School of Population Health

Exploring the Visual-Tactile Temporal Binding Window and Multisensory Influences on Sensorimotor Synchronization

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This thesis is presented for the Degree of Doctor of Philosophy - Psychology of Curtin University

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Declaration

To the best of my knowledge and belief this thesis contains no material previously published by any other person except where due acknowledgment has been made.

This thesis contains no material which has been accepted for the award of any other degree or diploma in any university.

Human Ethics (For projects involving human participants/tissue, etc)

The research presented and reported in this thesis was conducted in accordance with the National Health and Medical Research Council National Statement on Ethical Conduct in Human Research (2007) – updated March 2014. The proposed research study received human research ethics approval from the Curtin University Human Research Ethics Committee (EC00262), Approval Number HRE2018-0257.

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Article 2: Tactile Cues are More Intrinsically Linked to Motor Timing than Visual Cues i	n
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General Abstract

Moving around in our environment involves a complex interplay between sensory and motor functions. Each of these functions involves a subset of sensory-specific and motor-specific processes that both contribute to sensorimotor integration. In this thesis, I focus on a sensoryspecific process, known as the temporal binding window for multisensory integration, which refers to the period in which sensory information is bound into a single percept and attributed to an event in the environment. I also focus on a sensorimotor process known as sensorimotor synchronization, which involves synchronizing movement with incoming sensory information, a skill which is utilized frequently in our daily lives (e.g., playing sport or driving a car). Although there is a breadth of research characterizing the audio-visual temporal binding window, substantially less is known about the visual-tactile window. Specifically, there are few studies examining the width of the visual-tactile temporal binding window and the neural activity associated with the visual-tactile simultaneity task.

Chapter two of this thesis characterizes the width of the visual-tactile temporal binding window, as measured by the simultaneity judgment task. Then, chapter three uses electroencephalography to investigate functional connectivity between unisensory and multisensory neural regions during the simultaneity judgment task. It is important to characterize the width of the visual-tactile temporal binding window and functional connectivity between sensory regions involved in integrating these stimuli as visual-tactile information is crucial for motor control. I found the temporal binding window was significantly narrower when visual stimuli were presented before tactile stimuli (visualtactile) compared to tactile-visual stimuli. The functional connectivity results revealed connectivity was stronger between central-occipital and parietal-central sites when stimuli were perceived as non-simultaneous across theta, alpha and beta frequencies, whereas between parietal-occipital sites non-simultaneous perception was only stronger in the beta frequencies. We infer from our findings that stronger connectivity in theta and alpha

frequencies reflects the encoding of temporal differences between the cross-modal stimuli, and activity in the beta frequency reflects a violation of expectation that the stimuli will be simultaneous, conveying both feed forward and feedback information about the simultaneity status of cross-modal stimuli. Within these chapters, I examine the relationship between the width of the visual-tactile temporal binding window and autistic traits, sensory sensitivity, and unusual sensory experiences. In both chapters, I did not find evidence to suggest a relationship between these constructs in a neurotypical population.

Given the tight coupling of sensory and motor control, it is likely that the efficacy of temporal sensory binding is related to the successful execution of motor skills. Therefore, chapter four investigates unisensory and multisensory sensorimotor synchronization. Chapter four contains two experiments, Experiment 1 investigates sensorimotor synchronization with unimodal and cross-modal visual-tactile stimuli, and the relationship between sensorimotor synchronization and the width of the visual-tactile temporal binding window. Experiment 2 examines temporal error in sensorimotor synchronization between cross-modal stimuli presented inside the temporal binding window, and when one stimulus in the cross-modal pair is presented inside the window and the second stimulus presented outside the window. Across both experiments, I found that sensorimotor synchronization variability and temporal error was lower when participants moved in synchrony with cross-modal stimuli, compared to unimodal, and this effect was stronger for tactile-visual stimuli, than visual-tactile stimuli. These results suggest that in a finger-tapping sensorimotor synchronization task, tactile stimuli, whether presented as a unisensory stimulus or as part of a cross-modal pair, are weighted more reliably than visual stimuli.

