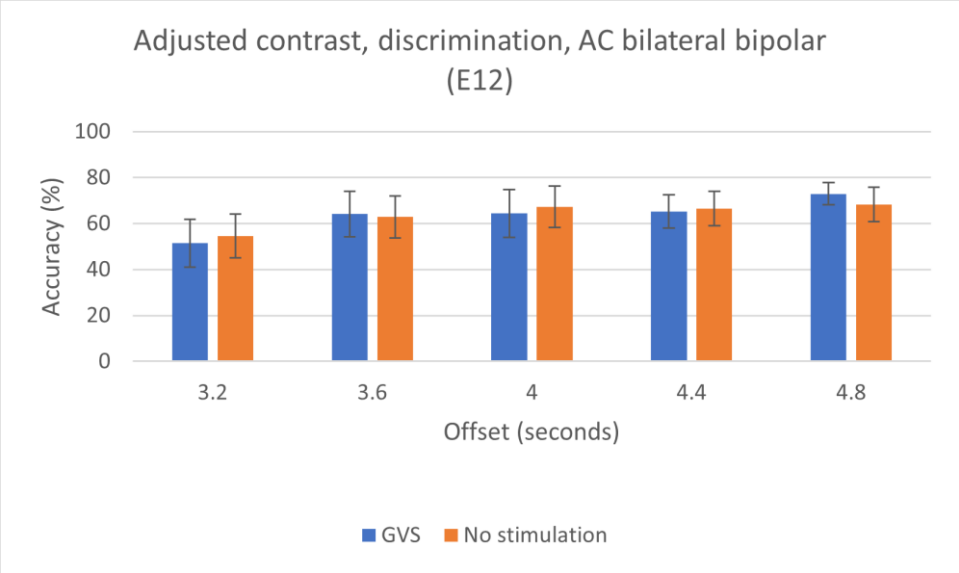

Figure 3.14: Response accuracy (%) in Experiment 12 as a function of Stimulation x Offset.

3.23 Discussion for Experiments 11 & 12

Experiment 11 assessed whether an AC bilateral bipolar induced an interference effect on visual detection when the conditions for multi-sensory facilitation were increased. The results showed that for median response time, neither Stimulation nor Offset revealed a significant effect, and that their interaction also failed to reach significance. In contrast, for response accuracy, responses during GVS were found to be more accurate compared to when there was no stimulation. However, the interaction between Stimulation and Offset failed to reach significance. The findings demonstrated that in the detection task, the interference effect was eliminated, and there was an overall improved performance in the response accuracy task.

Experiment 12 tested whether the same protocol eliminated the interference effect previously observed during visual discrimination experiments (E2, E6, E10). Consistent with predictions, enhancing the obscurity of the visual stimuli effectively mitigated the interference effect.

These data suggest that in degraded viewing conditions, when the visual system must rely more upon the vestibular system, the interference effect disappears. Therefore, one can argue that the vestibular signals were not, as perhaps first believed, inherently damaging. The detection data suggest that they may even enhance the possibility of visual detection. Furthermore, the lack of performance improvement in the discrimination experiment might be since the vestibular signal does not include information that informs visual identity. It does, however, provide temporal information, which may influence detection.

3.24 General Discussion

The current chapter further explored the inhibitory effect observed in the visual experiment from Chapter 2. The aim was to address the primary hypothesis of this thesis: if the visual system is attuned to the temporal Onset of vestibular signals, then would responses to visual stimuli be faster and/or more accurate when the visual signal coincides with the ongoing vestibular signal?

The visual discrimination experiment that utilised AC bilateral bipolar with positive Offset (E10) did not indicate a significant interaction between GVS and Offset for median response time. However, the data revealed a main effect of GVS and an interaction between GVS and Offset. A post-hoc analysis indicated that visual discrimination accuracy decreased significantly during active stimulation from the synchronous Offset onwards. This trend mirrored effects observed in the visual discrimination experiment that utilised AC bilateral bipolar (E6).The findings from E10 suggest that the source of the interference effect might not be unilateral, as the effect manifested in both AC bilateral bipolar configurations with zero and positive Offsets. More generally, the overall outcome of E6 and E10 are in line with the temporal rule, which states that stimuli with similar characteristics delivered at regular intervals will influence one another, albeit negatively in this case.

By reducing the contrast between the visual stimuli and their background (E11 and E12), conditions were identified that eliminate this inhibitory effect. These findings suggest that when both the temporal and stimulus effectiveness principles of multisensory integration are satisfied, the interaction of the vestibular system with visual attention differs from scenarios where only the principle of temporal coincidence is present. This experimental paradigm did not demonstrate multisensory enhancement, as one might anticipate according to the application of the inverse effectiveness rule; instead, it mitigated multisensory interference. There is still a need for empirical evidence demonstrating the capacity of coincident vestibular cues to enhance visual responses.

In the auditory discrimination task, AC bilateral bipolar (E7) resulted in a significant enhancement for the normative group, regardless of Offset. This enhancement surpassed that observed with DC bilateral bipolar (E4). While this provides evidence of vestibular-auditory coupling, it does no show modulation of this effect by temporal coincidence. This contrasts with the auditory-visual facilitation associated with the DAT. Moreover, this auditory discrimination advantage was not observed among participants with Auditory Processing Deficits. This lack of effect might suggest the broader challenges faced by individuals with ADHD/dyslexia in benefiting from cross-modal coupling, rather than being specific to visuo-vestibular interactions. This hypothesis requires further exploration.

Examining the visual experiments presented in Chapters 2 and 3, a distinct pattern emerges. A consistent inhibitory effect initiates from the synchronous Offset at timepoint 4, persisting through the subsequent Offsets at timepoints 4.4 and 4.8. Remarkably, this pattern exhibits in DC bilateral bipolar (E2), AC bilateral bipolar (E6), and AC bilateral bipolar with positive Offset (E10). Such findings suggest that the complex nature of this inhibitory effect is indifferent to waveform or polarity variations.

Central to these experiments were the Gabor patches, which were presented in full contrast. Gabor patches consist of sinusoidal gratings cloaked by a Gaussian and impart both orientation and spatial frequency details. Their effectiveness in stimulating the visual system is noteworthy, primarily because they reflect properties of natural visual stimuli. When subjected to the visual system, Gabor patches activate the early visual cortex (Stange, 2023; Albers et al., 2022).

A significant point of interest is that the combination of GVS with high-contrast Gabor patches could lead to an increased attentional load, thereby affecting performance and evoked brain potentials (Amir et al., 2022). The VOR uses vestibular signals about head motion to generate compensatory eye movements and maintain visual stability during head rotations via adaptive plasticity and multiple neural pathways (Lisberger & Pavelko, 1986; Ramachandran & Lisberger, 2006). Human psychophysical studies show visual and vestibular cues are integrated for self-motion perception in a statistically optimal Bayesian method, with cue weights proportional to reliability. This requires trial-to-trial re-weighting of cues based on reliability (Fetsch et al., 2009). As such, the relationship between the visual and vestibular systems, for instance, may cause a shift in visual attention. A perception of movement from the vestibular system even at the sub-sensory level could lead the visual system to allocate more resources towards stabilising visual stimuli. This incorporation potentially disrupts vestibulo-ocular reflex dynamics and modulates both spatial and non-spatial cognitive processing (Furman et al., 2003).

Moreover, when stimulus contrast is attenuated to almost invisible levels, it develops an ideal environment for multisensory integration, drawing on the principle of inverse effectiveness (Holmes, 2009). This principle hypothesises the brain's unparalleled efficiency in integrating weak sensory inputs, in this context the rhythmic vestibular signal, resulting in

an amplified collective response (Gil-Guevara et al., 2022). By calibrating contrast to such minimal levels, the brain becomes particularly receptive and responsive to the rhythm of the vestibular signals. Therefore, this amplifies overall subliminal perception, especially in situations where individual sensory inputs might be ambiguous.

Given the collected data and insights, I can conclude that the previously observed interference effect was more a product of the specific multisensory interactions determined by the viewing conditions rather than a consistent, underlying feature of visuo-vestibular interactions. However, as with earlier observations, there remains no concrete evidence that temporally coincident signals, specifically those aligning with the visual Onset, can enhance visual judgements.

A notable limitation of this study is the absence of individual threshold documentation and analysis for each participant. While participants were confirmed to be within the generic average hearing threshold, individual variances were not taken into account. Future research should consider capturing and assessing this individual threshold data to ensure a more comprehensive and representative understanding of the population.

An additional limitation concerns the relatively slow frequency of GVS, given that the predominant vestibular activation occurs within significantly condensed millisecond temporal spans. A potential approach to expanding the scope of this thesis involves the simultaneous incorporation of a higher-frequency carrier wave that is convolved with the slower wave presented here and which is required to match the longer ISIs needed for visual delayed match to sample tasks. This integration could be combined with the inclusion of supportive physiological measures, such as EEG recordings, which are skilled at capturing

neural dynamics occurring over brief temporal intervals. This measure would facilitate a reliable assessment of oscillatory cerebral responses during GVS (Saari et al., 2018).

Another limitation identified in Chapters 2 and 3 concerns the originally chosen statistical power of 0.80, guided by previous studies that adhered to Cohen's (1992) guidelines, whilst also taking into account practical factors such as time, resources, and the logistics of enlisting participants. In hindsight, this decision harboured the possibility of Type II errors, potentially affecting the wider applicability of the results. To tackle this issue, Chapter 4 introduced a corrective step by increasing the statistical power to 0.90, thereby reducing the likelihood of false negatives.

In the subsequent chapter, the study will examine the time course and componential nature of the visual interference effect using a behavioural paradigm with improved temporal precision.

Chapter 4 – Vestibular Modulation Within Millisecond Timeframes

Chapters 2 and 3 demonstrated that the temporal synchronicity of sinusoidal vestibular signals had a negative impact on visual processing. In both Experiments 6 and 10, response accuracy deteriorated from the synchronous timepoint (Offset 4) onwards, and the inhibitory effect persisted at Offsets 4.4 and 4.8. This overall pattern aligns with the DAT, albeit in a reversed manner. As discussed in Chapter 3 (Section 3.18), the type of visual stimuli used in the visual experiments of Chapters 2 and 3 may have played a role in creating this interference effect, and suggest that the effect is more closely associated with specific viewing conditions than being a consistent feature of visuo-vestibular interactions.

Although the DMTS paradigm employed in Chapters 2 and 3 repeatedly demonstrates the interference effect, it lacks the sensitivity required to offer more detailed insights into the temporal profile of visual response. This is because it only samples participants' responses once at every 400 ms which raises the question as to how visual processing is affected during the briefer time window between 0 ms and 400 ms from vestibular stimulus Onset.

The Rapid Serial Visual Presentation (RSVP) paradigm, first introduced by Ward and Rose in 1978, provides a methodological framework by which visual processing within brief, millisecond time windows can be accurately probed. Research has shown that the RSVP paradigm is capable of consistently identifying target stimuli presented within a time span of 100-800 ms (Chun & Potter, 1995; Potter et al., 2013). This effectiveness is linked to the paradigm's utilisation of a perceptual phenomenon known as the attentional blink (AB) as defined by Broadbent and Broadbent (1987).

The AB is a phenomenon where individuals find it challenging to recognise a second target stimulus when it appears shortly, typically between 200 and 500 ms, after a first target

stimulus in a rapid succession of visual stimuli (Kelly & Dux, 2011). During this interval, the recognition or identification of the second target is compromised. This phenomenon highlights constraints on humans' ability to process multiple closely spaced target stimuli, indicating potential limitations in attention and working memory (Pincham & Szűcs, 2012).

Various theories have emerged to explain the AB. For instance, Pincham and Szűcs (2012) propose that one contributing factor to AB is resource depletion, implying that processing the initial target uses the limited cognitive resources required for the subsequent one. However, they emphasise that this is not the only cause, as increasing resource demands on participants can mitigate AB. In contrast, Kelly and Dux (2011) suggest that AB occurs due to a temporary disruption in control processes triggered by the first target, which are essential for processing the second target. However, it is generally agreed that the extent of the AB is influenced by variables such as the interval between targets and cognitive load (Qiu et al., 2022).

To better understand the neural mechanisms that underlie the AB phenomenon, especially in the context of the visual disruptions observed in the vestibular experiments of Chapters 2 and 3, Chapter 4 explores the roles of diverse brain regions in AB, drawing upon EEG studies for insights.

Roles of diverse brain regions in AB have been examined using EEG studies, offering a deeper understanding of the neural correlates of the attentional blink, which may be linked to the visual processing anomalies observed in the earlier experiments. Studies indicate that AB is linked with decreased activity in the parietal cortex, a region responsible for attentional processing and working memory. On the contrary, increased activity in the prefrontal cortex,

which is tied to executive control and attentional selection, is associated with AB (Marois et al., 2004).

Another avenue of study has explored the relationship between AB and fluctuations in event-related potential (ERP) components. For instance, Kranczioch et al. (2007) found that AB corresponds with a decrease in the P3b amplitude, a component indicative of attentional processing and working memory allocation. Zhang et al. (2019) further investigated the neural underpinnings of AB in individuals with Autism Spectrum Disorder (ASD) using EEG. Their study revealed a reduced N2pc amplitude during the attentional blink in these individuals, suggesting difficulties in attentional selection and spatial attention allocation. Moreover, they found that cognitive training can enhance the N2pc amplitude and lessen AB severity in this group.

Building on this, Zhang et al. (2020) utilised EEG to examine the involvement of the prefrontal cortex in AB. Their findings emphasised increased activity in the dorsolateral prefrontal cortex (DLPFC) during the AB, highlighting the role of DLPFC in executive control and attentional selection. Furthermore, they discovered that applying transcranial direct current stimulation (tDCS) to the DLPFC could further improvements in AB, particularly in tasks that demand heightened attentional performance (Zhang et al., 2020).

The insights gained from these physiological studies emphasise a critical aspect of neural processing during attention-intensive tasks, which is directly relevant to the RSVP paradigm. The findings highlight how specific brain regions and their activities correlate with the capability to process rapid successions of visual stimuli, as is required in RSVP experiments. These studies suggest that alterations in brain activity, whether naturally

occurring or induced via interventions, can significantly impact the effectiveness of visual processing under conditions of rapid stimulus presentation.

Transitioning from this understanding of neural mechanisms, we can see how the RSVP framework provides an ideal experimental setting to further explore these concepts. As such, this makes it a suitable tool for investigating how the brain responses to rapid information processing, especially in relation to the attentional blink phenomenon.

In the RSVP framework, stimuli are presented in rapid succession, approximately 10 stimuli per second. Participants are asked to identify the targets. When the targets are presented for 100ms, the likelihood of reporting them correctly is higher (Shapiro et al., 1997). However, if the second target is presented in close proximity to each other, the chances of either detecting or identifying it correctly are considerably lower (Rolls, 1996).

In RSVP studies, three time points are tested, referred to as Lags. Given that stimuli are typically displayed with a frequency of one stimulus every 100ms, there are three distinct Lags that are of interest, including Lag 1 (100ms), Lag 3 (300ms), and Lag 8 (800ms), representing the time point at which the second target is shown after the first target (MacLean & Arnell, 2011). Lag 3 corresponds to the moment when the AB reaches its maximum depth.

One study of particular relevance to my study is the one conducted by Ronconi et al. (2016) who presented regular sounds with a frequency of 500 Hz, consistent with the rate of stimulus presentation in the RSVP paradigm. This rhythmic background auditory stimulus served as an external source of entrainment, just as the vestibular signal did in experiments of Chapters 2 and 3. They reported that visual stimuli that coincided with the same temporal frequency as the auditory stimuli exhibited enhanced response accuracy at Lag 3 compared to

instances where there was a temporal mismatch. In other words, the study showed that the attentional blink could be modulated via cross-sensory entrainment.

In this chapter, I therefore brought together insights from Chapters 2 (E6) and 3 (E10) and adopted a modified cross-over replication of Ronconi et al.'s (2016) study with one key difference: I replaced the rhythmic background auditory stimulus with a rhythmic background vestibular signal presented at a 10 Hz frequency, which is the same as the presentation rate of the visual target in the synchronous condition. I reasoned that if coincident vestibular information modules temporal attention within time windows shorter than 400ms then a modulatory effect may be observed on the depth of the attentional blink at Lag 3.

4.1 General Method

4.2 Participants

A total of 114 participants were recruited across 3 experiments with identical designs and procedures. Participants with an accuracy rate at or below 20% in T2|T1 detection were also excluded as chosen by Ronconi et al. (2016). Therefore, the final analysed sample consisted of 108 participants (22 male with average age of 21.32, *SD* = 3.71, range = 17, minimum = 18, maximum = 35 and 86 females with average age of 20.13, *SD* = 4.23, range = 29, minimum = 18, maximum = 47).

All studies were approved by the University of Kent's Psychology research ethics committee. Participants were treated in line with the Code of Conduct guidelines provided by the British Psychological Society (BPS).

4.3 Stimuli and apparatus

Testing occurred individually in a dimly lit room at the laboratory of the University of Kent. The experiment was programmed on PsychoPy and presented to participants on a 20-inch Dell monitor, refreshing at 100 Hz where they have seated approximately 57 centimetres away from the monitor with their eyes level with the centre of the screen. At the beginning of each trial, a fixation cross was presented in the centre of the monitor for 30 seconds. Possible targets were alphabetical letters excluding I, M, O, Q, and W, as instructed by Ronconi et al. (2016). Distractors were single digits excluding 0 and 1. Alphanumeric stimuli were always presented in white on a black background, except for the first target letter (T1), which was coloured in red (RGB: 255, 0, 0). Each alphanumeric stimulus was shown in 'Arial Rounded Bold' font. The subtended visual angle was 3.8 degrees vertically and 2.9 degrees horizontally.