Overall, this thesis offers novel insights into the visual-tactile temporal binding window by characterizing the width of the visual-tactile window and showing that functional connectivity between unisensory and multisensory neural regions is important for simultaneity perception in the simultaneity judgment task. Additionally, I established a link

between the temporal binding window and the temporal accuracy of motor execution in sensorimotor synchronization tasks, which is a unique contribution to this field of research. These findings contribute to advancing our understanding of sensory and motor integration. More specifically, they establish a foundation for studying the visual-tactile temporal binding, functional connectivity, and sensorimotor synchronization in populations with sensorimotor difficulties, such as individuals with autism.

COVID-19 Impact Statement

The COVID-19 pandemic impacted the direction of the research in this thesis. Prior to the pandemic, the studies contained in chapter two and three were conducted to understand the visual-tactile temporal binding window in neurotypical individuals and to establish appropriate protocols to replicate the studies in people with Autism Spectrum Disorder (ASD). The beginning of the pandemic in Australia coincided with the start of my maternity leave (March 2020), and when I returned from leave 6-months later there were restrictions in place from the University regarding conducting experimental studies in clinical populations. Unfortunately, these restrictions meant that I was unable to conduct experimental research in ASD and needed to develop an alternative third study. As an alternative study, we developed two experiments to thoroughly investigate the influence of unisensory and multisensory information on sensorimotor synchronization performance, including when stimuli are presented inside and outside the temporal binding window, and the relationship between the temporal binding window and sensorimotor synchronization.

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List of Abbreviations

ASD	Autism Spectrum Disorder
AQ	Autism Quotient
CNS	Central Nervous System
dWPLI	Debiased Weighted Phase Lag Index
EEG	Electroencephalography
GSQ	Glasgow Sensory Questionnaire
IAF	Individual Alpha Frequency
ISI	Interstimulus interval
LMM	Linear Mixed Model
MLE	Maximum Likelihood Estimation
MUSEQ	Multi-modality Unusual Sensory Experiences Questionnaire
SMS	Sensorimotor Synchronization
SOA	Stimulus Onset Asynchrony
TBW	Temporal Binding Window
TT-TBW	Tactile-Tactile Temporal Binding Window
TV-TBW	Tactile-Visual Temporal Binding Window
VT-TBW	Visual-Tactile Temporal Binding Window
VV-TBW	Visual-Visual Temporal Binding Window

Chapter 1: General Introduction

1.1 Introduction

Imagine yourself at the beach. You can feel the sand between your toes as you walk towards the ocean. Your feet touch the water; you wade in past your knees and eventually dive under an oncoming wave. You feel the cold water surround you as you swim across the ocean surface. You hear the waves crashing on the shore and smell the salt water in the air. This beach encounter involves a multitude of sensory and motor experiences, such as walking and feeling the sand, the sensation of water temperature and its level on your body, diving under the wave and swimming to the surface. These sensorimotor control processes play a key role in shaping your overall perception.

Sensorimotor control refers to the tightly coupled relationship between sensory input and motor function (Franklin & Wolpert, 2011; Todorov, 2004). Within this complex relationship, sensory information from various modalities is processed and integrated in unisensory and multisensory neural regions. The integrated multisensory information is transmitted to motor areas of the brain involved in planning, preparing, and executing actions. This dynamic interplay between sensory and motor processes is fundamental to our ability to perform a wide range of everyday activities, from basic movements (e.g., grasping a cup), to complex tasks requiring precise coordination (e.g., driving a car). The term 'sensorimotor' somewhat oversimplifies the individual 'sensory' and 'motor' components that contribute to sensorimotor control. Specifically, sensory components involve sensory perception, processing and integration of unisensory and multisensory experiences. This thesis will focus on two key components of sensorimotor control, 1) the temporal binding window for multisensory integration, and 2) motor execution in sensorimotor synchronization tasks (discussed later). There are various complementary theoretical models that seek to explain the sensory and motor processes involved in the temporal binding window and sensorimotor synchronization. These models include the linear phrase correction model, the maximum likelihood estimation model, causal inference, Bayesian causal inference and predictive

coding (see Figure 1.1). It is important to note that these models provide different perspectives for understanding how various sensory inputs and motor responses are integrated and processed by the CNS to optimize motor performance. Each model brings a unique lens through which one can examine and explain the complex interplay of sensory perception, motor planning, and execution.



Figure 1.1. This figure shows the various theoretical models that seek to explain sensorimotor control. Specifically, it illustrates the temporal binding window (TBW) and sensorimotor synchronization (SMS).

The linear phase correction model posits that the central nervous system (CNS) aligns our actions with incoming sensory information (Schulze & Vorberg, 2002). When the brain detects a discrepancy in the timing of the action and the sensory information, the (CNS) phase shifts the timing of the action to align the action with the sensory information, thereby reducing error. Building on this model, the maximum likelihood estimation (MLE) model assigns weights to sensory cues, which provides an estimate of the unisensory and/or multisensory stimuli in the environment (Alais & Burr, 2004; Ernst & Banks, 2002). The multisensory estimates are assigned higher weights than unisensory stimuli, leading to higher reliability for multisensory stimuli that are used by the motor system to plan and execute actions. Extending the MLE model, causal inference and Bayesian causal inference models suggest that the brain combines information from multiple sensory modalities in the environment with prior knowledge to make predictions about the common cause of the sensory information (Körding et al., 2007; Parise et al., 2012). This 'prior' would have already been weighted by the CNS based on internal and external feedback about the success of an action. Bayesian causal inference models use the 'prior' to determine whether the multisensory cues arise from the same causal source, and assign a probability to the likelihood of the sources (Kayser & Shams, 2015; Körding et al., 2007; Körding & Wolpert, 2006). Linked to Bayesian causal inference, in predictive coding the 'prior' is used to make predictions about incoming sensory information (Friston & Kiebel, 2009). When sensory input conflicts with the prediction it creates a prediction error that is used to update the existing prior with the new information. The updated existing prior is used to improve the performance of future actions. Below is an example of how the above-mentioned models explain the sensory and motor components of a basketball player dribbling a ball down the court (See Figure 1.2).

	Example	Basketball player dribbles the ball down the court, with opposition players attempting to intercept the ball. The player passes the ball to another team member before the ball is intercepted.
	Linear phase	The player adjusts and temporally aligns the movement
	correction	and force of their hand and arm with the speed and
		and force of their hand and and and with the speed and $\frac{1}{2}$
	model	velocity of the ball to effectively dribble the ball down the
		court. They use sensory feedback to temporally adjust the
		action and relies on the integration of, and feedback from,
		sensory and motor processes.
	Maximum	Visual, tactile, proprioceptive, and auditory cues provide
	likelihood	information about proximity between the player and the
	estimation	ball, and the success of the dribbling action. The sensory
	model	cues are assigned a weight according to their reliability
Multiple		estimate (e.g. in effectively dribbling the ball)
theoretical	Causal	Player dribbling the ball identifies if there is a common
frameworks	inference	source for the sensory cues/signals. Sensory cues arising
underlie the	micrenee	from the same source are combined/integrated into a
coupling of		non the same source are combined/integrated into a
		perceptual whole. This process is useful to help the player
multisensory		differentiate between various cross-modal percepts, such
integration		as the difference between the sight, sound and feeling of
and motor		the ball bouncing, and the sight and sound of an
execution		opposition player running nearby. These individual cross-
		modal percepts with the same causal source are crucial for
		focused actions during the game.
	Bayesian	During a fast-paced dribble down the court, a basketball
	causal	player combines visual and proprioceptive information to
	inference	anticipate an opposition player's attempt to block the
		dribble. Current reliability estimates form the players prior
		belief. This 'prior' is updated with new sensory
		information/feedback as the game unfolds, known as the
		'likelihood'. Based on the likelihood, the player decides to
		pass the ball to another player.
	Predictive	Player dribbling the ball anticipates and predicts the
	coding	incoming multisensory information that is likely to arise
	8	(based on their prior) from dribbling the ball. When the
		sensory information aligns with their predictions, the brain
		minimises prediction error which reinforces the existing
		nrior When the sensory information is unexpected for
		avample, when an opponent player upovportedly tries to
		example, when an opponent player unexpectedly tries to
		intercept the ball, the prediction error increases. The
		player uses this unexpected information to update the
		existing prior, which allows for more accurate predictions
		and motor responses as the game continues.

Figure 1.2: This figure shows the complementary theoretical models underlying multisensory integration (i.e., the temporal binding window) and motor execution in an example of a basketball player engaged in dribbling a ball.

The different models described above and in Figure 1.2 emphasize different aspects of the sensory and motor processes involved in a basketball player's action, illustrating the complex and multifaceted nature of sensorimotor integration. They are not mutually exclusive and instead provide complementary frameworks to understand sensorimotor

integration. These models are discussed later in this thesis when discussing experimental results in chapter four and the General Discussion of the thesis.