4.4 GVS Protocol

The GVS protocol was identical to the method employed in Chapters 2 and 3 of this thesis, as explained in Sections 2.5 to 2.7. Following a modified replication of Ronconi et al. (2016), I substituted the rhythmic auditory tone with a rhythmic sub-sensory GVS pulse, resulting in the creation of three distinct conditions, as outlined below: (1) In the synchronous condition for experiments RSVP-1 and RSVP-3, the GVS pulse was administered at a frequency of 10 Hz, matching the frequency of the visual target presented at 100ms. However, in RSVP-2, the synchronous condition administered the GVS pulse at a frequency of 12 Hz, matching the frequency of the visual target presented at 83.33ms (2) In the asynchronous condition for experiments RSVP-1 and RSVP-3, participants received GVS stimulation at a frequency of 12 Hz, which did not align with the 10 Hz presentation rate of

the visual targets. In RSVP-2, the asynchronous condition utilised a 10 Hz GVS pulse (3) In the no stimulation condition, participants did not receive any stimulation.

4.5 GVS Sensory Thresholding

To find the sub-sensory threshold level for each participant, I delivered the adapted version of the Up-and-Down method suggested by Dixon (1965), which was identical to the stimulation protocol used in experiments in Chapters 2 and 3 (as explained in Section 2.6).

4.6 Experimental Procedure

Before starting the experiment, participants completed a block of 40 practice trials. After the practice phase, the main blocks began. There were three possible pre-RSVP entrainment conditions which occurred during fixation presentation. In the synchronous condition, a stream of AC bilateral bipolar with a frequency of 10 Hz, each of 20ms duration, was presented. The first pulse was presented in synchrony with fixation Onset. In the asynchronous condition, a stream of AC bilateral bipolar with a frequency of 12 Hz. In the no stimulation condition, the device was set to disable, and participants did not receive any stimulation. After the Offset of the fixation and the concurrent end of GVS entrainment, the RSVP stream began.

Each RSVP stream contained 15 items (2 targets and 13 distractors) that were presented one after the other in the centre of the monitor. At the end of each stream, participants were given unlimited time to report the target letters in the correct order and were required to guess if they were unsure. Distractors were presented for 100ms, and target letters were presented for 60ms, followed by a 40-ms hash (#) mask followed by no inter-stimulus interval (ISI).

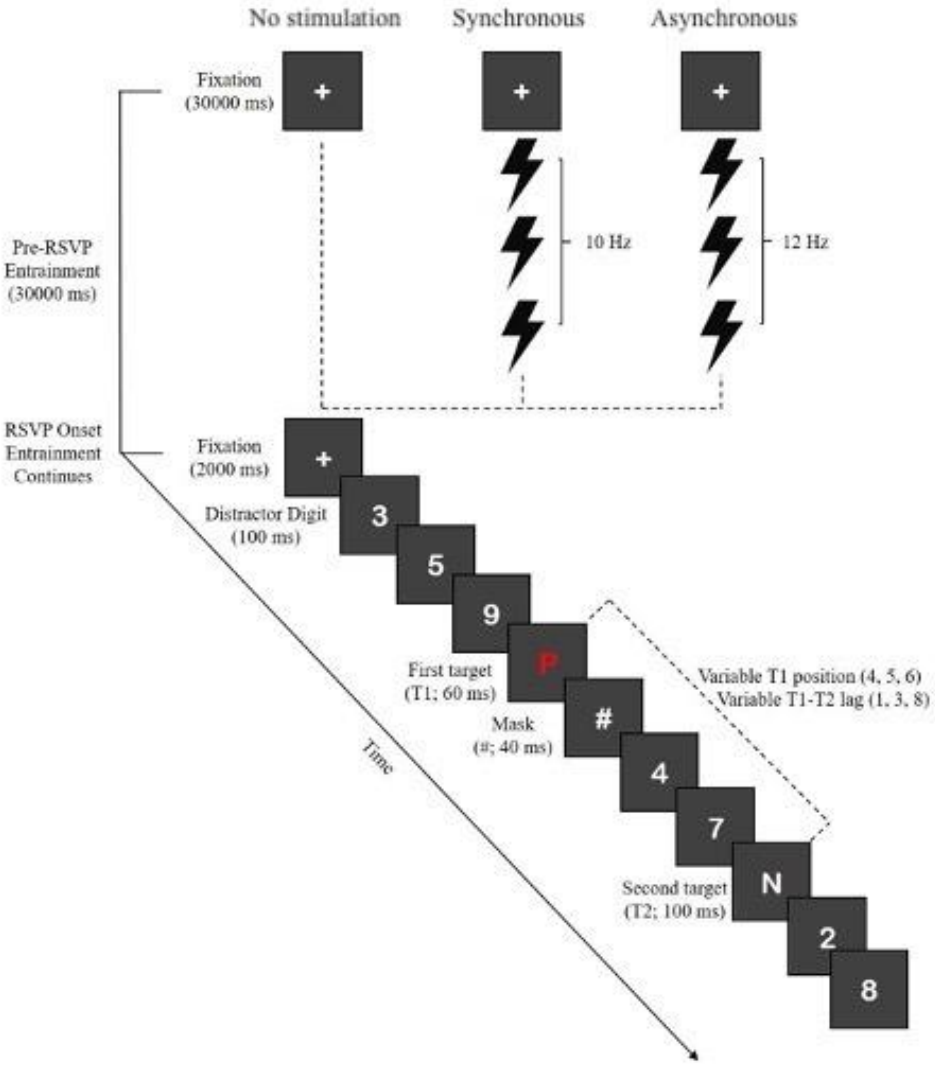

Figure 4.1: Visual representation of the attentional blink (AB) task used in the RSVP1 and RSVP3, where participants had to report the identity of the two target letters displayed among digit distractors while receiving vestibular stimulation.

The identities of the target letters and digit distractors were randomly assigned on each trial, with the restriction that successive items could not be the same. To prevent predictability, the first target (T1) appeared randomly as the fourth, fifth, or sixth item in the stream. The second target letter (T2) appeared at Lags 1, 3, or 8 with equal frequency. The experiment consisted of a total of 198 trials, divided into three blocks of 66 trials each. This included 180 T2-present trials (with 6 absent trials in all three entrainment conditions), resulting in a total of 18 T2-absent trials (catch trials). All trials were randomly intermixed.

4.7 Planned analysis

ANOVA was utilised to interrogate both the main effects and interactions. A Greenhouse- Geisser correction was applied where the assumption of sphericity was violated. Bonferroni-corrected pairwise comparisons were used via SPSS software (Version 25) to explore the interaction term.

Correct responses were determined based on the accurate identification of both target letters (T1, T2) and the correct reporting order. Analysis of trials was limited to cases where T1 was correctly identified. The chance level of accuracy, corresponding to a selection from 21 possible target letter choices, was 4.76% (1/21 response choices). T1 accuracy was utilised to exclude participants who performed at or below the chance level (≤ 4.76%, n = 0) or below the acceptable performance threshold of 20% (n = 0), as specified by Ronconi et al. (2016).

An a priori sample size estimation was performed using the G*Power software package (version 3.1.9.3) during the planning and design of the trial. The input parameters were the following: statistical test = ANOVA: repeated measures, within factors; effect size f = 0.25; α err prob = 0.05; power (1 ß err prob) = 0.90; number of groups = 3; number of measures = 3; correlation among repeated measures = 0.5; non-sphericity correction e = 1. These conditions pre-determined a sample size of n = 36. The stopping rule for in this Chapter was based upon maintaining a statistical power in excess of 0.80 as recommended by Cohen's (1992), resulting in a minimum sample size of n = 30.

4.8 Introduction to Experiment 1 of the RSVP series

Experiment RSVP1 was a modified replication of Ronconi et al.'s (2016) study, where they investigated the impact of rhythmic auditory entrainment on temporal attention. Their

task included three distinct RSVP auditory entrainment conditions implemented during the fixation presentation phase. In the synchronous condition, a sequence of twenty 500 Hz auditory tones, each lasting 20ms, was delivered via headphones. The Onset of the first tone was synchronised with the Onset of visual fixation, and subsequent tones followed at a consistent ISI of 80ms, resulting in a rhythmic presentation of one tone every 100ms. In the asynchronous condition, twenty 500 Hz auditory tones of the same duration were presented through headphones, but with irregular ISIs ranging from 0 to 130ms, introducing variability in the timing between successive tones. In their "baseline" condition, no auditory stimuli were presented, serving as a control condition for comparison. Their findings suggested that the synchronous condition resulted in a more effective reduction in the effects of attentional blink when compared to both the baseline and asynchronous conditions.

Based on these findings, the current experiment replaced the auditory stimulus with a vestibular pulse, creating synchronous (10 Hz), asynchronous (12 Hz), and no stimulation conditions, similar to the task protocol conducted by Ronconi et al. (2016) to investigate the effect of rhythmic entrainment on temporal attention. I hypothesised that if synchronised GVS exerts a similar effect to that of synchronous auditory tones on the AB, then in the condition where the visual and vestibular frequencies are aligned, I should expect a decrease in the effects of the AB. This reduction is anticipated to be particularly noticeable between 200-500ms, corresponding to Lag 3.

4.9 RSVP-1

A 3 (Lag: 1 vs 3 vs 8) x 3 (Stimulation: 10 Hz vs 12 Hz vs no stimulation) repeated measures ANOVA with Greenhouse-Geisser correction on percentage of accurate responses (conditional T2 on T1) did not show a main effect of Stimulation [F (1.943, 66.072) = 0.429, p = 0.647, η_p^2= 0.012], however the interaction [F (3.202, 108.858) = 5.659, p = 0.001, η_p^2=

0.143] as well as the main effect of Lag [F (1.496, 50.862) = 62.264, $p < 0.001$, $\eta_p^2 = 0.647$] reached statistical significance (Figure 4.2).

Post-hoc pairwise comparisons on the main effect of Lag using the Bonferroni correction revealed several significant differences in response accuracy. The response accuracy for Lag 1 (M = 0.716, SD = 0.146) was significantly higher than that for both Lag 2 (M = 0.337, SD = 0.164), t(34) = 14.037, $p < 0.001$, and Lag 3 (M = 0.556, SD = 0.235), t(34) = 3.721, p = 0.002. Additionally, the response accuracy for Lag 3 (M = 0.556, SD = 0.235) was significantly higher than for Lag 2 (M = 0.337, SD = 0.164), t(34) = 7.097, $p < 0.001$ (Table 4.1).

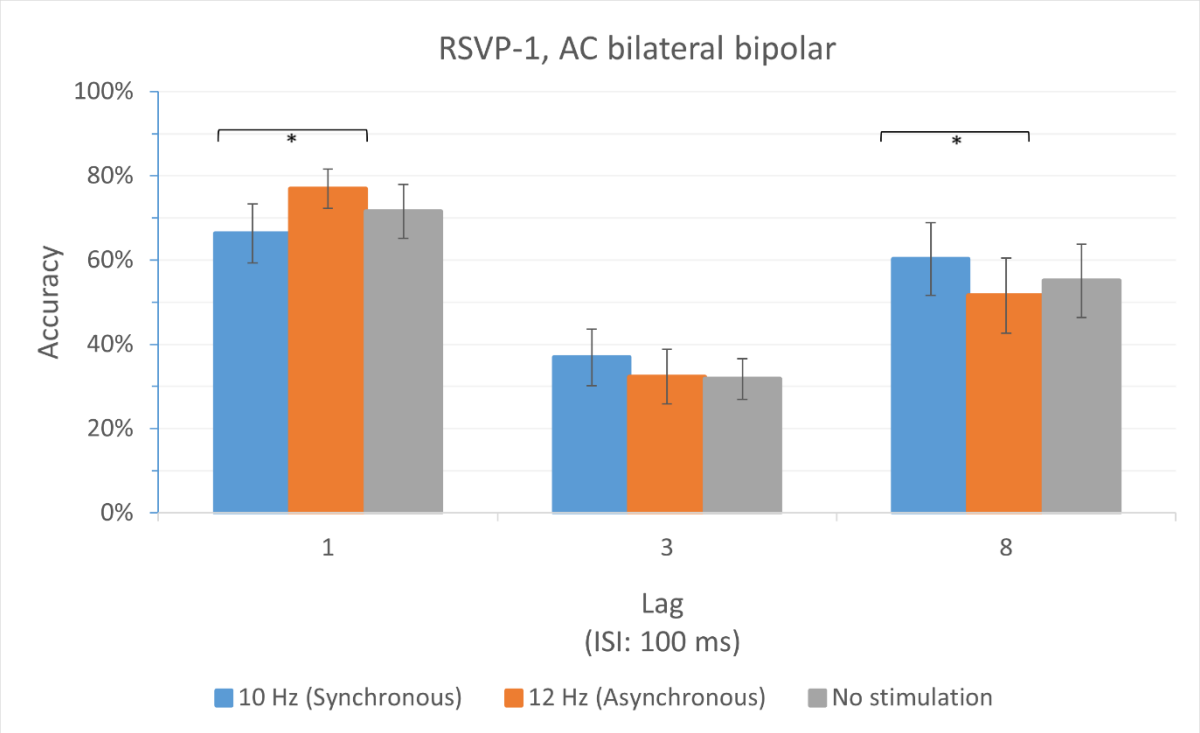

Figure 4.2: Mean accuracy rates of T2|T1 identification as a function of stimulus condition and Lag in RSVP1. Bars represent 95 % confidence intervals. An asterisk (*) shows significance at $p \leq .05$.

Lag	Lag	t value	Sig.	95% CI	
				Lower Bound	Upper Bound
1	**2**	14.037	<.001	0.312	0.446
1	**3**	3.721	0.002	0.052	0.267
3	**2**	7.097	<.001	0.141	0.298

Table 4.1: Post-hoc statistical analysis of pairwise comparisons for the main effect of Lag in RSVP-1

Pairwise comparisons examined mean difference in response accuracy between different Stimulation conditions (10 Hz Synchronous, 12 Hz Asynchronous, and no stimulation) at three levels of Lags (1, 3, and 8) (Appendix B.4.1): At Lag 1, response accuracy was higher in the 12 Hz (Asynchronous) condition (M = 0.769, SD = 0.142) relative to the 10 Hz (Synchronous) condition (M = 0.663, SD = 0.211), [$t(34) = 3.212$, $p = 0.009$]. However, there was no significant difference in response accuracy between no stimulation condition (M = 0.715, SD = 0.193) and the 12 Hz (Asynchronous) condition (M = 0.769, SD = 0.142), [$t(34) = 2.160$, $p = 0.126$] or the 10 Hz (Synchronous) condition (M = 0.663, SD = 0.211), [$t(34) = 1.333$, $p = 0.573$].

At Lag 3, there was no significant difference in response accuracy between the 10 Hz (Synchronous) condition (M = 0.369, SD = 0.202) and the 12 Hz (Asynchronous) condition (M = 0.323, SD = 0.195), [$t(34) = 1.917$, $p = 0.201$] or no stimulation condition (M = 0.318, SD = 0.146), [$t(34) = 2.125$, $p = 0.119$]. There was also no difference between the 12 Hz (Asynchronous) condition (M = 0.323, SD = 0.195) and the no stimulation condition (M = 0.318, SD = 0.146), [$t(34) = 0.227$, $p = 1$].

At Lag 8, response accuracy was higher in the 10 Hz (Synchronous) condition (M = 0.602, SD = 0.26) relative to the 12 Hz (Asynchronous) condition (M = 0.516, SD = 0.269), [$t(34) = 3.000$, $p = 0.017$]. However, there was no significant difference in response accuracy between the no stimulation condition (M = 0.318, SD = 0.146), and 10 Hz (Synchronous)

condition (*M* = 0.602, *SD* = 0.26), [*t*(34) = 1.333, *p* = 0.566] or the 12 Hz (Asynchronous) condition (*M* = 0.516, *SD* = 0.269), [*t*(34) = 0.946, *p* =1].

Pairwise comparisons also examined response differed between levels of Lag at each Stimulation condition (Appendix C.4.2): Under synchronised GVS (10 Hz) condition, there was a significant difference between Lag 3 (*M* = 0.369, *SD* = 0.202) and Lag 1 (*M* = 0.663, *SD* = 0.211), [*t*(34) = 7.171, *p* < 0.001] and between Lag 3 (*M* = 0.369, *SD* = 0.202) and Lag 8 (*M* = 0.602, *SD* = 0.26), [*t*(34) = 5.419, *p* = <.001]. However, there was no difference between Lag 1 (*M* = 0.663, *SD* = 0.211) and Lag 8 (*M* = 0.602, *SD* = 0.26), *t*(34) = 1.245, *p* = 0.666 (see Figure 4.3).

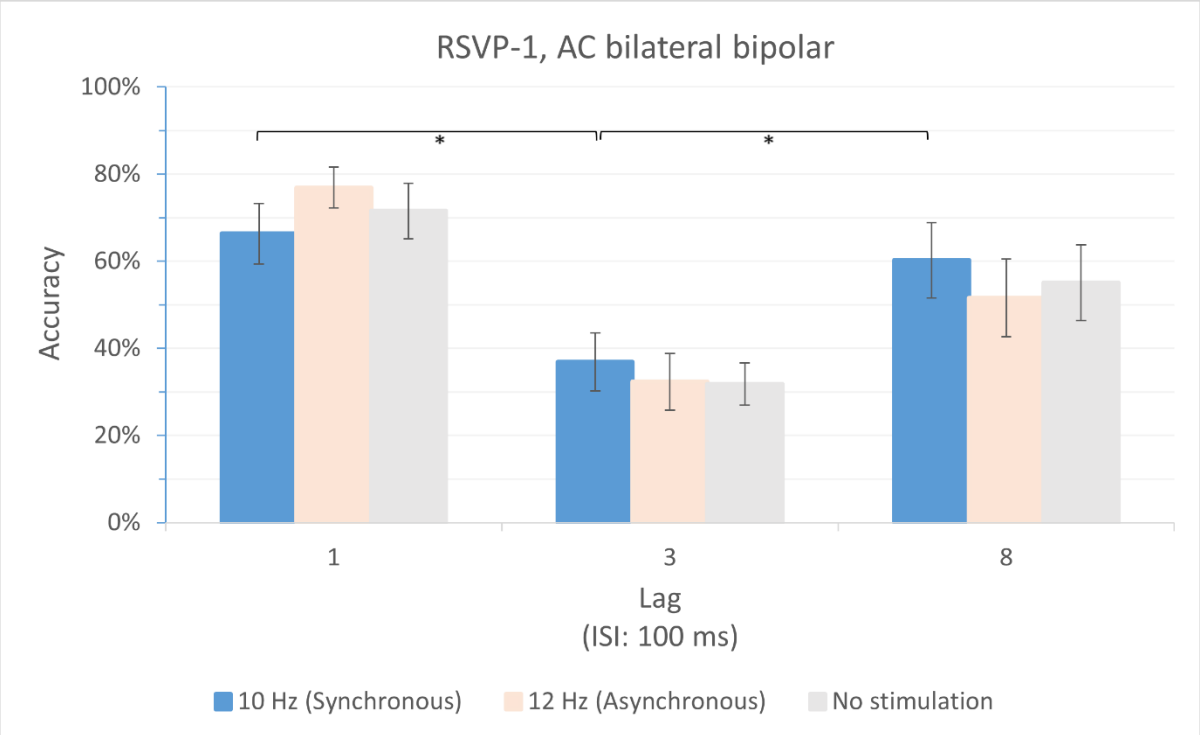

Figure 4.3: Mean accuracy rates of T2|T1 identification as a function of between Lag conditions at each synchronous condition. Bars represent 95 % confidence intervals.

Under asynchronised GVS (12 Hz) condition, there was a significant difference between Lag 1 (*M* = 0.769, *SD* = 0.142) and Lag 3 (*M* = 0.323, *SD* = 0.195) conditions,[*t* (34) = 14.867, *p* = <0.001], Lag 1 (*M* = 0.769, *SD* = 0.142) and Lag 8 (*M* = 0.516, *SD* =

0.269) conditions, [t (34) = 5.163, p <0.001] as well as Lag 3 (M = 0.323, SD = 0.195) and Lag 8 (M = 0.516, SD = 0.269) conditions, [t (34) = 5.216, p <0.001] (see Figure 4.4).

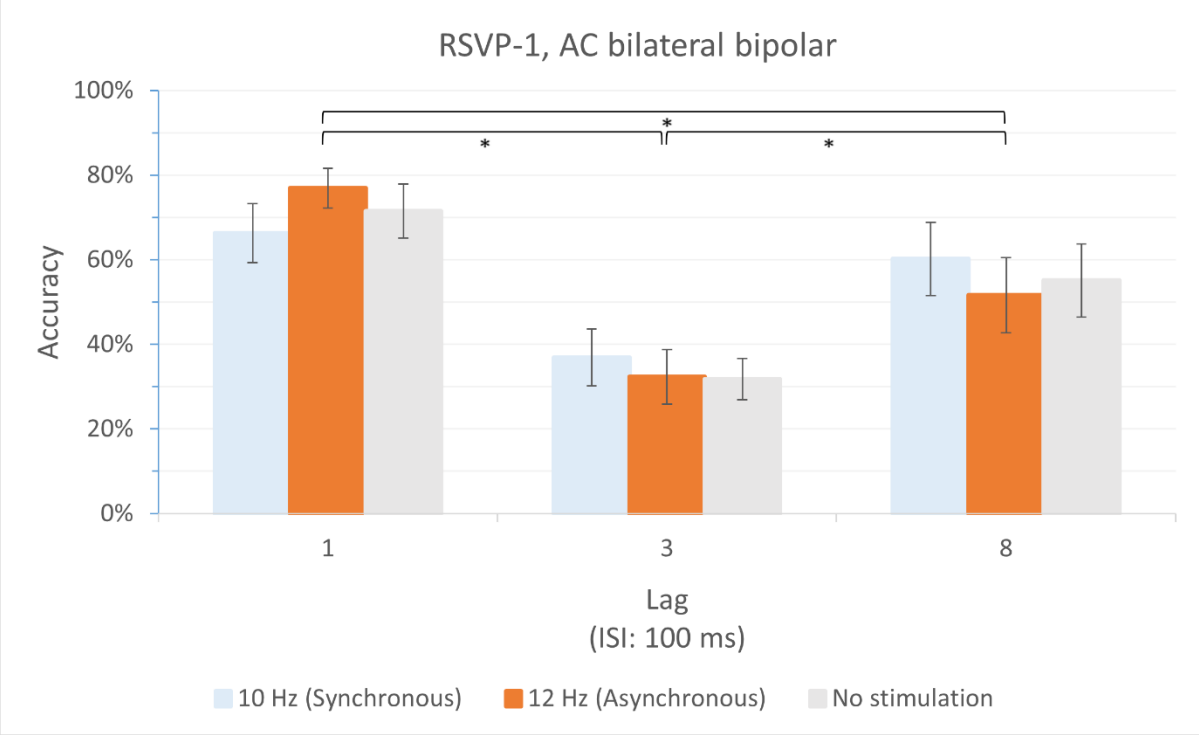

Figure 4.4: Mean accuracy rates of T2|T1 identification as a function of between Lag conditions at each asynchronous condition. Bars represent 95 % confidence intervals.

Under no stimulation condition, there was a significant difference between Lag 1 (M = 0.715, SD = 0.193) and Lag 3 (M = 0.318, SD = 0.146), [t (34) = 11.343, p <0.001], and Lag 1 (M = 0.715, SD = 0.193) and Lag 8 (M = 0.551, SD = 0.262),[t (34) = 3.000, p = 0.014 as well as Lag 8 (M = 0.551, SD = 0.262) and Lag 3 (M = 0.318, SD = 0.146) conditions, t (34) = 6.657, p <0.001 (see Figure 4.5).

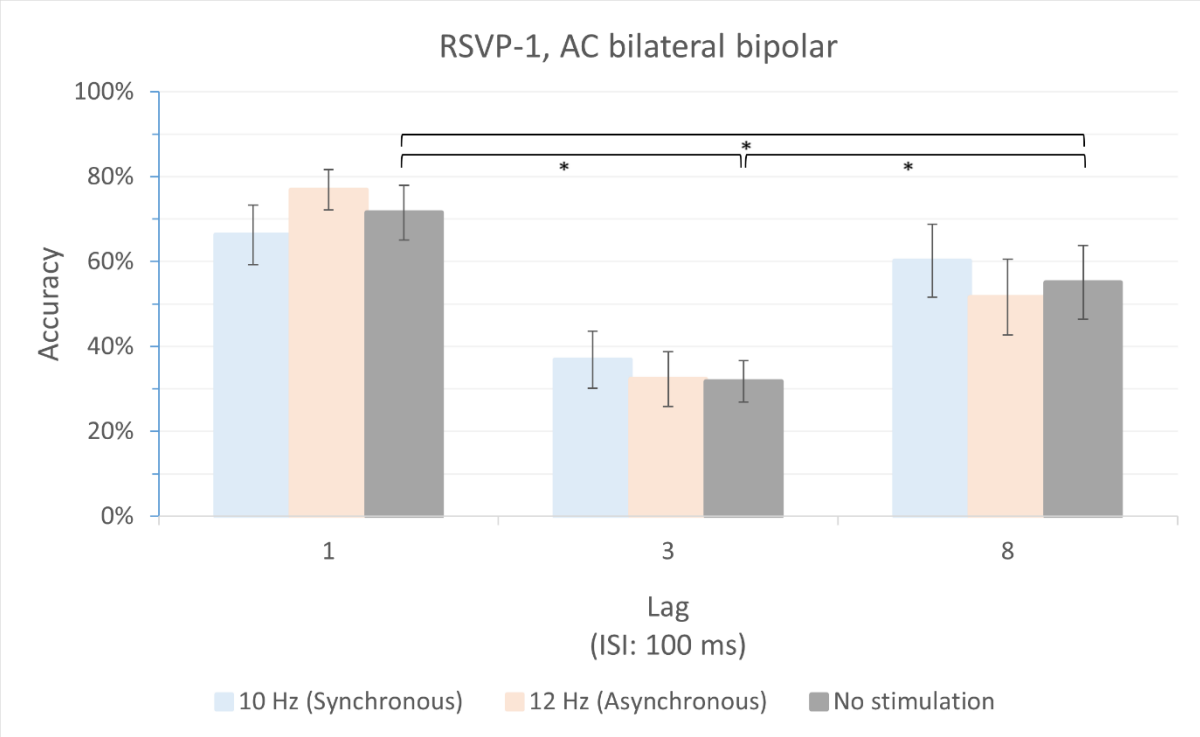

Figure 4.5: Mean accuracy rates of T2|T1 identification as a function of between Lag conditions at each no stimulation condition. Bars represent 95 % confidence intervals.

4.10 Discussion to RSVP-1

The primary aim of Experiment RSVP1 was to examine whether a synchronous presentation of visual stimuli with the GVS pulse, both occurring at the same frequency as the visual target presentation rate, could induce entrainment and subsequently reduce the AB effect anticipated at Lag 3. A reduction in the AB would be evident as a statistically significant enhancement in accuracy compared to the no stimulation condition.

In evaluating the accuracy of responses in RSVP-1 across Stimulation conditions between Lags, noticeable patterns became evident. At Lag 1, the 12 Hz (Asynchronous) condition revealed a significant increase in accuracy compared to the 10 Hz (Synchronous) condition. In contrast, at Lag 8, the 10 Hz (Synchronous) condition showed higher accuracy relative to the 12 Hz (Asynchronous) condition.

However, no statistically significant differences were observed at Lag 3 among the Stimulation conditions. This outcome at Lag 3 challenges the null hypothesis in RSVP-1. It is worth noting that a Bonferroni correction was utilised during RSVP-1's post-hoc analysis. This is different from the original study by Ronconi et al. (2016), which did not adopt any corrections for their post-hoc analysis. Given this, outcomes comparable to the original study would have been observed if similar analytical techniques had been applied.

In evaluating the accuracy of responses in RSVP-1 between Stimulation conditions across Lags, under the 10 Hz (Synchronised) condition, Lag 1 and Lag 8 performances were similar. However, in the 12 Hz (Asynchronised) and no stimulation conditions, Lag 1 performance exceeded Lag 8 by 32.89% and 22.96%, respectively.

For Lag 1, our findings indicate an improvement in performance with 12 Hz asynchronous GVS. For Lag 1, our findings indicate an improvement in performance with 12 Hz asynchronous GVS. A comparative analysis between the outcomes of RSVP-1 and Ronconi et al.'s (2016) work raises the possibility that the distinctions observed between active stimulation and no stimulation conditions may be attributed to overarching facilitatory effects associated with GVS, rather than any specific interactions between temporal Lags and GVS.

Furthermore, the data indicates that the average accuracy at Lag 1 is considerably higher, suggesting that the 12 Hz asynchronous condition might be a stronger entrainer overall than 10 Hz synchronous condition. However, within the experimental framework, under the condition of a 10 Hz Synchronous GVS at Lag 8, a response accuracy of 60.2% was observed. These empirical findings, if supported in subsequent experimental repetitions, would suggest that the interference effect seen within the temporal window of 400ms to 800

ms in the DMTS paradigm (as explained in Chapters 2 and 3) does not characterise an universal trait of visuo-vestibular interactions. Instead, it could be indicative of a task-dependent distinctiveness. In the DMTS paradigm, the measured visual responses are contingent upon stimuli showing alongside or following the vestibular signal, whereas the RSVP paradigm evaluates the visual response in relation to a downstream stimulus, specifically at T2.

The results imply that 12 Hz asynchronous GVS might bolster performance—an observation not documented in the delayed matching-to-sample paradigm discussed in Chapters 2 and 3. This performance enhancement might originate from the higher alpha band oscillations in the RSVP paradigm. Such oscillations are associated with sensory suppression and attention modulation—functions that actively inhibit irrelevant or distracting information while bolstering selective attention across sensory systems (Foxe & Snyder, 2011; Klimesch, 2012). Furthermore, studies have suggested that alpha band oscillations contribute to brain gating mechanisms. An increase in alpha power in the visual cortex correlates with reduced neuronal excitability and reduced processing of irrelevant or distracting stimuli (Foxe & Snyder, 2011; Zhigalov & Jensen, 2020). This aligns with the argument that 12 Hz GVS stimulation enhances overall performance, irrespective of the Lag, and with the hypothesis that 12 Hz GVS is unlikely to alter the attentional blink in this experimental context.

4.11 Introduction to Experiment 2 of the RSVP series

In Experiment 1 of the RSVP series, the use of 12 Hz (Asynchronous) GVS led to a 16.4% higher response accuracy at Lag 1 compared to the 10 Hz (Synchronous) GVS. In contrast, at Lag 8, the 10 Hz (Synchronous) GVS resulted in a 16.2% higher response accuracy compared to the 12 Hz (Asynchronous) GVS. Overall, the data suggests that the 12 Hz (Asynchronous) GVS frequency may be slightly more effective in enhancing

response accuracy across Lag intervals. The observed differences, albeit minor, lead to investigation here in Experiment 2 into whether the frequency-specific effects are due to a mere coincidence of matching the frequency of the visual stimuli or if the GVS influence the performance independently of the simultaneous visual signals. This latter possibility would suggest the presence of an entraining effect.

Accordingly, in the present experiment, the frequency of the visual stimuli was adjusted from 10 Hz (100 ms) to 12 Hz (83.33 ms) to further investigate this phenomenon. Consequently, within RSVP-2, the Synchronous condition corresponds to 12 Hz, while the Asynchronous condition is set at 10 Hz. Preliminary findings from the pilot study indicated that a heightened visual presentation rate of 12 Hz enabled reasonably precise behavioural responses. Specifically, accuracy for the first target (T1) ranged between 60% and 90%. For the second target (T2), following an accurately identified first target (T2|T1), the accuracy remained at a chance level (4.76%). This performance is consistent with the 20% arbitrary performance threshold proposed by Ronconi (2016). Given these results, I conducted a replication of the RSVP-1, adjusting the synchronous and asynchronous conditions to incorporate 12 Hz and 10 Hz frequencies, respectively.

4.12 RSVP-2

A 3 (Lag: 1 vs 3 vs 8) x 3 (Stimulation: 12 Hz vs 10 Hz vs no stimulation) repeated measures ANOVA with Greenhouse-Geisser correction on the percentage of accurate responses (conditional T2 on T1) did not show a main effect of Stimulation (F (1.820, 65.517) = 1.533, p = 0.225, η_p^2= 0.041), or interaction [F (2.883, 103.793) = 1.122, p = 0.343, η_p^2= 0.030]. The main effect of Lag [F (1.653, 59.524) =69.727, p= 0.001, η_p^2= 0.660] did however reach statistical significance.

Post-hoc pairwise comparisons on the main effect of Lag using the Bonferroni correction revealed several significant differences in response accuracy. The response accuracy for Lag 1 (M = 0.617, SD = 0.165) was significantly higher than that for both Lag 2 (M = 0.276, , SD = 0.171), $t(36) = 14.208$, $p < 0.001$, and Lag 3 (M = 0.339, SD = 0.221), $t(36) = 7.722$, $p < 0.001$ (Table 4.2).

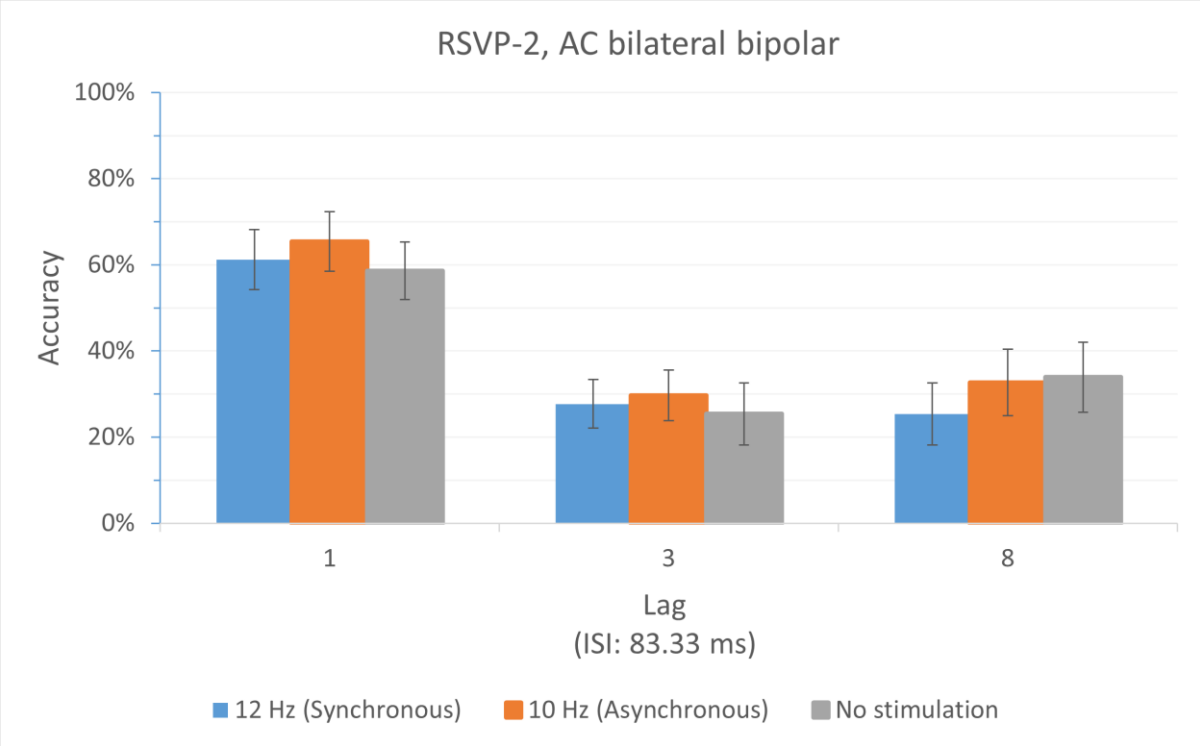

Figure 4.6: Mean accuracy rates of T2|T1 identification as a function of stimulus condition and Lag in RSVP2. Bars represent 95 % confidence intervals.