1.2 Measuring the Temporal Binding Window

The sensation of being at the beach is created by quickly integrating multisensory stimuli from the environment within a brief time-window and attributing the stimuli to the perceptual experience of being at the beach. This time-window is referred to as the temporal binding window (TBW) for multisensory integration. Multisensory information received within the TBW is bound —or rather, integrated— into a single percept and attributed to an event in the environment (Powers et al., 2009; Spence & Squire, 2003; Vroomen & Keetels, 2010). Thus, binding multisensory information from our surroundings across the TBW helps form our everyday perceptual experiences.

The TBW is typically measured using the simultaneity judgment task (Powers et al., 2009; Spence & Squire, 2003). In the simultaneity judgment task, two sensory stimuli are presented simultaneously and at various stimulus onset asynchronies (SOAs). After presentation of the two stimuli, participants are asked "were the stimuli simultaneous?" and they respond yes or no (see Figure 3; Vroomen & Keetels, 2010). For each participant, the number of simultaneous responses for each SOA is calculated, plotted on a distribution and a psychometric function (e.g., Gaussian or sigmoid) is fitted to the data (Costantini et al., 2016; Hillock-Dunn & Wallace, 2012; Hillock et al., 2011; Migliorati et al., 2020; Moro & Steeves, 2018; Noel et al., 2016; Noel et al., 2017a; Powers et al., 2009; Stevenson et al., 2018; Stevenson et al., 2014a; Stevenson & Wallace, 2013; Venskus et al., 2021) – this is referred to as the rate of perceived simultaneity. The rate of perceived simultaneity is then averaged across a group to determine the average width of the TBW (see Figure 1.3 bottom). However, the exact method for determining the width of TBW after fitting the data varies across studies. For example, the 50% rate of perceived simultaneity (Ikeda & Morishita, 2020;

Stevenson & Wallace, 2013; Stevenson et al., 2012b), the 75% ("3/4 maximum") rate of perceived simultaneity (Butera et al., 2018; De Niear et al., 2018; Dunham et al., 2020; Feldman et al., 2020; Hillock-Dunn & Wallace, 2012; Hillock et al., 2011; Peter et al., 2019; Venskus et al., 2021; Wallace & Stevenson, 2014), and the standard deviation of the curve of the distribution (Borgolte et al., 2021; Donohue et al., 2012; Ikumi et al., 2019; Noel et al., 2017b; Tagini et al., 2020; Vroomen & Keetels, 2010) have all been used to determine the width of the TBW.





Figure 1.3: The top image shows the layout of the trials for the simultaneity judgment task. The bottom image shows how the temporal binding window can be calculated from the simultaneity judgment task.

This chapter contains a brief review of studies that have used the simultaneity judgment task to examine the width of the TBW for simple and complex sensory stimuli, along with changes in the size of the window that occur with aging and in neurodiverse populations. Then, I will examine research using electroencephalography (EEG) to measure neural activity associated with the simultaneity judgment task. A considerable amount of research has focused on the aforementioned aspects of the TBW in the audio-visual domain, with limited knowledge gained about these aspects in the visual-tactile domain. This thesis aims to bridge this gap by characterizing the size of the visual-tactile TBW and investigating neural activity occurring during and immediately after stimulus presentation in the visualtactile simultaneity judgement task. In this chapter, I will also discuss the relationship between the visual-tactile TBW and sensorimotor synchronization.

Sensorimotor synchronization is an important cognitive and neural process that involves anticipating the timing of incoming sensory stimuli from our environment and synchronising our own movement with the stimuli (Mates et al., 1994). For example, in the context of tennis, an athlete needs to observe the flight of the ball, predict its velocity and the timing of its arrival at the point of interception, and synchronize the movement of their body with the ball's trajectory to effectivity return the serve to their opponent. Given that our ability to interact with our environment relies on using multisensory information from our environment, it is likely that the time-range in which multisensory stimuli is integrated across (i.e., the width of the TBW) influences the temporal accuracy of movement execution, particularly in sensorimotor synchronization tasks. Despite the integral role that visual-tactile information plays in motor control, there are limited studies examining sensorimotor synchronization with visual-tactile stimuli. Additionally, the relationship between synchronization performance and the size of the visual-tactile TBW remains under explored. This thesis investigates visual-tactile sensorimotor synchronization performance with unimodal and cross-modal stimuli. These stimuli are presented both inside and outside the TBW. Additionally, it explores the relationship between sensorimotor synchronization and the width of the visual-tactile TBW.