Lag	**Lag**	**t value**	**Sig.**	**95% CI**	
				Lower Bound	Upper Bound
1	**2**	14.208	<.001	0.281	0.401
1	**3**	7.722	<.001	0.187	0.37
3	**2**	2.032	0.144	-0.014	0.14

Table 4.2: Post-hoc statistical analysis of pairwise comparisons for the main effect of Lag in RSVP-2

4.13 Discussion to RSVP-2

RSVP-2 aimed to replicate RSVP-1 by investigating whether 12 Hz GVS, synchronised with the RSVP stimuli, would diminish the attentional blink (AB) effect and enhance attention by improving response accuracy. However, the results of this experiment did not reveal any significant main effect of Stimulation or an interaction. It appears that the modulation observed in the previous experiment depends on the frequency of the visual stimulus, considering that the GVS frequencies remained unchanged, albeit paired differently with the GVS stimulus.

The absence of statistically significant effects makes it challenging to shed further light on the interference effect observed in the delayed matching-to-sample task. Nevertheless, these findings may suggest that the interaction between vestibular and visual processes on brief timescales critically relies on external factors such as frequency and task difficulty.

One possible explanation for this lack of statistical significance is the rapid presentation of stimuli, combined with the extended duration of the study. The data at hand confirm that this combination resulted in performance levels at baseline that were close to chance (< 4.76%). Furthermore, speculative evidence suggests that when two targets emerge in close temporal proximity, the processing of the first target might interrupt the processing of the second and third targets (Badcock & Kidd, 2015). Thus, this may eliminate the Lag 3 advantage observed in the previous experiment of this chapter. These findings indicate that higher-level processing is unable to withstand the AB, implying that perceptual processing is disrupted by the AB (Zivony et al., 2018).

Another explanation for these results can be found in the work of Hanslmayr et al. (2011), who argue that alpha power tends to decrease when task-relevant visual stimuli occur in very close proximity to one another (i.e., at 12 Hz). Therefore, one could argue that the 12 Hz stimulation induced an alpha rhythm that made participants more susceptible to distraction.

4.14 Introduction to Experiment 3 of the RSVP series

Attentional deficits and anomalies in temporal processing are hallmark features of neuropsychological conditions such as ADHD and dyslexia. The AB phenomenon has been a key method for investigating these irregularities in affected populations (Amador-Campos et al., 2015). Research initiated by Sams et al. (1991) began the exploration of attentional blink differences in individuals with dyslexia. This study was later broadened by McLean et al. (2010), who utilised dual-target RSVP paradigms to further investigate the visual temporal attentional processing. Their results showed an atypical attentional blink pattern in dyslexic individuals. Furthermore, both ADHD and dyslexic individuals displayed an extended attentional retention duration of 700ms, as opposed to the 540ms observed in the normative group, regardless of the time gap between the two targeted stimuli.

The RSVP-1 paradigm provided preliminary evidence that 12 Hz GVS entrainment at the upper alpha band frequency has the potential to enhance temporal attention in a normative population at Lag 1. Building on these findings, the RSVP-3 intervention was designed to explore whether the overall facilitatory effects observed in RSVP-1 could be replicated within a clinical population. The hypothesis driving this investigation centred on the potential therapeutic benefits of GVS entrainment for individuals in this group.

In the overarching framework of sensory processing difficulties, there is a correlation between ADHD, dyslexia, atypical multisensory integration, and deficiencies in temporal processing (Clements et al., 2014; Panagiotidi et al., 2017). This association stems from a reduced capacity to identify and recognise unisensory inputs, attributed to impairments within the midbrain superior colliculus (SC) (Dean et al., 1989; Dokka et al., 2015). Such impairments subsequently cause disruptions in the temporal window of integration (Panagiotidi et al., 2018; Brown et al., 2020).

Considering these connections, it raises the question of whether rhythmic background vestibular entrainment presented at the same visual frequency might modulate temporal attention. If this is the case, it presents possible therapeutic avenues for individuals with ADHD, dyslexia, or a combination of both, potentially alleviating sensory deficiency and enhancing sensory integration. Investigating the influence of this entrainment on temporal attention is therefore crucial for the development of targeted treatments tailored to the unique sensory processing challenges faced by these populations.

In refining the research approach, particular emphasis was placed on the advantages at Lag 1 in the 12 Hz asynchronous condition, contrasting with the Lag 8 in the 10 Hz synchronous condition. This decision was based on empirical results, where the asynchronous condition demonstrated a higher response accuracy compared to the synchronous condition in RSVP-1. This disparities in performance suggested the potential benefits of the asynchronous condition, particularly in visual cognitive processing within the RSVP paradigm.

4.15 RSVP-3

RSVP-3, which utilised the identical experimental paradigm and protocol as RSVP-1, was administered to the clinical population as a component of the clinical test battery. The remaining tasks within the clinical test battery are outlined in Chapter 3.

A 3 (Lag: 1 vs 3 vs 8) x 3 (Stimulation: 12 Hz vs 10 Hz vs no stimulation) repeated measures ANOVA with Greenhouse-Geisser correction on the percentage of accurate responses (conditional T2 on T1) did not show a main effect of Stimulation [F (1.615, 53.293) = 1.705, p = 0.196, η_p^2= 0.049], or interaction [F (3.283, 108.331) = 0.969, p = 0.416, η_p^2= 0.029]. The main effect of Lag [F (1.439, 47.482) = 57.355, p < 0.001, η_p^2= 0.635] did however reach statistical significance.

Post-hoc pairwise comparisons on the main effect of Lag using the Bonferroni correction revealed several significant differences in response accuracy. The response accuracy for Lag 1 (M = 0.666, SD = 0.221) was significantly higher than that for both Lag 2 (M = 0.307, SD = 0.198), t(33) = 9.972, p < 0.001, and Lag 3 (M = 0.532, SD = 0.201), t(33) = 3.268, p = 0.007. Additionally, the response accuracy for Lag 3 (M = 0.532, SD = 0.201) was significantly higher than for Lag 2 (M = 0.307, SD = 0.198), t(33) = 10.714, p < 0.001 (Table 4.3).

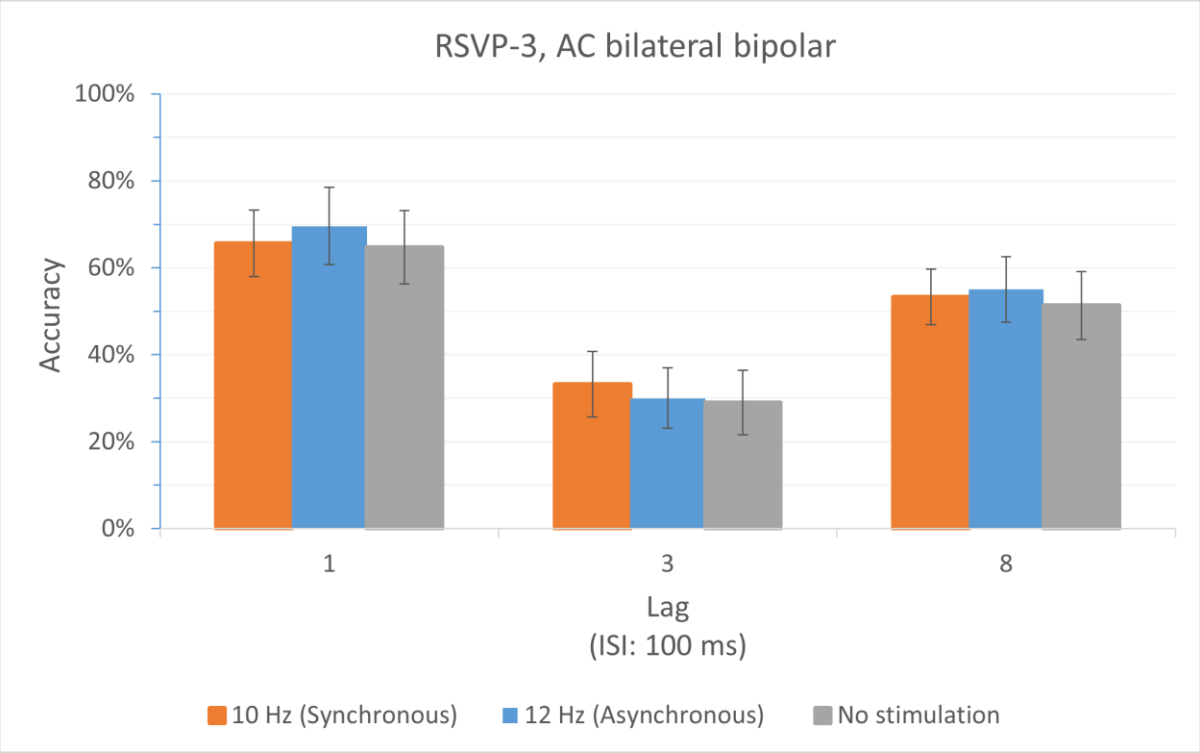

Figure 4.7: Mean accuracy rates of T2|T1 identification as a function of stimulus condition and Lag in RSVP3. Bars represent 95 % confidence intervals.

Lag	Lag	t value	Sig.	95% CI	
				Lower Bound	Upper Bound
1	**2**	9.972	<.001	0.267	0.451
1	**3**	3.268	0.007	0.031	0.237
3	**2**	10.714	<.001	0.171	0.279

Table 4.3: Post-hoc statistical analysis of pairwise comparisons for the main effect of Lag in RSVP-3

4.16 Joint analyses of RSVP-1 & RSVP-3

RSVP-1 and RSVP-3 contained identical experiments conducted within both the healthy control and clinical populations. As a result, an exploratory joint analysis was conducted to compare the performance of the two groups and to reveal shared and distinct responses within the normative RSVP-1 sample and the clinical RSVP-3 sample.

A 3 (Lag: 1 vs 3 vs 8) x 3 (Stimulation: 10 Hz vs 12 Hz vs no stimulation) x 2 (Population: Healthy Control vs Clinical Group) repeated measures ANOVA with Greenhouse-Geisser correction on percentage of accurate responses (conditional T2 on T1)

did not show a main effect of Stimulation [$F(1.821, 122.018) = 1.640$, $p = 0.200$, $\eta_p^2 = 0.024$], however the two-way interaction between Stimulation and Lag [$F(3.202, 222.626) = 4.959$, $p = 0.002$, $\eta_p^2 = 0.069$] as well as the main effect of Lag [$F(1.562, 104.664) = 119.423$, $p < 0.001$, $\eta_p^2 = 0.641$], reached statistical significance.

Post-hoc pairwise comparisons on the main effect of Lag using the Bonferroni correction revealed several significant differences in response accuracy. The response accuracy for Lag 1 ($M = 0.691$, $SD = 0.187$) was significantly higher than that for both Lag 2 ($M = 0.322$, $SD = 0.182$), $t(67) = 16.773$, $p < 0.001$, and Lag 3 ($M = 0.544$, $SD = 0.219$), $t(67) = 4.900$, $p < 0.001$. Additionally, the response accuracy for Lag 3 ($M = 0.544$, $SD = 0.219$) was significantly higher than for Lag 2 ($M = 0.322$, $SD = 0.182$), $t(67) = 11.684$, $p < 0.001$ (Table 4.4).

Lag	**Lag**	**t value**	**Sig.**	**95% CI**	
				Lower Bound	Upper Bound
1	**2**	16.773	<.001	0.314	0.424
1	**3**	4.900	<.001	0.074	0.219
3	**2**	11.684	<.001	0.176	0.269

Table 4.4: Post-hoc statistical analysis of pairwise comparisons for the main effect of Lag in RSVP-1 and RSVP-3

The two-way interactions between Stimulation and Population [$F(1.821, 122.018) = 0.467$, $p = 0.628$, $\eta_p^2 = .007$] and Lag and Population [$F(1.562, 104.664) = 0.154$, $p = 0.804$, $\eta_p^2 = 0.002$] failed to reach statistical significance. However, the two-way interactions between Stimulation and Lag [$F(3.323, 222.626) = 4.959$, $p = 0.002$, $\eta_p^2 = 0.069$] reached statistical significance (Figure 4.8).

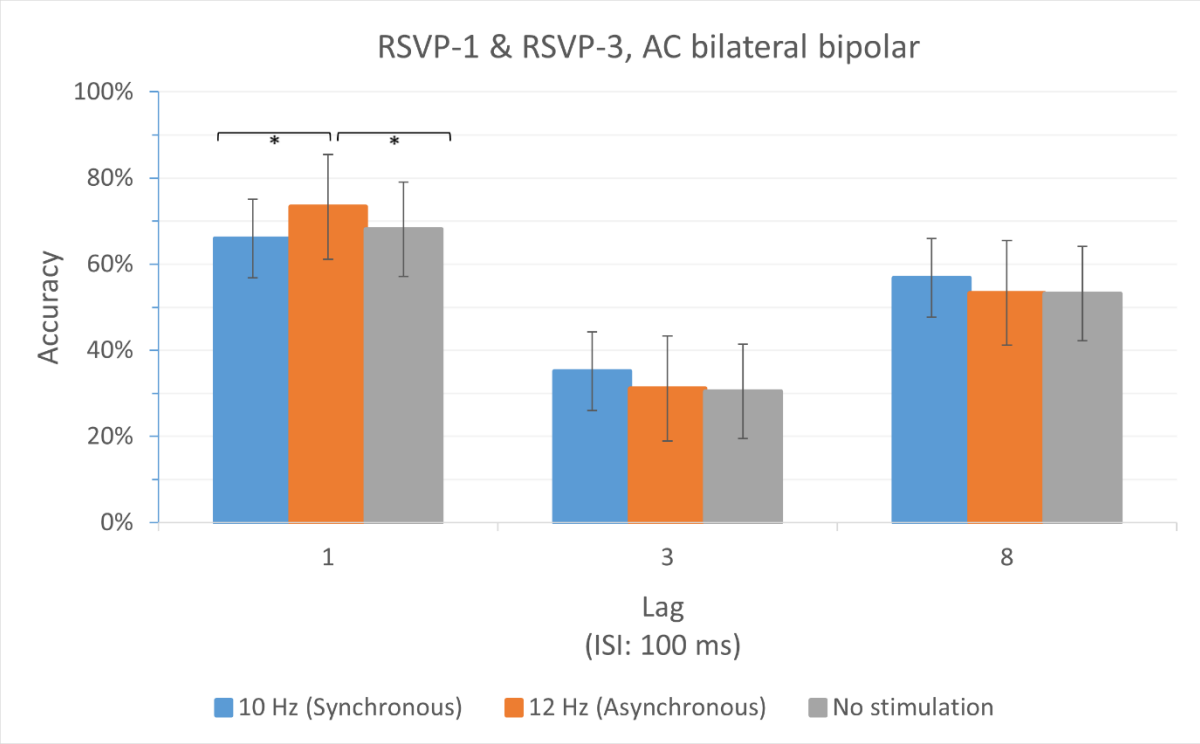

Figure 4.8: Mean accuracy rates of T2|T1 identification as a function of stimulus condition and Lag. Bars represent 95 % confidence intervals.

Pairwise comparisons examined mean difference for response accuracy between different Stimulation conditions (10 Hz synchronous, 12 Hz asynchronous, and no stimulation) at three levels of Lags (1, 3, and 8) (Appendix B.4.3): At Lag 1, response accuracy was higher in the 12 Hz (Asynchronous) condition (M = 0.733, SD = 0.213) relative to the 10 Hz (Synchronous) condition (M = 0.659, SD = 0.217), [$t(67) = 3.174$, $p = 0.007$]. Similarly, response accuracy was higher in the 12 Hz (Asynchronous) condition (M = 0.733, SD = 0.213) relative to the no stimulation condition (M = 0.681, SD = 0.225), [$t(67) = 2.737$, $p = 0.024$]. However, there was no significant difference between no stimulation condition (M = 0.681, SD = 0.225), and the 10 Hz (Synchronous) condition (M = 0.659, SD = 0.217), [$t(67) = 0.786$, $p = 1$].

At Lag 3, the mean difference for accuracy failed to reach significance between 10 Hz (Synchronous) condition (M = 0.351, SD = 0.213) relative to the 12 Hz (Asynchronous) condition (M = 0.311, SD = 0.200), [$t(67) = 2.167$, $p = 0.085$] and no stimulation condition

(*M* = 0.304, *SD* = 0.184) , [*t*(67) = 2.474, *p* = 0.052]. The difference between 12 Hz (Asynchronous) condition (*M* = 0.311, *SD* = 0.200) and no stimulation condition (*M* = 0.304, *SD* = 0.184) also failed to reach statistical significance [*t*(67) = 0.438, *p* = 1].

At Lag 8, the mean difference for accuracy failed to reach significance between 10 Hz (Synchronous) condition (*M* = 0.568, *SD* = 0.229) relative to the 12 Hz (Asynchronous) condition (*M* = 0.533, *SD* = 0.247), [*t*(67) = 2.059, *p* = 0.142] and no stimulation condition (*M* = 0.532, *SD* = 0.247), [*t*(67) = 1.565, *p* = 0.364]. The difference between 12 Hz (Asynchronous) condition (*M* = 0.533, *SD* = 0.247) and no stimulation condition (*M* = 0.532, *SD* = 0.247) also failed to reach statistical significance [*t*(67) = 0.042, *p* = 1].

Pairwise comparisons also examined response accuracy between levels of Lag at each Stimulation condition. For ease of interpretation, the means and standard deviations for each Offset during each condition are presented in Table 4.5 below and (Appendix B.4.4).

	10 Hz (Synchronous)		**12 Hz (Asynchronous)**		**No Stimulation**	
Lag	Mean	SD	Mean	SD	Mean	SD
1	0.659	0.217	0.733	0.213	0.681	0.225
3	0.351	0.213	0.311	0.200	0.304	0.184
8	0.532	0.247	0.533	0.247	0.532	0.247

Table 4.5: Presenting means and SD for each Lag during each condition. RSVP-1 & RSVP-3

Under the 10 Hz (Synchronous) condition, there was a significant difference between Lag 1 (*M* = 0.659, *SD* = 0.217) and Lag 3 (*M* = 0.351, *SD* = 0.213), [*t* (67) = 10.300, *p* <0.001], and Lag 1 (*M* = 0.659, *SD* = 0.217) and Lag 8 (*M* = 0.532, *SD* = 0.247), [*t* (67) = 2.788, *p* = 0.002 as well as Lag 8 (*M* = 0.532, *SD* = 0.247), and Lag 3 (*M* = 0.351, *SD* = 0.213), conditions, *t* (67) = 8.346, *p* <0.001 (see Figure 4.9).

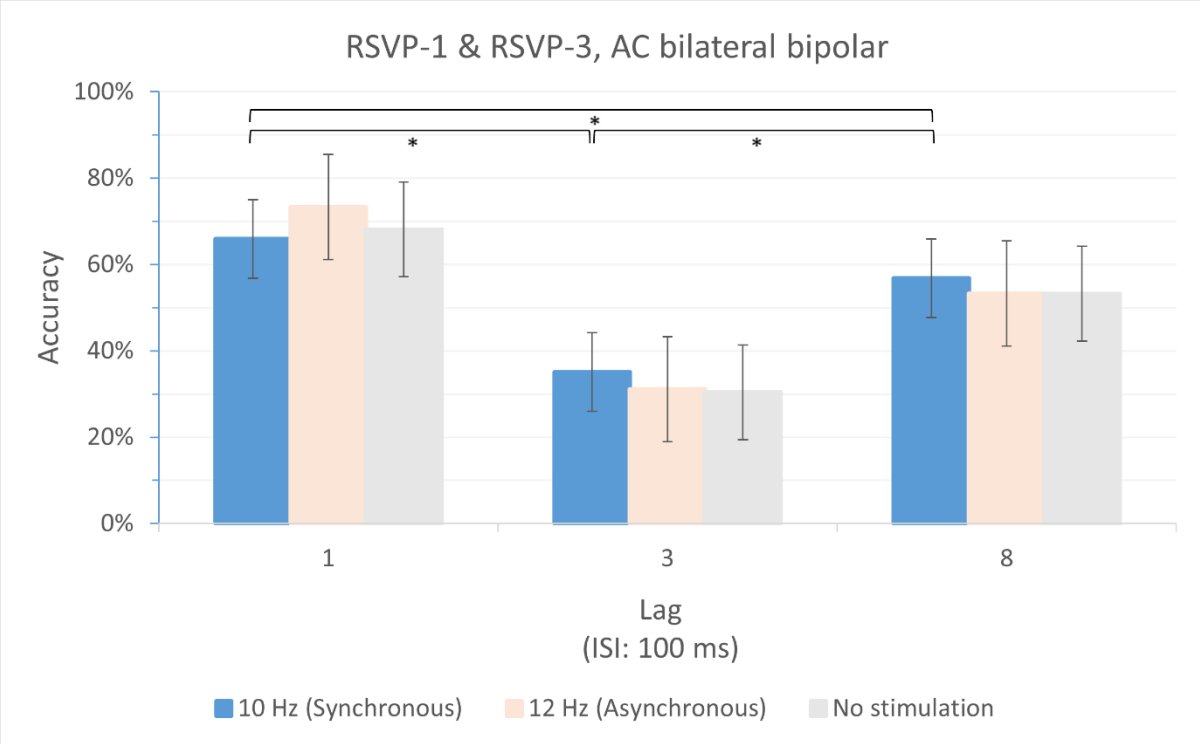

Figure 4.9: Mean accuracy rates of T2|T1 identification as a function of between Lag conditions at each synchronous condition. Bars represent 95 % confidence intervals.

Under the 12 Hz (Asynchronous) condition, there was a significant difference between Lag 1 (M = 0.733, SD = 0.213) and Lag 3 (M = 0.311, SD = 0.200), [t (67) = 16.192, p <0.001], and Lag 1 (M = 0.733, SD = 0.213) and Lag 8 (M = 0.533, SD = 0.247), [t (67) = 5.882, p < 0.001 as well as Lag 8 (M = 0.533, SD = 0.247), and Lag 3 (M = 0.311, SD = 0.200), conditions, t (67) = 10.091, p <0.001 (see Figure 4.10).

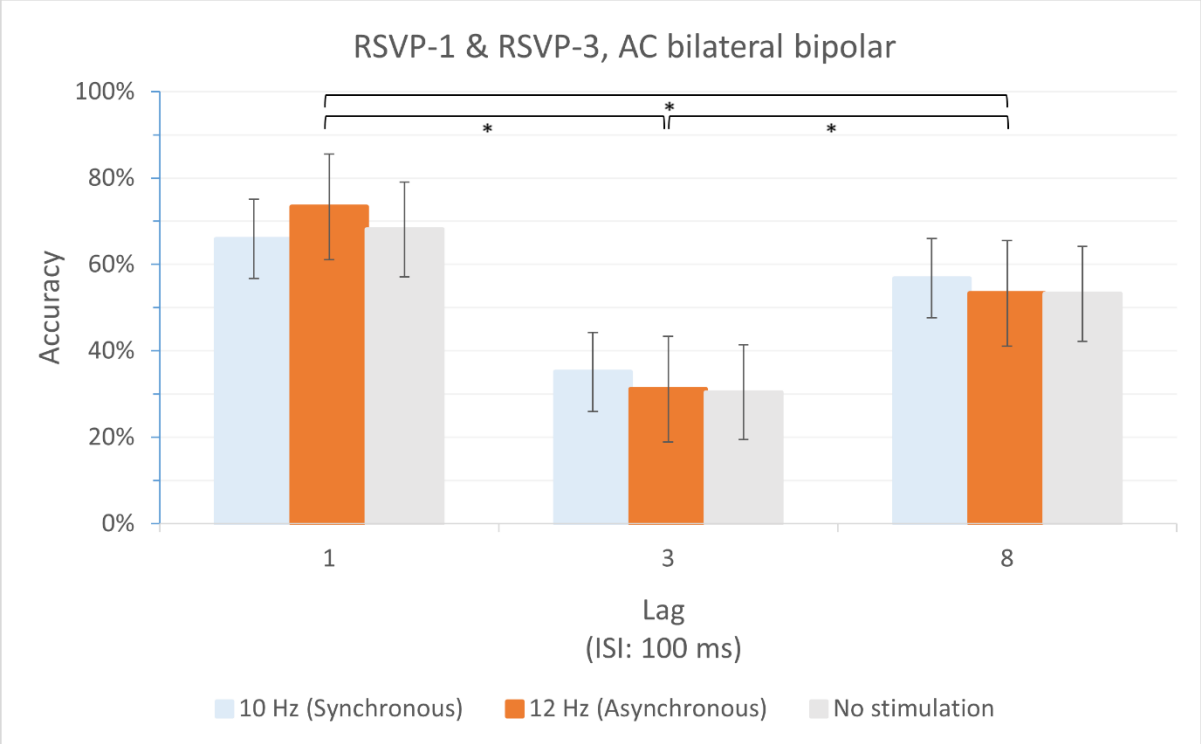

Figure 4.10: Mean accuracy rates of T2|T1 identification as a function of between Lag conditions at each Asynchronous condition. Bars represent 95 % confidence intervals.

Under the no stimulation condition, there was a significant difference between Lag 1 (M = 0.681, SD = 0.225) and Lag 3 (M = 0.304, SD = 0.184), [t (67) = 14.500, p <0.001], and Lag 1 (M = 0.681, SD = 0.225) and Lag 8 (M = 0.532, SD = 0.247), [t (67) = 3.921, p < 0.001 as well as Lag 8 (M = 0.532, SD = 0.247), and Lag 3 (M = 0.304, SD = 0.184), conditions, t (67) = 9.120, p <0.001 (see Figure 4.11).

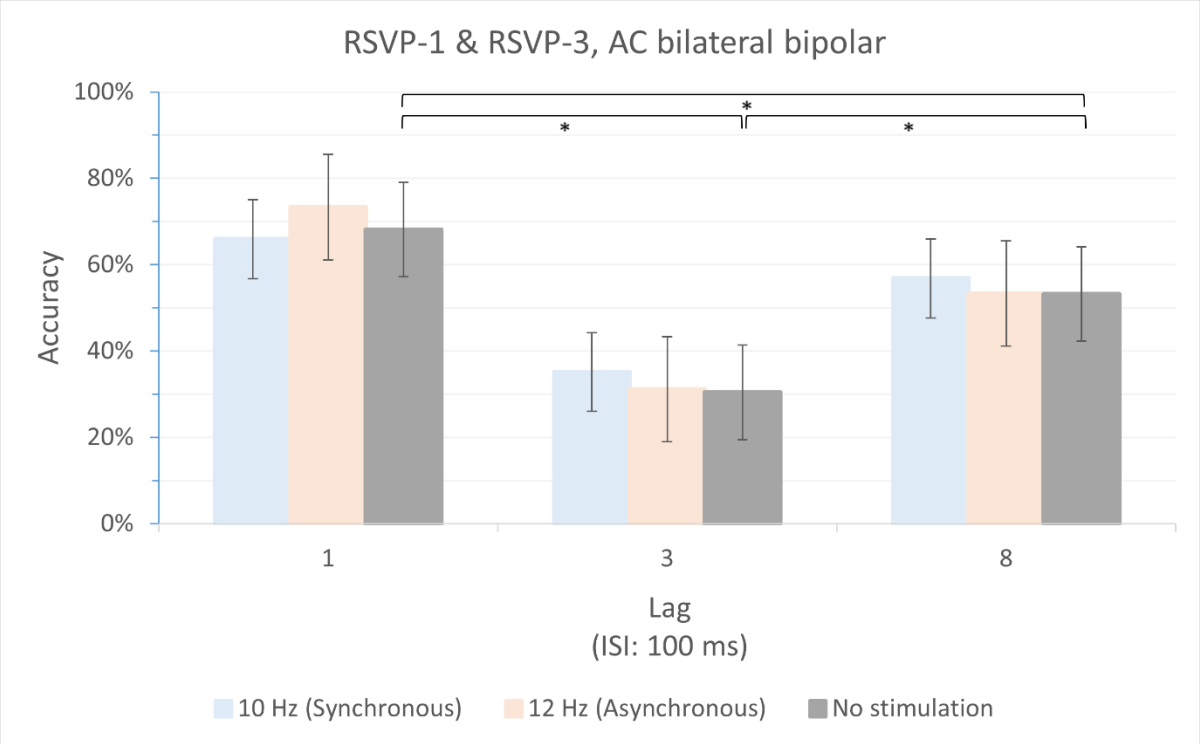

Figure 4.11: Mean accuracy rates of T2|T1 identification as a function of between Lag conditions at each no stimulation condition. Bars represent 95 % confidence intervals.

The three-way interaction between Stimulation, Lag, and Population failed to reach statistical significance, $F(3.323, 222.626) = 2.221$, $p = 0.080$, $\eta_p^2 = 0.032$ (Figure 4.12).

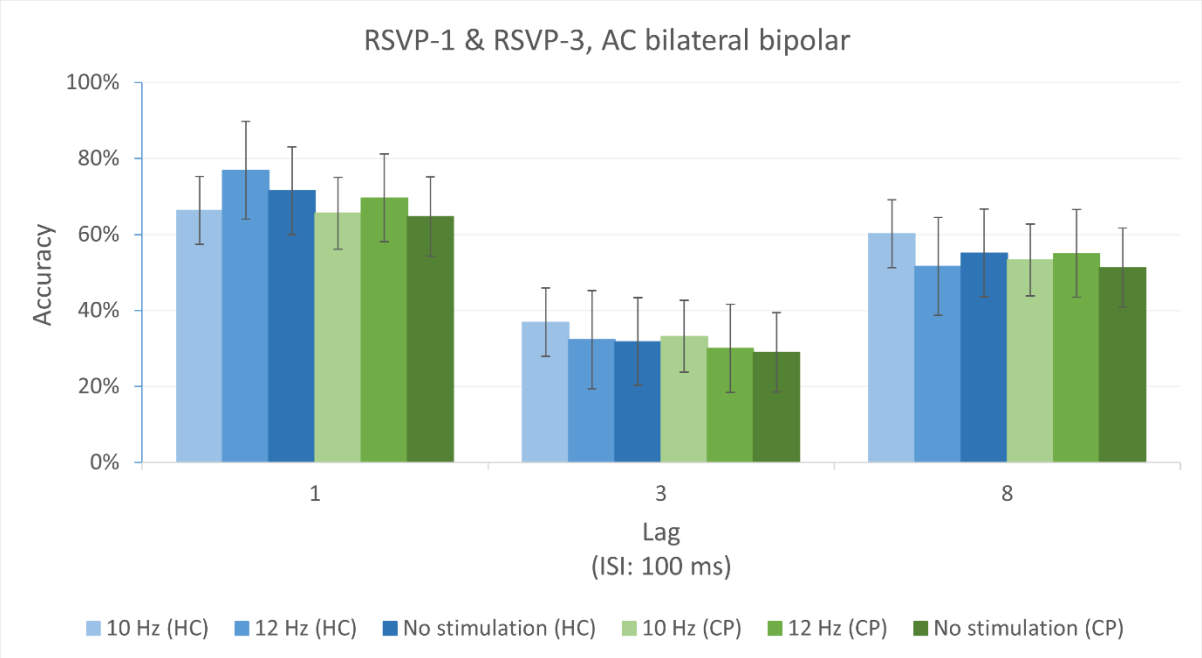

Figure 4.12: Mean accuracy rates of T2|T1 identification as a function of three-way interaction between Stimulation, Lag, and Population. HC stands for Healthy Control and CP stands for Clinical Population. Bars represent 95 % confidence intervals.

4.17 Discussion to Experiment 3 of the RSVP series

The outcomes of the RSVP-3 experiment did not reveal a significant main effect of Stimulation or an indicative interaction effect, suggesting a lack of potential benefits of the asynchronous condition in visual cognitive processing within the RSVP paradigm.

The results of joint analysis (RSVP-1 & RSVP-3), aimed to further evaluate the impact of different Stimulation conditions on response accuracy between Lags, several patterns appear. At Lag 1, the 12 Hz (Asynchronous) condition outperformed the 10 Hz (Synchronous) condition by 11.23% ($p = 0.007$) and exceeded the no-stimulation condition by 7.63% ($p = 0.024$). This suggests that at Lag 1, 12 Hz (Asynchronous) condition significantly enhanced performance.

Preliminary predictions for the clinical group (RSVP-3) suggested a pronounced AB effect due to the unique neural processing and attentional regulation in individuals with ADHD. These variations affect how rapid sequences of stimuli are processed, resulting in a diminished ability to detect the second target compared to the normative group. Interestingly, the findings from RSVP-3 indicate a trend towards normalisation within the clinical participants. Contrary to expectations, the data did not support the hypothesis that entrainment through rhythmic GVS, synchronised with the frequency of visual target presentation, would attenuate the AB effect, thereby improving performance. This might suggest that the clinical population exhibits a reduced sensitivity to rhythmic vestibular entrainment. Consequently, the results of this study do not provide support for the use of GVS within the RSVP paradigm as a therapeutic intervention. The principal inference to be drawn from these findings is that the experimental paradigm elicited a comparable response to stimulation in both the clinical cohort (RSVP-3) and the normative cohort (RSVP-1). This suggests a uniformity in the processing of vestibular signals across the two groups. Such a

result may be indicative of the notion that the visuo-vestibular interaction under investigation is not the point of the deficit observed in the clinical population.

While significant group differences were not observed, it is crucial to emphasise the significant enhancement observed at Lag 1 in both groups under the 12 Hz Asynchronous GVS conditions during the joint analysis. This observation implies the existence of a generic effect that may not be linked directly to the frequency of the vestibular waveform. Exploring this enhancement further could yield valuable insights into the underlying mechanisms and potentially guide future research directions.

4.18 General Discussion

The current chapter focused on exploring the interaction between the vestibular system and attentional blink processes. In Chapters 2 and 3, an interference effect was observed within the DMTS paradigm, lasting for 800ms. However, due to the limited temporal sensitivity of the DMTS paradigm, it was challenging to pinpoint the exact timing of visual process disruption or determine the duration required for recovery to a baseline performance level. To address this limitation, Chapter 4 introduced the RSVP paradigm with enhanced temporal sensitivity. This new approach was designed to detect any effects within the 100-800 milliseconds temporal window, which aligns with the timeframe when visual processing was impacted in Chapters 2 and 3. This investigation aimed to shed light on the underlying mechanisms that might have resulted in the previously seen inhibitory effect.

In the RSVP-1 experiment, a modified version of the study by Ronconi et al. (2016) was employed to investigate the effects of rhythmic entrainment on temporal attention. This study incorporated GVS into the RSVP stream, outlining three distinct conditions: Synchronous (10 Hz), Asynchronous (12 Hz), and a no stimulation condition. The central

hypothesis assumed that GVS entrainment would mitigate the AB effect, with a particular emphasis on Lag 3, identified as the 200-500ms interval between two target presentations.

The AB magnitude may be heightened by early interference effects during RSVP tasks, resulting in reduced visual attention under cognitive strain (Raymond et al., 1992; Bermeitinger & Frings, 2015). The Resource Sharing Model suggests this is due to the division of limited attentional resources between tasks, impairing T2 detection when T1 processing consumes these resources (Hommel et al., 2006; Bermeitinger & Frings, 2015).

According to the DAT, rhythmic stimuli can synchronise attentional rhythms, facilitating more efficient processing at expected times. In the context of AB, this theory explains how aligning attentional resources with the timing of T2 through a rhythmic cue can diminish the AB effect, offering a potential mitigation strategy (Bermeitinger & Frings, 2015). Theories vary on the AB's occurrence stage; some suggest it happens during T1's perceptual processing, impacting T2, while others propose a later stage, with T1's working memory representation hindering T2 (Vogel et al., 1998; Jolicoeur and Dell'Acqua, 2000; Bermeitinger & Frings, 2015).

Contrary to expectations, the results did not evidence a reduction in the AB effect at Lag 3. This outcome could be due to the multisensory facilitation where the unisensory signals were relatively weak by virtue of their brief presentation and high target-distractor similarity (Roy et al., 2020; Cederblad et al., 2022).