1.3 Examining the temporal binding window for audio-visual integration.

The simultaneity judgment task has been widely used to characterize the size of the TBW for audio-visual integration (See Reviews Sanders et al., 2019; Zhou et al., 2020). To measure the TBW, studies have used stimuli of varying complexities (Ikeda & Morishita, 2020; Johnston et al., 2022; Stevenson & Wallace, 2013; Stevenson et al., 2012b), altered the spatial, temporal and visual field components of the stimuli (Noel et al., 2018a; Opoku-Baah & Wallace, 2021; Stevenson et al., 2012a; Takeshima, 2021; Van der Stoep et al., 2020), and measured age-related changes in the size of the TBW (Hillock-Dunn & Wallace, 2012; Hillock et al., 2011; Stevenson et al., 2018). Further, research continues to measure the audio-visual TBW in various clinical populations and uses perceptual training and neurophysiological techniques to alter the width of the audio-visual TBW.

1.3.1 Stimulus complexity.

Stimulus complexity in audio-visual simultaneity judgment tasks influences the size of the TBW. When complex audio-visual stimuli are presented, the TBW is wider than when simple stimuli are presented (Vroomen & Keetels, 2010). A wider TBW indicates that multisensory information is integrated across a longer time-period, which provides an opportunity for relevant and irrelevant information to be bound together in a single percept (Wallace & Stevenson, 2014). The binding of irrelevant information can distort the perceptual accuracy of the relevant information, which can make it difficult for individuals with wider TBWs to interact with their environment (Iarocci & McDonald, 2006). Using simple stimuli, such as flashes and beeps presented for short durations (< 15 ms), research shows the width of the whole audio-visual TBW is on average between 320 ms and 390 ms (Johnston et al., 2022; Stevenson & Wallace, 2013; Stevenson et al., 2012b). This width is similar to other simple stimuli, such as the combined image and sound of a tool (e.g., the sight and sound of a hammer) presented at longer durations (1 sec), which showed the whole width was on average 317 ms (Stevenson & Wallace, 2013). For more complex stimuli, such as speech sounds, the width of the window is longer compared to simple stimuli. Speech sounds, presented at longer durations (2 sec), have produced a TBW that was approximately 461 ms (Stevenson & Wallace, 2013). However, the width of the TBW can vary between different types of complex stimuli. When comparing the size of the TBW between spoken sentences and melodies played on different musical instruments, the whole width of the window was substantially wider for sentences (400 ms) than for instruments (227 ms) (Ikeda & Morishita, 2020).

The size of the audio-visual TBW is also influenced by visual factors, including distance (Van der Stoep et al., 2020), visual field (Stevenson et al., 2012a; Takeshima, 2021), and binocular and monocular vision (Opoku-Baah & Wallace, 2021). When audio-visual stimuli are presented at a closer distance to an individual, the TBW is wider compared to when stimuli are presented further away (Noel et al., 2018a; Van der Stoep et al., 2020). As stimuli move from central to peripheral vision, simultaneity perception becomes less accurate (Stevenson et al., 2012a), which means the size of the TBW increases as stimuli move further into the periphery. These results combined indicate that the width of the TBW is malleable, and that stimulus complexity and location are just some of the factors that influence its width. In addition to these factors, development and ageing also influence the size of the TBW.

1.3.2 Age-related changes in the audio-visual temporal binding window.

The simultaneity judgment task has been used in populations from 5 to 80 years old to examine development changes in the width of the audio-visual TBW (Hillock-Dunn & Wallace, 2012; Hillock et al., 2011). It is worth noting that the current research has

predominantly focused on using simple audio-visual stimuli to examine developmental changes in the width of the TBW, rather than a variety of stimulus complexities. It is perhaps not too surprising that the width of the TBW is largest during the main developmental years - childhood and adolescence - with the width of the TBW ranging from an average of 399 to 413 ms for 9-14 year olds (Hillock-Dunn & Wallace, 2012; Hillock et al., 2011). In adulthood around 20-26 years old, the width of the TBW tends to narrow, with audio-visual windows ranging from 290-300 ms (Hillock-Dunn & Wallace, 2012; Hillock et al., 2011). However, it has been reported that the width of the TBW is at its narrowest around middle adulthood (40-59 years old), yet in older adulthood (60+ years) it is at a similar width as childhood and adolescents (Stevenson et al., 2018). These age-related changes in the size of the TBW indicate that the neural changes that occur during development and aging influence the binding of multisensory information.

1.4 Examining the temporal binding window for visual-tactile integration.

1.4.1 Stimulus complexity.

Despite the abundance of literature examining the audio-visual TBW, less is known about the visual-tactile TBW. Research using the simultaneity judgment task to measure the visual-tactile TBW has primarily used simple stimuli. Using a light emitting diode (LED) as a visual stimulus and electrical stimulation as a tactile stimulus in the simultaneity judgment task, research shows that the width of the whole TBW was on average 345 ms (visual leading:169 ms, tactile leading: 176 ms) (Migliorati et al., 2020). A further study using an LED and a supra-threshold solenoid tapper (Costantini et al., 2016) for tactile stimuli found the width of the visual-tactile TBW was around 200 ms (Costantini et al., 2016). However, it is somewhat difficult to interpret these results as it is unclear if the 200 ms estimate relates to the whole distribution, which includes both visual leading *and* tactile leading visual-tactile stimuli, or for half the distribution, which includes either visual leading *or* tactile leading visual-tactile stimuli. It is imperative that studies report whether the size of the TBW includes the whole or half the distribution to help us understand whether the leading sensory modality influences the size of the TBW.

1.4.2 Age-related changes in the visual-tactile temporal binding window.

When comparing the width of the visual-tactile TBW between children and adults, children have a much wider window compared to adults (Chen et al., 2018). Similar to the audio-visual TBW, the visual-tactile TBW is widest in younger children (~ 7 yrs old) and becomes narrower during development into early adolescents (~ 13 yrs old), and continues to narrow into early-middle adulthood (Chen et al., 2018). These developmental and age-related changes in the size of the visual-tactile TBW are consistent with the research with audio-visual stimuli. As such, it seems there are common underlying neural mechanisms associated with binding multisensory stimuli that change due to maturation, regardless of the sensory modality. Further, the narrowing of the TBW during childhood and adolescence indicates that multisensory integration is fine-tuned throughout development.

1.5 Clinical populations and the temporal binding window.

The simultaneity judgment task has been used to measure the audio-visual TBW in individuals with autism spectrum disorder (ASD) and schizophrenia. For both ASD and schizophrenia, the audio-visual TBW is wider compared to neurotypical controls (Noel et al., 2018b; Noel et al., 2018c; Stevenson et al., 2017; Wallace & Stevenson, 2014). For example, for simple flash beep stimuli, individuals with schizophrenia had an average TBW width of 550 ms, compared to controls who had an average TBW width of 240 ms (Stevenson et al., 2017). Similarly, for speech stimuli, individuals with schizophrenia had an average TBW width of 682 ms, compared to controls who had an average TBW width of 432 ms (Stevenson et al., 2017). The width of the TBW has been associated with symptoms of these conditions,

such that wider windows were associated with greater severity of hallucinations in schizophrenia (Stevenson et al., 2017), and social communication deficits in ASD (Stevenson et al., 2014a; Zhou et al., 2018). In contrast, some individuals with ASD demonstrate narrower TBWs than neurotypical individuals, and these narrower TBWs have been associated with higher attention to detail in ASD (Zhou et al., 2021b), which further supports the notion that symptoms of ASD are related to the size of the TBW. Despite the widespread use of the simultaneity judgment task to characterize the audio-visual TBWs in ASD and schizophrenia, there is minimal evidence characterizing the visual-tactile TBW in these populations. However, there is some evidence from alternative (yet similar) tasks, such as the rubber hand illusion and the temporal order judgment task, indicating that visual-tactile information is integrated is atypical in ASD (Cascio et al., 2012; Greenfield et al., 2015; Paton et al., 2012; Ropar et al., 2018; Wada et al., 2020). Hence, research using the simultaneity judgment task with visual-tactile stimuli is needed to establish whether the visual-tactile TBW is extended in these clinical populations. This thesis aims to address this gap by investigating the relationship between the width of the visual-tactile TBW and autistic traits in a neurotypical population. Further, I aim to investigate neural activity associated with the visual-tactile TBW by recording electroencephalography (EEG) during the simultaneity judgment task.