A key result from the RSVP-1 experiment highlighted that the highest performance accuracy was seen at Lag 1 during the 12 Hz (Asynchronous) condition. This indicates that the potential for improving performance might be especially strong within very short time

frames. Assenza and Lazzaro (2015) and Jiang et al. (2023) have shown that upper alpha band oscillations are associated with various cognitive functions, including attention and perception, playing a role in the overall organisation of neural activities. When it comes to visual perception, Ronconi et al. (2018) discovered that alpha-band sensory engagement can modify the duration of these temporal windows, affecting how stimuli are integrated or separated over time. Furthermore, Klimesch et al. (2001) conducted an EEG study indicating that increased alpha power enhances synchronisation, which includes sensory perception and controlled processing and is associated with selective attention. In contrast, reduced alpha power leads to desynchronisation and is linked to overall awareness of input and output processes.

RSVP-2 was characterised by an adaptation of the visual stimulus stream to maintain synchrony with the concurrent 12 Hz GVS pulse. RSVP-2 did not show evidence of the predicted AB effect. The take-home from RSVP-1 and RSVP-2 is that the frequency of the visual stimuli was more important than the frequency of the vestibular stimuli. One consideration for the results observed in RSVP-2 could be attributed to the increased task complexity and temporal constraints due to the very brief presentation rate of the stimuli (83.33 ms) imposed on the participants.

The RSVP-3 experiment was a direct replication of the RSVP-1. However, the participants in RSVP-3 consisted of a clinical cohort with documented histories of temporal attentional deficits. While the RSVP-3 results did not conclusively demonstrate a therapeutic advantage, the data suggested normalisation in the clinical population. Upon comparing the clinical data to that of the normative control group, there was an observable trend nearing significance at Lag 3 in the 10 Hz (Synchronous) condition. This result may suggest a potential modulatory effect on the attentional blink phenomenon. However, it is crucial to

note that the observed effect did not reach the conventional threshold for statistical significance, with a p-value of 0.052.

The results derived from the three conducted experiments in Chapter 4 diverge from the interference effect seen in Chapters 2 and 3. Contrary to prior findings, the current results do not indicate that this interference effect is a consequence of the sensory and perceptual processes activated by the RSVP, nor is it associated with the attentional blink. The results of the RSVP-1 study provide preliminary evidence that GVS entrainment at the upper alpha frequency—specifically, the synchronisation of cerebral oscillations within the 10-12 Hz range, as observed in both Lag 1 and 8—may enhance performance when visual stimuli are presented with an ISI of 100ms. Although these results do not confirm the hypothesis presented in this chapter, they are still noteworthy.

I cannot conclude this chapter without reflecting on the limitations of these studies. The methodology and procedures of the current chapter presented several areas where limitations could have influenced the results. A notable starting point is the potential inconsistency in the phase of the alpha during the oscillatory cycle when presenting visual stimuli. While I attempted to synchronise the frequency of the vestibular signal with the presentation rate of the visual target and utilised an oscilloscope for verification, only a one-directional trigger (specifically trigger 128) was employed to communicate with the GVS box. This trigger was sent at intervals as prescribed by the timings listed in the Excel trial sheet integrated into PsychoPy, designed to manage stimulus presentation timings.

To achieve true synchronous and consistent phase-locking of the visual stimulus Onset with the AC peak, future research should contemplate incorporating a second peak detector into the experimental setup. The output from this peak detector could be observed

via the parallel port linked to the PC. If the GVS box lacks the capability to support peak detection and the return of triggers, a viable alternative would involve introducing a second parallel card to the PC. Such a setup would allow one line to oversee signal transmission while the other line analyses signal reception, facilitating simultaneous bidirectional operation. With this configuration, it becomes feasible to establish a truly synchronised condition for the Onset of the visual stimulus at the desired oscillatory phase of the signal from the GVS box and to promptly receive a corresponding feedback signal once the phase of the peak has been detected.

A further limitation of this research relates to the integration of RSVP-3 into a clinical test battery. This battery was administered to participants with a documented history of hyperactivity and attentional deficits, requiring them to engage in tasks lasting an hour, concurrent with exposure to GVS from additional experimental protocols. Prolonged exposure to GVS may induce adaptation or reduced sensitivity, which has the potential to confound the experimental results, though the literature in this area remains limited. Additionally, the decision to incorporate RSVP-3 into the test battery, especially when the results of RSVP-1 were not markedly substantial, is a consideration that future studies might wish to re-evaluate.

An additional limitation of this study concerns to the insufficient characterisation of the clinical population under investigation. Given the heterogeneous nature of ADHD and dyslexia, it is imperative to emphasise that these conditions are not homogenous. The sensory response patterns might exhibit variations depending on distinct subgroups within each condition, each manifesting differential attributes and underlying cognitive impairments (Ghanizadeh, 2008; Wang et al., 2022).

As a concluding limitation, in order to gain a more accurate insight into the electrophysiological changes associated with the AB function during vestibular entrainment at different frequency bands, for future research it is advisable to consider incorporating ERP measures, with a specific focus on the P300 component (Martens et al., 2006). Measuring the P300 component allows for an investigation of EEG studies indicating that the P300 component is eliminated after T2 at shorter target separations, implying that T2 tends to reach working memory at shorter T1–T2 gaps when there is a higher likelihood of T1 target detection. Martens et al. (2006) demonstrated that a low probability of T1 detection contributes to a higher chance of observing the P300 component and, consequently, a more pronounced AB effect. Therefore, the inclusion of ERP measures would help clarify the cognitive and neuropsychological associations between the role of GVS and its impact on the temporal limitations of attention.

Chapter 5 – General Discussion

5.1 Overview

An increasing number of studies show that vestibular dysfunction disrupts cognitive performance. Brain imaging studies have further supported this evidence by demonstrating wide-spread activation of cortical networks from the vestibular system (Bigelow & Agrawal, 2015). However, the effects of vestibular signals on specific aspects of cognitive function are still not thoroughly understood, and as a result, their influence is frequently minimised in cognitive models. This thesis made use of non-invasive artificial vestibular stimulation to investigate if and how vestibular information modulates temporal attention in a normative and a clinical population. Theoretical implication aside this, in turn, might highlight novel therapeutic avenues for psychological disorder.

5.2 Theoretical Insights and Summary of Results

The published literature shows that temporal expectancies can be induced in one sensory domain by the delivery of temporally regular stimuli in another, affecting both perceptual and motor behaviour (Correa et al., 2006; Bollimunta et al., 2011; Rohenkohl et al., 2012; MacLean et al., 2013). This thesis aimed to contribute to a gap in literature by providing insight into the impact of rhythmic sub-sensory vestibular signals on visual and auditory temporal processes in normative and clinical population. More specifically, the experiments explored whether the visual or auditory systems could benefit from the temporal rhythm of the vestibular signals to better process incoming visual or auditory information.

Chapter 2 explored the principles of the Dynamic Attending Theory (DAT) through a delayed matching-to-sample (DMTS) paradigm to determine if the synchronisation of visual and auditory stimuli with individual vestibular signals could enhance attentional judgments. As such, 144 participants from a normative population engaged in a series of visual and auditory

experiments, which involved both detection and discrimination tasks while receiving DC bilateral bipolar or AC bilateral bipolar GVS. The detection tasks focused on the presence or absence of visual stimuli, whereas the discrimination tasks were designed to investigate attentional identification processes.

The primary objective of Chapter 2, explored through Experiments 1 and 2, was to investigate the potential of a DC bilateral bipolar waveform, with box-car shape to mirror the structure of auditory stimuli used in allied experiments, to prime visual responsiveness. This theory is grounded in the principles of the DAT proposed by Jones and Boltz (1989). It was hypothesised that DC-GVS waveform would enhance visual attentional processes, as evidenced by improved performance in attention-based, detection and discrimination working memory tasks. Such improvements were anticipated when visual stimuli were presented in synchrony with the Onset of the DC-GVS, leveraging the temporal characteristics of the vestibular system. In the visual detection task (E1), the results did not achieve statistical significance, thereby at this stage remained inconclusive. In the visual discrimination task (E2), the results revealed initial indications of an interference effect on response times at Offset 4.4 and Offset 4.8, following synchronous Offset. This pattern offered partial support for the hypothesis, which predicted a visuo-vestibular interaction albeit facilitative in nature at Offset 4 (i.e. where the visual stimuli aligned with the Onset of DC-GVS).

Experiments 3 and 4 examined whether this same DC bilateral bipolar stimulation, which had previously shown inhibitory effects in the visual domain, also influenced auditory performance when synchronised with the Onset of the DC-GVS pulse. In the auditory detection task (E3), the results did not achieve statistical significance, thereby at this stage remained inconclusive. However, the findings of E4 demonstrated a main effect of Stimulation on the response time, with responses significantly shorter during GVS compared to instances with no

Stimulation, regardless of the Offset condition. However, this finding does not provide support for the hypothesis. This preliminary result may suggest that the auditory and visual systems process identical vestibular signals in a distinct qualitative manner. Notably, the auditory system appears unaffected by the incongruent characteristics of a GVS signal. Furthermore, this could represent a non-specific regulatory enhancement of auditory functions, as similarly observed in a subsequent GVS paradigm within this thesis, as outlined in Experiment 7. This may represent the first instance in research literature where a study proposes a general improvement in auditory capabilities facilitated by GVS.

Given that my previous experimental attempts to enhance responses by synchronising visual or auditory stimuli with vestibular pulses failed to yield positive results, a different approach was needed. In Experiments 5 and 6, I therefore changed the DC signal to an AC signal. This was driven by evidence that an alternating current may be more effective in inducing cross-frequency coupling and oscillatory entrainment than a direct current (Moreno-Duarte et al., 2014; Dowsett & Herrmann, 2016; Cole & Voytek, 2017; Żebrowska et al., 2020). No effect was seen in the visual detection task (E5) which may simply be the very high accuracy rate. However, the outcome of E6, the visual discrimination task, showed a significant change compared to no stimulation. During GVS, response times were shorter at Offset 3.6 (an effect that did not prove replicable) while accuracy rates were lower when the Onset of the delayed visual sample task was synchronised with the vestibular signal at Offset (4). Furthermore, this inhibitory effect carried over to negatively impact post-synchronous Offsets (4.4 and 4.8). This interference effect partially supports the visuo-vestibular interaction predicted by the DAT hypothesis. Interestingly, when the same AC bilateral bipolar protocol was implemented within the auditory domain (E7, as explored in Chapter 3), the results distinctly differed. A general facilitatory effect of GVS was apparent, devoid of any pronounced interaction with the Offset. This finding once again proposes that the

auditory and visual systems treat the same vestibular signal qualitatively differently, with the auditory system remaining clearly undisrupted by the incongruent nature of a GVS signal.

This observed interference effect provides evidence for a reciprocal inhibition mechanism playing a role in managing sensory conflicts and coordinating responses. The importance of this reciprocal inhibition becomes clearer when considering the implications of conflicting sensory inputs on cognitive function. Such conflicts can cause perceptual uncertainty and require the additional allocation of attentional resources to resolve — in this case, high-contrast Gabor patches (Bigelow et al., 2015; Smith et al., 2022). To manage these conflicts, the brain tends to prioritise one particular sensory modality (Da Moreira Teixeira et al., 2021). Interestingly, interference effects were consistent across different stimulation protocols, although it was more prominent during AC than DC stimulation which fits with the idea that AC signals have a more pervasive effect on neuronal response. The observed facilitatory outcomes in the auditory domain suggest that the inhibitory effects found in the visual tasks are not a universal feature of vestibular stimulation and, rather are sensory specific.

Taken together, the results in Chapter 2 indicate that distinct sensory modalities (i.e., visual and auditory) exhibit differential responses to temporally induced expectancies generated by the vestibular system. These differences manifest not merely in terms of facilitatory or inhibitory effects, but also with respect to their sensitivity to the timing of the stimulus. It is notable to mention that facilitatory interactions between the auditory and vestibular system have been previously documented under comparable experimental conditions (Schmidt-Kassow et al., 2013).

Chapter 3 further explored the incorporation of GVS within the DAT framework by comparing unilateral and bilateral AC signals on visual and auditory responses in normative and clinical groups. In Experiment 7, the primary objective was to investigate whether the general

facilitatory effect on audition observed in Experiment 4 could be replicated and potentially strengthened by employing the more powerful entrainer of AC. If found to be the case then it would suggest that DC-GVS is not a prerequisite for auditory-vestibular enhancement. Rather, it would indicate that any waveform shape may suffice. Experiment 7 also sought to explore whether the inhibitory effect seen in the visual experiments (E2 and E6) is modality-specific. The results of Experiment 7 demonstrated that the application of an AC bilateral bipolar protocol during the auditory discrimination task led to a generalised facilitatory effect when active GVS was employed, as opposed to conditions with no stimulation. This effect was observed without any significant interaction with the Offset parameter. As such, the results of E7 serve to further support the hypothesis that the auditory system exhibits heightened sensitivity to GVS, irrespective of Offset, compared to the visual system when administered as an alternating current. Notably, the facilitation effect observed in E7 is more pronounced than the results of E4. This may imply that the level of facilitation relies on the shape of the waveform and/or the active stimulation of both cerebral hemispheres.

Experiment 8 was excluded from this thesis and subsequent analyses due to a scripting error that compromised its results' validity. Consequently, comparing the results of Experiment 9 with a normative group (E8) was not feasible. However, E9 demonstrated that individuals with ADHD exhibited lower auditory response accuracy under GVS compared to no stimulation. This outcome is in line with research suggesting that ADHD is associated with heightened sensory sensitivities, which can be exacerbated rather than facilitated by such stimulation (Micoulaud-Franchi et al., 2015).

Experiment 10 explored the possibility of the interference effect observed in E6 being hemisphere-specific by employing AC stimulation with a positive Offset that exclusively delivered cathodal stimulation to the right hemisphere and anodal stimulation to the left

hemisphere. In contrast, Experiment 6 utilised AC bilateral bipolar stimulation during a visual discrimination task which successively stimulated both hemispheres. The results of E10 indicate that performance once again declined noticeably from Offset 4 onwards, reaching its lowest point at Offsets 4.4 and 4.8. This result confirmed the replicability of this previously unreported psychological interference effect, and also indicated that it is not contingent upon both cerebral hemispheres actively receiving GVS.

To further investigate the nature of this interference effect, Experiments 11 and 12 sought to determine if they were reliant on incidental viewing conditions. This was motivated by a principle of inverse effectiveness which states that multi-sensory facilitation may be strongest when signals in one sensory domain are relatively weak and ambiguous (Meredith & Stein, 1987). In the present context, it may be that I had not observed vestibular facilitation because the visual stimuli were strong and unambiguous. Accordingly, in Experiments 11 and 12, the visual stimuli were presented under degraded viewing conditions. Experiment 11, a detection task, showed an overall enhancement in target detection, while Experiment 12, a discrimination task, eliminated the inhibitory effect. This suggests that under specific conditions with near-threshold visibility, where the visual system relies more on the vestibular system, the interference effect disappears, and that for basic detection processes some benefit may also emerge. This phenomenon aligns with the principles of multisensory integration, suggesting that the integration of different sensory cues produces a more pronounced neural response compared to the effect of isolated stimuli. The experimental frameworks outlined in Chapters 2 and 3 were designed with the objective of exploring whether this amplification of response extends to functions such as visual and auditory discrimination is applicable beyond the functions of the superior colliculus and can be modulated by vestibular inputs. This highlights the increased sensitivity of an organism to events when it can access information from multiple sources, illustrating the combined impact on brain processing and behavioural reactions (Meredith & Stein, 1987).

Chapter 4 further informed the thesis question by demonstrating that the interference effect did not originate within the processes engaged by the attentional blink paradigm. Previous research discovered that the presence of a background rhythmic auditory stimulus modulated the AB whereby visual stimuli occurring at the same temporal frequency as the auditory stimuli were identified more accurately at Lag 3 (Ronconi et al., 2016). According to Fellinger et al. (2012), the flow of information improves when two continuous streams of information coordinate their oscillatory cycles over time, resulting in completely synchronised excitability cycles (Cardin et al., 2009; Bollimunta et al., 2011; Mathewson et al., 2011).

As such, in Chapter 4, RSVP-1 experiment was designed to elucidate the temporal dynamics of the visual interference effect previously seen in Experiments 6 and 10. In these earlier experiments, the effect was observed to persist for 800ms following a synchronous GVS pulse. Although the 800ms estimate provided a general indication of the duration of the effect, it was limited by the temporal insensitivity of the delayed matching-to-sample paradigm that had been employed. As a result, no insights were gained into changes in visual processing that might have occurred during this window.

To overcome this limitation, a RSVP paradigm, known for its high temporal specificity, was utilised. This allowed for the identification of transient visual-vestibular cross-modal interactions on a much finer timescale. The efficacy of RSVP in this context was enhanced by its exploitation of the AB, a perceptual phenomenon that served as a valuable tool for probing visual processing within brief time intervals. Specifically, the AB captures the cognitive challenge associated with identifying a second stimulus in a rapid sequence of visual events, thereby revealing characteristic limitations in both attention and working memory.

Accordingly, RSVP-1 aimed to investigate whether synchronising the presentation of visual stimuli with GVS pulses (10Hz) at the same frequency as the visual target rate (100ms) could lead to entrainment and, consequently, reduce the expected AB effect at Lag 3. If successful, this would be manifested as a significant improvement in accuracy compared to asynchronous (12Hz) or no stimulation conditions. The results of RSVP-1 did not support the hypothesis regarding the modulation of AB at Lag 3. However, overall, Lag 1 consistently exhibited the best performance across various stimulation conditions, demonstrating a significant 33% improvement in the 12 Hz (Asynchronous) condition compared to other Lags. In the case of Lag 8 at 10 Hz, there was a notable 17% increase in accuracy compared to the 12 Hz condition. Nevertheless, Lag 1 remained the top-performing Lag in this task.

The improved performance accuracy during a 12 Hz frequency could possibly be due to a beneficial effect of GVS at very short time lags. This finding aligns with previous research linking alpha band oscillations to reduced sensory disturbances and improved attention (Foxe & Snyder, 2011; Klimesch, 2012). Elevated alpha activity in the visual cortex is also associated with decreased neuronal responsiveness and reduced processing of distractions (Foxe & Snyder, 2011; Zhigalov & Jensen, 2020). The observed variances raise questions about whether the 12 Hz frequency coincidentally aligns with the visual stimuli or if GVS independently influences cognitive performance, suggesting a possible entrainment effect.

In examining the integration of vestibular and visual processes, the RSVP-2 experiment built on the findings of RSVP-1, investigating whether the frequency-specific effects observed were a coincidence or indicative of a deeper interaction. However, the results from RSVP-2, did not show any notable effects, suggesting that the modulation seen in RSVP-1 was likely tied to the frequency of the visual stimulus rather than an independent effect of GVS. These outcomes imply that the interaction between vestibular and visual mechanisms over short periods is instead

influenced by non-vestibular factors like visual frequency and task complexity. This suggests an optimal frequency range for the effective integration of vestibular and visual information, beyond which the coupling may be disrupted, possibly due to inadequate time for effective information processing.

Supporting these findings, Cardelli et al. (2023) highlighted the reciprocal influence between optic flow changes and vestibular system activity, suggesting an adaptive yet constrained relationship between these sensory systems. In particular, the task complexity and high frequency of stimuli, specifically referencing the use of 12 Hz in RSVP-2 as opposed to the 10 Hz used in RSVP-1, emphasise the challenges posed to cognitive processing. As Malcolm et al. (2018) suggest, this adaptability is limited, especially under high cognitive demands, such as the use of 12 Hz GVS and the same rate of visual presentation in tasks (83.33ms per stimulus), which can impair the brain's information processing efficiency, evident in increased cortical activation and a reduction in alpha power.

Furthermore, Hanslmayr et al. (2011) observed a decrease in alpha power when processing closely spaced, task-relevant visual stimuli, indicating that the brain's ability to function effectively is challenged during cognitive overload. While these studies did not pinpoint the exact cause of the interference effect observed in previous experiments, they opened up the possibility that this phenomenon might be task-specific and influenced by the frequency and complexity of the stimuli presented

RSVP-3 investigated whether the frequency-dependent facilitatory effects observed in the normative group in RSVP-1 could be replicated in a clinical population characterised by established deficits in temporal attention. The hypothesis implied potential therapeutic benefits of GVS for the clinical group, particularly in modulating AB. Contrary to expectations, the RSVP-3

data did not show a significant modulatory effect. Although a joint analysis with RSVP-1 indicated a trend towards such an effect, it fell short of statistical significance with a p-value of 0.052. Hence, the hypothesis remains inconclusive. Nevertheless, the joint analysis did indicate a uniformity in the processing of vestibular signals across both groups, and a significant enhancement observed at Lag 1 under the 12 Hz GVS condition. Other studies have suggested that GVS may enhance resting state neural activity by enhancing functional connectivity in the temporoparietal regions responsible for processing vestibular inputs (Helmchen et al., 2020). This modulation has the potential to mitigate atypical visuo-vestibular interactions and facilitate compensation for deficient perceptual processes in a clinical population (Helmchen et al., 2020). Additionally, GVS has been observed to increase resting state neural activity in specific regions across both clinical and normative populations. Nonetheless, findings of the RSVP series suggest a generic effect that warrants further investigation; however, they do not directly support the central hypothesis.

This constitutes a novel finding, as the data presented do not reveal a deficit that could account for the clinical features observed in the clinical group. Furthermore, there is no indication of a differential response to vestibular stimulation. The absence of expected outcomes indicates new avenues for understanding the complexities of this clinical population and its interaction with sensory processing. Data from Chapter 4, which compared the ADHD clinical group to normative cohorts, suggested a normalisation and uniformity in the processing of vestibular signals across the two groups. Although the relatively subtle enhancement observed at Lag 1 lacks clinical significance (with a p-value of 0.052), it is possible that more naturalistic stimulation techniques may increase efficacy. These techniques include Sensory Integration Therapy (SIT) which incorporates vestibular stimulation exercises like swinging or balance activities (Dąbrowska & Biernacki, 2023), and physical activities such as ballet or dance which inherently involve vestibular stimulation and are highly effective for improving symptoms and functional abilities in

individuals with vestibular dysfunction and impairments (Heusel-Gillig & Hall, 2023). Furthermore, Virtual Reality Therapy (VRT) could provide controlled and safe vestibular stimulation experiences, presenting a novel approach to vestibular rehabilitation in a clinical population with a known temporal deficit (Sana et al., 2023). These approaches could offer a more engaging and less invasive means of exploring naturalistic methods of vestibular stimulation within the clinical cohort, suggesting promising directions for future research.

5.3 Limitations

A number of major limitations apply to the conclusions drawn from this thesis. Although many of these have been discussed in the discussion sections of each chapter, this section aims to address a collective insight into the issues raised in this thesis and suggest a direction for future research.

In Chapters 2 and 3, the research methodology followed the approach used by Jones and Boltz (1989) within the DAT framework and, as such, employed response accuracy and reaction time measures. However, the limitations of the detection task methodology became clear. The straightforward nature of the task led to ceiling effects, which concealed finer variations in performance. Participants consistently achieved high levels of accuracy, rendering traditional performance metrics, such as reaction time and response accuracy, inadequate for capturing subtle differences. This ceiling effect indicates that the participants reached their maximum capacity for detection, thereby making it challenging to draw meaningful theoretical inferences. To overcome this limitation, future studies could consider making the task harder and also incorporating Signal Detection Theory (SDT) into their research design. This mathematical framework allows for the separation of an individual's perceptual sensitivity from their response bias, thereby providing a more nuanced understanding of cognitive processes. Utilising metrics like d-prime could offer valuable insights into the attentional dynamics affecting an individual's ability to detect

experimental stimuli, particularly when performance reaches saturation levels. This methodological shift could facilitate more precise analyses and comparisons with other studies, enhancing our understanding of dynamic attending mechanisms.

Another limitation is the absence of documentation for individualised threshold data. During these studies, a thresholding procedure was systematically carried out for each participant to assess their respective sub-sensory thresholds. However, it is important to note that the subsequent analysis primarily presents data on the range of sensory thresholds (upper and lower threshold bands) observed and the corresponding levels of electrical currents. In retrospect, it becomes evident that including this data in the analysis was necessary. Future research should consider incorporating individualised sub-sensory thresholding data, as this would enable a deeper understanding of the variability in subliminal somatosensory perception and its potential impact on GVS outcomes (Yang et al., 2015). Furthermore, this incorporation allows for the consideration of individual differences in somatosensory perception, thereby enhancing the generalisability of the findings (Bauer et al., 2023). This approach enables a more comprehensive comprehension of the effects of GVS across distinct individuals and populations.

Another limitation evident in Chapters 2 and 3 relates to the initially selected statistical power of 0.80, influenced by prior research following Cohen's (1992) recommendations, while also accounting for practical considerations such as time, resources, and participant recruitment logistics. Upon reflection, this choice carried the potential for Type II errors, which could have impacts on the generalisability of the findings. To address this concern, Chapter 4 implemented a corrective measure by elevating the statistical power to 0.90, thus mitigating the risk of false negatives.

In evaluating the efficacy of GVS, it is crucial to consider the temporal characteristics of the applied stimulus in comparison to naturally occurring vestibular stimuli. As such further limitation impacting Chapters 2 and 3, is that the frequency of the GVS may have been suboptimal, particularly in relation to its temporal alignment with naturally elicited vestibular activities since the vestibular system is generally activated by head movements that occur within millisecond time frames. As such, the slower frequency utilised in the GVS protocol may not adequately replicate the rapid temporal dynamics that characterise organic vestibular stimulation. This temporal incompatibility may therefore limit the generalisability of the findings and should be taken into account in future experimental designs.

In considering the limitations of this study, it is crucial to mention the size of the electrodes used, particularly when implementing a sub-sensory stimulation protocol. The electrodes utilised in the experiments in Chapters 2, 3, and 4 were larger than the newer versions currently available. Both large and small electrodes offer specific advantages and disadvantages. Large electrodes, when positioned on the vestibular nerve beneath the mastoid, have the benefit of accommodating inter-individual variability in the location of the vestibular nerve across participants (McLaren et al., 2023). On the contrary, Truong et al. (2023) argue that the use of larger electrodes results in greater current loss across the scalp, leading to less efficient current flow. Smaller electrodes are favoured for facilitating higher current flow and induced electric fields, particularly in brain regions such as the cerebellum and temporal area. Nonetheless, it is imperative to acknowledge that transcutaneous electrical stimulation modalities, irrespective of mastoidal or alternative electrode placement strategies, fundamentally possess the potential to activate a heterogeneous range of sensory afferent pathways (Vallar et al., 1996; Lafosse et al., 2003; Zhang et al., 2022). As such, any observed physiological or behavioural outcomes should not be explicitly attributed to isolated vestibular activation; rather, it is highly plausible that these outcomes incorporate a vestibular component amongst a multifaceted sensory response. This

methodological consideration is not confined to the studies addressed in this thesis but extends to the broader body of literature employing GVS techniques.

Additionally, the study did not provide a sufficiently detailed characterisation of the clinical population, especially given the diverse nature of ADHD and dyslexia. Existing research shows that there are different sensory response profiles and cognitive deficits among specific subgroups within each disorder (Ghanizadeh, 2008; Wang et al., 2022). A more detailed classification of the clinical cohort would have added depth and specificity to the findings of the study. Future research should focus on explaining the subtypes of ADHD and dyslexia. ADHD is classically categorised into three primary subtypes: inattentive, hyperactive-impulsive, and combined (Saad et al., 2020). Dyslexia, on the other hand, manifests in forms such as phonological, surface, and mixed dyslexia (Friedmann & Lukov, 2008). Exploring these subtypes would provide critical insights into the varying manifestations of these disorders. Moreover, it is essential to consider the comorbidity profiles of these populations. The frequent co-occurrence of conditions such as anxiety disorders, depression, and learning disorders with ADHD and dyslexia necessitates a comprehensive understanding of these interrelations (Willcutt et al., 2005; Leyfer et al., 2013). Detailing these comorbidities within the clinical population could provide a more inclusive perspective on the challenges and treatment responses encountered. Additionally, further assessing a range of cognitive functions, including working memory, executive functioning, processing speed, and auditory and visual processing, is crucial for a comprehensive understanding of the broader cognitive profile of individuals with these neurodevelopmental disorders (Ziegler et al., 2021; Hong et al., 2021; Cai et al., 2022). Incorporating these cognitive aspects into future research would enhance our understanding of ADHD and dyslexia. This, in turn, would improve the specificity and applicability of the findings of the study, offering more targeted approaches for intervention and support for individuals affected by these conditions.

A notable methodological limitation that requires attention in subsequent investigations concerns the suboptimal alignment of timing and phase congruency between the Onset of the AC/DC vestibular signal and the experimental stimuli. This limitation further manifests as variable phase consistency in the AC/DC signal during the oscillatory cycle concurrent with stimulus presentation. Despite detailed efforts to synchronise the Onset of the vestibular signal with that of the visual/auditory stimuli—such as frequency alignment of the vestibular signal with target presentation and real-time monitoring via an oscilloscope—the experimental design was confined to a unidirectional triggering system. Specifically, this was implemented through an Excel-based timing sheet integrated into the PsychoPy script, which communicated with the DC-stimulator device.

To enhance temporal alignment and phase-locking, it is advisable for future studies to incorporate a secondary peak detector into the experimental design. This can be interfaced with the parallel port of the computer; if the DC-stimulator device lacks peak detection capability, as was the case with the device used in this study, an additional parallel card could be installed in the computer. Such an arrangement would facilitate bidirectional communication, thereby achieving true phase-locking between the stimulus Onset and peak signal. Implementing this modification is likely to result in more robust phase-locking, which would contribute to more reliable testing of the hypothesis. It is noteworthy to mention that, despite the potential misalignment of the peaks, the frequencies of stimulus presentation remained consistent.

Furthermore, future research could benefit from integrating a high-frequency carrier wave alongside established physiological metrics such as EEG. The EEG is advantageous due to its temporal resolution, capturing neural activity in millisecond intervals. This incorporation could provide a more granular assessment of oscillatory brain responses during GVS. Recent literature corroborates the utility of EEG in exploring oscillatory patterns in temporal attentional tasks

(Ismail & Karwowski, 2020; Petit et al., 2021), thus supporting the validity of its application in the context of this thesis.

In considering opportunities for future replications for the experiment in the healthy controls group, it is worth noting a valuable lesson learned during this study regarding the quality and accuracy of data from the healthy control group (E8 - data excluded from this thesis). This experience emphasises the importance of implementing continuous checks and validation procedures throughout the data collection process. Real-time monitoring of each participant's data is essential for promptly identifying and rectifying any errors or anomalies. This approach not only enhances the scientific precision of the study, but also demonstrates a commitment to respecting the time and effort contributed by participants, ensuring the effective utilisation of their data. Additionally, the complexity of the visual stimuli, particularly Gabor patches, may present a limitation in the DMTS paradigm. Alternatively, simpler stimuli like sinusoidal gratings with reduced variation in orientation or frequency may be less cognitively demanding and thereby mitigate potential aftereffects, a phenomenon documented in prior studies (Kobayashi et al., 2012).

5.4 Conclusion

The current thesis endeavours to expand the empirical understanding of the multidimensional relationship between the vestibular system and both visual and auditory temporal attentional processes. Several experimental chapters in this research work offer novel insights into how the rhythmic properties of the vestibular system modulate attentional mechanisms in the visual and auditory domains. Nevertheless, it has become clear that the effects of such modulation are neither homogeneous nor universal; they differ significantly across various tasks and time courses.

A critical finding is that the facilitatory effects associated with the DAT across the visual and auditory domains do not apply to visuo-vestibular or auditory-vestibular interactions. This may simply be because the artificial, unexpected nature of the GVS signal does not allow the brain to meaningfully relate it to concurrent visual or auditory input. Applying a more naturalistic stimulus, such as ballet, dancing, cycling, skating, skipping rope, ice skating, and balancing on uneven terrain, where the vestibular signal conveys information about head movement that is congruent with information from other concurrent sensory inputs, may increase its modulatory effect (Thompson et al., 2017; Rosa et al., 2023; Swaminathan et al., 2023). In its current state, the vestibular signal may appear nonsensical to the brain, potentially leading to its down-weighting in favour of more coherent and expected input from other sensory channels.

Alternatively, it may be that the vestibular system interacts with the other senses in a somewhat unique fashion. Interestingly, a consistent trend of negative interference was observed within the visual domain, an effect that is enhanced by the use of sinusoidal vestibular stimuli. This interference can be attenuated by reducing the visibility of the visual stimuli and thereby re-weighting allied vestibular stimuli more strongly. On the other hand, this thesis provides preliminary evidence that GVS can, under certain conditions, enhance auditory responses. Although this magnitude effect does not indicate immediate clinical relevance, it is possible that it may be more apparent in a different clinical population or following a longer or more intensive stimulation protocol. Nevertheless, the visual and auditory systems seem to share bespoke relationships with the vestibular system.

This thesis has highlighted the novel and striking influences of the vestibular system on the processing mechanisms of both visual and auditory stimuli. The experimental conditions deployed here show that the vestibular system interacts with other sensory systems in a pervasive and unique manner. The findings extend the boundaries of our current understanding, suggesting that

vestibular influences are deeply embedded within the multisensory processing framework. Thus, a fundamental avenue for future research will be to further investigate the governing dynamics of these interactions, with a particular focus on determining the conditions that underpin their facilitative or detrimental impact on sub-sensory perception.

The principle of inverse effectiveness suggests that when multiple unisensory stimuli are integrated, even if they are individually weak, they can lead to an enhanced neural response greater than the sum of strong stimuli (Meredith & Stein, 1986). This principle could provide a pathway to addressing the unresolved quest of this thesis, which is to identify instances of visuo-vestibular enhancement. So far, it has been observed that applying the inverse effectiveness rule by reducing visual contrast could eliminate interference, but it has not yielded significant results. The synergistic effect of combining sensory stimuli, such as subtle visual cues with reliable vestibular inputs, not only increases reliance on vestibular rhythms but also results in a stronger neural response than that observed with more powerful individual stimuli. This phenomenon suggests that, instead of causing sensory overload, the integration of weaker stimuli fosters a more effective sensory response (Stanford and Stein, 2007; Miller et al., 2017).

Furthermore, the inverse effectiveness principle sheds light on the brain's strategy for optimising sensory integration. It proposes that the CNS employs a probabilistic model to modulate the integration of sensory inputs, adjusting the weighting of cues according to their contextual reliability (Gu et al., 2008; Angelaki et al., 2011; DeAngelis & Angelaki, 2012), emphasising the idea that multi-sensory enhancement seems to be a pervasive attribute of neural functionality. Therefore, any difficulties in detecting it within the experimental framework of this thesis may be attributed to task-specific and stimulus-related variables, rather than fundamental functional principles.

Exploring the cerebral mechanisms responsible for the incorporation of subliminal vestibular stimuli promises to significantly advance our understanding of the subconscious aspects of sensory integration. I anticipate that this enhanced understanding will drive the development of innovative therapeutic approaches to vestibular dysfunctions and provide guidance for engineering advanced artificial sensory interfaces.

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Appendices

Appendix A

1) Participant information sheet

You are invited to take part in a research study. Before you decide it is important for you to understand why the research is being done and what it will involve. Please take time to read the following information carefully. Please ask if anything is unclear, and do not feel rushed into making a decision.

Study Background

The purpose of this study is to assess whether vestibular stimulation can enhance the ability to make temporal auditory judgements. The technique we will use is called Galvanic Vestibular Stimulation. This involves applying gentle electrical currents to parts of the scalp behind the ears. Galvanic vestibular stimulation is able to engage various brain structures without direct contact and using currents which are so small that you cannot feel them.

Do I have to take part?

No. It is up to you to decide whether or not to take part. If you do, you will be given this information sheet to keep and will be asked to sign a consent form. You are still free to withdraw at any time without giving a reason.

What will happen to me if I take part?

Firstly, we need to double-check that you are eligible to participate:
This is a clinical trial; therefore, you need to have an official diagnosis from a professional for ADHD or dyslexia. Secondly, we are going to ask you a number of questions to make sure you can receive GVS. Such as:

1. Are you currently pregnant?
2. Do you have any history of neurological conditions (e.g., seizure/convulsion, epilepsy, fainting/syncope, brain injury)?
3. Have you previously had any heart problems?
4. Do you have any problems with your hearing or your balance?
5. Do you have any permanent hair accessories (i.e., weave, cornrows, toupees, extensions)?

Then you will be tested for normal hearing. Pure-tone audiometry is a behavioural test used to measure hearing sensitivity. If eligible, we will begin by gently rub the scalp with a gel to remove any dead skin and ensure good conductivity. This might induce some redness and/or a feeling of warmth. We will then apply two GVS electrodes to the skin (which look like simple auto-adhesive plasters). Then be asked to complete four simple auditory tasks and one memory task with and/ or without stimulation. At the end of the experiment, the aims of the study will be fully explained to you, and any questions which you might have will be answered.

What are the side effects?

The stimulation may cause you to experience temporary sensations of dizziness or tingling/ itching/ warmth. There is also a small risk of burn at the electrode sites if they become detached for a prolonged period. To prevent this, we will check that they are properly attached at several points throughout the experiment. Although the risk is small, other unexpected or previously unreported side effects may also occur. If you have unusual sensations or side effects, then you should inform one of the experimenters straight away. If any side effects appear later after you have left, please get in touch again.

What are the possible benefits of taking part?

Your contribution to this project will help enhance knowledge about Galvanic Vestibular Stimulation in a controlled environment. You may also learn something new about your own thinking skills.

What if there is a problem?

If you require further information relating to the study or you have a concern about any aspect of the study, then you can email Saghi Arabi, PhD student, sa813@kent.ac.uk. If you remain unhappy and wish to complain formally, you can do this through the Chair of the University of Kent School of Psychology ethics committee on 01227 824775.

Will my taking part in this study be kept confidential?

Information collected for the purpose of this research study will be kept confidential as required by law. Your study records will be held in password-protected computer programs and locked file cabinets to which only the study investigators can access. All data forms will bear a study number in place of your name. All personal data will be destroyed after one year. The results of this study will be used to determine whether our neurostimulation treatment interacts with different cognitive functions.

The results of the present study may be published for scientific purposes, but your records or identity will not be revealed.

Who has reviewed this study?

This study was given a favourable ethical opinion for conduct by the ethics committee of the University of Kent, School of Psychology.

We thank you for taking the time to read this sheet. If you decide to participate in the study, then you will receive a copy of this Information Sheet and the consent form that you must later sign.

2) Screening

Age (years):

Biological sex: Male Female

Do you have epilepsy, or have you had seizures/convulsions?

- Yes
- No

Have you ever had a brain injury (with loss of consciousness)?

- Yes
- No

Have you ever had neurosurgery (including brain or spinal cord)?

- Yes
- No

Do you have hearing problems or ringing in your ears?

- Yes
- No

Do you have any metal in your body, such as shrapnel, surgical clips or fragments from welding or metalwork?

- Yes
- No

Do you have a diagnosis of ADHD or dyslexia?

- Yes
- No

3) Self-reported perception of Galvanic Vestibular Stimulation

Please help us to understand your perceptions of the stimulation that you received.

Q1) How strong was the sensation of the stimulation?

- I could not feel anything at all.
- Slight sensation, but unsure if it was the result of the stimulation
- Felt a definite sensation of being stimulated
- A strong feeling of being stimulated
- Currents were too strong; stimulation was overpowering.

Q2) What did the stimulation feel like?I could not feel anything at all

- A brief pulsating sensation behind the ears
- A continuous sensation or wave of activity behind the ears

Q3) If you felt any sensation throughout the experiment, how often did you notice the stimulation?

Q4) If you felt any sensation throughout the experiment, did you notice any patterns in the stimulation?

Q5) If you felt any sensation, in which of the test blocks did you feel it (tick all that apply)?

First block

Second block

Third block

Fourth block

4) **Debriefing sheet**

This study was an investigation into the relationship between the vestibular system and temporal predictions in visual attention. Participants completed a visual discrimination experiment, which was asked to make visual judgments. At the same time, vestibular signals were induced via gentle galvanic stimulation on the part of the scalp overlying the vestibular nerves. In one condition, they have received galvanic signals, while in the other condition, no galvanic signal was delivered at all. We hope to show that judgments of the auditory stimuli were quicker and more accurate when they received vestibular signals compared to the 'no stimulation' conditions. If so, then it will tell us that visual attention processes information from complementary signals in the vestibular system.

Should you have any concerns or questions, please feel free to contact the researcher, Saghi Arabi, PhD student, at sa813@kent.ac.uk. If you remain unhappy and wish to complain formally, you can do this through the Chair of the University of Kent School of Psychology ethics committee on 01227 824775.

Appendix B

Chapter 2 Tables

Stim	Offset (I)	Offset (J)	t value	df	Sig.	95% CI	
						Lower Bound	Upper Bound
GVS	3.2	3.6	0.000	21	1	-0.004	0.003
		4	-2.800	21	0.118	-0.03	0.002
		4.4	-2.583	21	0.173	-0.069	0.007
		4.8	-2.727	21	0.153	-0.066	0.006
	3.6	4	-2.800	21	0.109	-0.029	0.002
		4.4	-2.583	21	0.172	-0.068	0.006
		4.8	-2.727	21	0.151	-0.065	0.005
	4	4.4	-2.429	21	0.347	-0.04	0.007
		4.8	-2.286	21	0.324	-0.038	0.006
	4.4	4.8	1.000	21	1	-0.003	0.005
No Stim	3.2	3.6	1.000	21	1	-0.002	0.005
		4	-1.000	21	1	-0.016	0.008
		4.4	-1.286	21	1	-0.032	0.014
		4.8	-1.286	21	1	-0.032	0.014
	3.6	4	-1.250	21	1	-0.019	0.008
		4.4	-1.250	21	1	-0.035	0.014
		4.8	-1.250	21	1	-0.035	0.014
	4	4.4	-1.250	21	1	-0.018	0.007
		4.8	-1.250	21	1	-0.017	0.007
	4.4	4.8	0.000	21	1	-0.003	0.003

Table B.2.1: post-hoc statistical analysis of pairwise comparisons breaking down interaction by Offset. E2, response time

Stim	Offset (I)	Offset (J)	t value	df	Sig.	95% CI	
						Lower bound	Upper bound
Active GVS	3.2	3.6	0.780	23	1.000	-0.043	0.072
		4	-0.868	23	1.000	-0.038	0.022
		4.4	-4.807	23	0.001	-0.208	-0.045
		4.8	-5.579	23	<.001	-0.181	-0.052
	3.6	4	-1.136	23	1.000	-0.085	0.040
		4.4	-4.143	23	0.004	-0.246	-0.035
		4.8	-4.267	23	0.003	-0.226	-0.036
	4	4.4	-4.959	23	0.001	-0.226	-0.044
		4.8	-5.917	23	<.001	-0.165	-0.051

	4.4	4.8	0.474	23	1.000	-0.055	0.075
No Stim	3.2	3.6	0.212	23	1.000	-0.035	0.040
		4	-1.299	23	1.000	-0.091	0.037
		4.4	-3.865	23	0.008	-0.124	-0.013
		4.8	-4.222	23	0.003	-0.161	-0.024
	3.6	4	-1.525	23	1.000	-0.089	0.030
		4.4	-4.348	23	0.002	-0.122	-0.021
		4.8	-4.206	23	0.003	-0.165	-0.025
	4	4.4	-2.743	23	0.116	-0.089	0.006
		4.8	-3.983	23	0.006	-0.117	-0.014
	4.4	4.8	-1.918	23	0.676	-0.063	0.015

Table B.2.2: post-hoc statistical analysis of pairwise comparisons for E6, response time

Stim	**Offset (I)**	**Offset (J)**	**t value**	**df**	**Sig.**	**95% CI**	
						Lower bound	Upper bound
Active GVS	3.2	3.6	0.197	23	1.000	-4.909	5.576
		4	5.267	23	<.001	4.691	18.155
		4.4	4.946	23	0.001	9.348	40.860
		4.8	5.992	23	<.001	13.785	43.420
	3.6	4	4.528	23	0.002	3.487	18.692
		4.4	4.523	23	0.002	7.771	41.770
		4.8	5.580	23	<.001	12.543	43.995
	4	4.4	3.694	23	0.012	2.187	25.176
		4.8	4.832	23	0.001	6.144	28.215
	4.4	4.8	1.800	23	0.849	-2.533	9.530
No Stim	3.2	3.6	-0.970	23	1.000	-7.657	4.011
		4	1.567	23	1.000	-3.231	9.817
		4.4	1.501	23	1.000	-4.641	13.335
		4.8	3.277	23	0.033	0.465	17.172
	3.6	4	2.957	23	0.071	-0.254	10.486
		4.4	2.657	23	0.141	-1.038	13.379
		4.8	4.860	23	0.001	3.844	17.439
	4	4.4	0.475	23	1.000	-5.841	7.950
		4.8	3.098	23	0.051	-0.011	11.063
	4.4	4.8	3.483	23	0.020	0.487	8.456

Table B.2.3: post-hoc statistical analysis of pairwise comparisons for E6, response accuracy

Chapter 3 Tables

Stim	Offset	Offset	t value	Sig.	95% CI	
					Lower Bound	Upper Bound
Active GVS	3.2	3.6	0.975	1.000	-3.849	7.374
		4	3.787	0.010	1.128	11.372
		4.4	10.396	<.001	15.175	28.095
		4.8	14.322	<.001	24.352	37.828
	3.6	4	1.922	0.670	-2.759	11.733
		4.4	8.965	<.001	12.992	26.752
		4.8	10.752	<.001	20.860	37.793
	4	4.4	9.592	<.001	10.406	20.363
		4.8	15.490	<.001	19.862	29.817
	4.4	4.8	6.627	<.001	5.027	13.884
No Stim	3.2	3.6	-3.278	0.033	-9.984	-0.272
		4	2.282	0.321	-1.385	9.078
		4.4	8.676	<.001	14.100	29.810
		4.8	10.410	<.001	17.658	32.662
	3.6	4	5.934	<.001	4.280	13.668
		4.4	12.881	<.001	20.557	33.610
		4.8	15.385	<.001	24.178	36.399
	4	4.4	9.252	<.001	12.033	24.184
		4.8	10.704	<.001	15.133	27.495
	4.4	4.8	1.872	0.739	-2.108	8.518

Table B.3.1: post-hoc statistical analysis of pairwise comparisons for E9, response accuracy

Stim	(I) Offset	(J) Offset	t value	Sig.	95% CI	
					Lower Bound	Upper Bound
Active GVS	3.2	3.6	0.129	1	-4.784	5.196
		4	6.166	<.001	6.072	18.64
		4.4	5.140	<.001	9.016	37.229
		4.8	5.983	<.001	12.628	40.433
	3.6	4	4.653	0.001	3.964	20.336
		4.4	4.438	0.002	6.725	39.108
		4.8	5.302	<.001	10.757	41.892
	4	4.4	3.463	0.023	1.02	20.514
		4.8	4.644	0.001	4.606	23.743
	4.4	4.8	1.999	0.587	-1.936	8.752

No Stim	3.2	4	4.208	0.004	1.534	10.51
		4.4	2.527	0.196	-1.158	10.781
		4.8	5.252	<.001	4.27	16.915
	3.6	3.2	0.148	1	-2.963	3.258
		4	7.880	<.001	3.716	8.623
		4.4	2.423	0.246	-1.46	11.378
		4.8	5.480	<.001	4.594	16.886
	4	4.8	2.326	0.301	-1.59	10.731
	4.4	4	0.542	1	-5.788	8.209
		4.8	3.654	0.015	0.82	10.741

Table B.3.2: Post-hoc statistical analysis of pairwise comparisons for E9, response accuracy

Chapter 4 Tables

Lag	(I) Stim	(J) Stim	t value	Sig.	95% CI	
					Lower Bound	Upper Bound
1	Async (12 Hz)	Sync (10 Hz)	3.212	0.009	0.022	0.189
	Async (12 Hz)	No stim	2.160	0.126	-0.01	0.118
	No stim	Sync (10 Hz)	1.333	0.573	-0.046	0.15
3	Sync (10 Hz)	Async (12 Hz)	1.917	0.201	-0.015	0.108
	Sync (10 Hz)	No stim	2.125	0.119	-0.009	0.111
	Async (12 Hz)	No stim	0.227	1	-0.05	0.059
8	Sync (10 Hz)	Async (12 Hz)	3.000	0.017	0.013	0.16
	Sync (10 Hz)	No stim	1.333	0.566	-0.045	0.149
	No stim	Async (12 Hz)	0.946	1	-0.059	0.128

Table B.4.1: Post-hoc statistical analysis of pairwise comparisons for RSVP-1 showing between stimulation conditions at each Lag level

Stim	(I) Lag	(J) Lag	t value	Sig.	95% CI	
					Lower Bound	Upper Bound
Sync (10 Hz)	1	3	7.171	<.001	0.191	0.397
	1	8	1.245	0.666	-0.062	0.184
	8	3	5.419	<.001	0.124	0.342
Async (12 Hz)	1	3	14.867	<.001	0.37	0.522
	1	8	5.163	<.001	0.129	0.378
	8	3	5.216	<.001	0.101	0.285
No Stim	1	3	11.343	<.001	0.309	0.486
	1	8	3.000	0.014	0.027	0.302
	8	3	6.657	<.001	0.144	0.321

Table B.4.2: Post-hoc statistical analysis of pairwise comparisons for RSVP-1 showing comparisons between levels of Lag at each Stimulation condition

Lag	(I) Stim	(J) Stim	t value	Sig.	95% CI	
					Lower Bound	Upper Bound
1	12 Hz (Async)	10 Hz (Sync)	3.174	0.007	0.017	0.13
	12 Hz (Async)	No Stim	2.737	0.024	0.005	0.098
	No Stim	10 Hz (Sync)	0.786	1	-0.047	0.091
3	10 Hz (Sync)	12 Hz (Async)	2.167	0.085	-0.004	0.083
	10 Hz (Sync)	No Stim	2.474	0.052	0	0.094
	12 Hz (Async)	No Stim	0.438	1	-0.032	0.046
8	10 Hz (Sync)	12 Hz (Async)	2.059	0.142	-0.008	0.078
	10 Hz (Sync)	No Stim	1.565	0.364	-0.02	0.093
	12 Hz (Async)	No Stim	0.042	1	-0.057	0.059

Table B.4.3: Post-hoc statistical analysis of pairwise comparisons for RSVP-1& RSVP-3 showing between Stimulation conditions at each Lag level

Stim	(I) Lag	(J) Lag	t value	Sig.	95% CI	
					Lower Bound	Upper Bound
10 Hz (Sync)	1	3	10.300	<.001	0.234	0.383
	1	8	2.788	0.02	0.011	0.172
	8	3	8.346	<.001	0.153	0.281
12 Hz (Async)	1	3	16.192	<.001	0.358	0.485
	1	8	5.882	<.001	0.115	0.284
	8	3	10.091	<.001	0.168	0.275
No Stim	1	3	14.500	<.001	0.313	0.441
	1	8	3.921	<.001	0.056	0.242
	8	3	9.120	<.001	0.167	0.288

Table B.4.4: Post-hoc statistical analysis of pairwise comparisons for RSVP-1 and RSVP-3 showing comparisons between levels of Lag at each Stimulation condition

Appendix C

ID	Orientation (degrees)	Phase (cycles)	Spatial frequency (Cycles per pixel)
1	130	0	0.044
2	160	0	0.09
3	-110	0	0.07
4	90	0	0.02
5	90	0	0.055
6	-110	0	0.055
7	-110	0	0.057
8	130	0	0.055
9	-140	0	0.055
10	-110	0	0.066
11	-110	0	0.04
12	180	0	0.066
13	180	0	0.055
14	160	0	0.044
15	-140	0	0.03
16	-140	0	0.09
17	90	0	0.07
18	130	0	0.06
19	130	0	0.052
20	155	0	0.09
21	-140	0	0.05
22	90	0	0.052

23	-110	0	0.05
24	130	0	0.03
25	130	0	0.09
26	180	0	0.07
27	160	0	0.055
28	90	0	0.04
29	-110	0	0.044
30	-110	0	0.09
31	180	0	0.04
32	155	0	0.055

Figure C.1.1: Properties of the 32 Gabor patches used in visual modality experiments.

Appendix D

Participant ID		Block_1	Block_2	Block_3
1	25	No stimulation	Main (10 Hz)	Async (12 Hz)
2	26	Main (10 Hz)	Async (12 Hz)	No stimulation
3	27	Async (12 Hz)	No stimulation	Main (10 Hz)
4	28	No stimulation	Main (10 Hz)	Async (12 Hz)
5	29	Main (10 Hz)	Async (12 Hz)	No stimulation
6	30	Async (12 Hz)	No stimulation	Main (10 Hz)
7	31	No stimulation	Main (10 Hz)	Async (12 Hz)
8	32	Main (10 Hz)	Async (12 Hz)	No stimulation
9	33	Async (12 Hz)	No stimulation	Main (10 Hz)
10	34	No stimulation	Main (10 Hz)	Async (12 Hz)
11	35	Main (10 Hz)	Async (12 Hz)	No stimulation
12	36	Async (12 Hz)	No stimulation	Main (10 Hz)
13	37	No stimulation	Main (10 Hz)	Async (12 Hz)
14	38	Main (10 Hz)	Async (12 Hz)	No stimulation
15	39	Async (12 Hz)	No stimulation	Main (10 Hz)
16	40	No stimulation	Main (10 Hz)	Async (12 Hz)
17	41	Main (10 Hz)	Async (12 Hz)	No stimulation
18	42	Async (12 Hz)	No stimulation	Main (10 Hz)
19	43	No stimulation	Main (10 Hz)	Async (12 Hz)
20	44	Main (10 Hz)	Async (12 Hz)	No stimulation
21	45	Async (12 Hz)	No stimulation	Main (10 Hz)
22	46	No stimulation	Main (10 Hz)	Async (12 Hz)

23	47	Main (10 Hz)	Async (12 Hz)	No stimulation
24	48	Async (12 Hz)	No stimulation	Main (10 Hz)

Figure D.1.1: Counterbalancing Latin square.