1.6 Electroencephalography and the simultaneity judgment task

Neural oscillations play important, yet different, roles in facilitating the integration of sensory information from different modalities. In the context of multisensory integration, activity in the lower frequency bands, such as theta (4-7 Hz) and alpha (7-12 Hz), is associated with maintaining attention on relevant stimuli, encoding the temporal components of sensory information (Alais et al., 2010; Keil & Senkowski, 2018), and making predictions about the timing of sensory stimuli (Arnal & Giraud, 2012). Whereas, activity in higher

frequency bands, such as beta-low (12-20 Hz) and beta-high (20-30 Hz), is associated with identifying and processing the type of stimulus presented (Arnal & Giraud, 2012), and the feed-forward and feedback of information about characteristics of sensory information between various regions of the brain (Alais et al., 2010; Keil & Senkowski, 2018). Broadly, neural oscillations play various roles in cognitive function, which is also relevant for sensory integration and motor control. Oscillations in the theta frequency are important for memory and encoding new information, particularly the spatial and temporal aspects of stimuli (Klimesch, 1999; Korotkova et al., 2018), which are important for learning new motor skills and encoding sensory information. Alpha oscillations are thought to be associated with longterm memory, that is, searching and retrieval information from memory (Klimesch, 1999), which aids in motor planning and execution. Higher frequency activity (12-20 Hz) in the beta-band range is associated with motor control, including the prediction, preparation and execution of actions, and processing sensory information (Engel & Fries, 2010) and facilitating working memory processes (Schmidt et al., 2019). Gamma oscillations are typically associated with processing sensory stimuli from different sensory modalities (Başar et al., 2001; Fries, 2009). Despite the role gamma oscillations play in sensory processing, this thesis will only focus on theta, alpha and beta frequencies as these oscillations are involved in sensory and motor function, which is more relevant for this thesis. Although neural oscillations in different frequencies aid in integrating multisensory information (Senkowski et al., 2008), further investigation is needed to understand how functional connectivity affects multisensory integration (Keil & Senkowski, 2018), particularly for visual-tactile information during stimulus presentation. Chapter three aims to address this gap by measuring functional connectivity across frequencies ranging from 4-30 Hz during and immediately following stimulus presentation in a visual-tactile simultaneity judgment task. The purpose of this study is to examine the strength of functional connectivity between unisensory and multisensory regions to understand the role of connectivity in the perception of visual-tactile simultaneity.

1.6.1 Pre-stimulus neural activity

Simultaneity perception, that is, whether an individual perceives stimuli as occurring simultaneously even with a temporal delay, has been shown to be influenced by the state of the brain prior to the onset of the first stimulus. In particular, it has been shown that the speed of an individual's alpha oscillation (7-12 Hz) - known as individual alpha frequency (IAF) (Klimesch, 1999) - predicts whether stimuli will be perceived as simultaneous or nonsimultaneous. Previous research recorded EEG during the simultaneity judgment task to investigate whether IAF was associated with simultaneity perception (Bastiaansen et al., 2020; Ikumi et al., 2019; Migliorati et al., 2020; Yuan et al., 2016). For both audio-visual and visual-tactile stimuli, higher IAF (e.g., faster alpha oscillations) was related to narrower audio-visual and visual-tactile TBWs (Bastiaansen et al., 2020; Migliorati et al., 2020), which means participants are accurately able to distinguish between simultaneous and nonsimultaneous stimuli with high degrees of accuracy. Despite only examining pre-stimulus neural activity and not activity during the task, it seems that alpha oscillatory activity influences the width of the TBW. In addition to IAF, pre-stimulus alpha oscillatory phase and power has been shown to influence the perception of audio-visual simultaneity, as well as activity in beta and gamma frequencies.

Pre-stimulus oscillatory power in the beta (14 - 28 Hz) and gamma (55 – 80 Hz) frequency bands has been associated with the perception of simultaneity for audio-visual stimuli (Bastiaansen et al., 2020; Ikumi et al., 2019; Yuan et al., 2016). However, the strength of oscillatory power differed depending on which sensory modality was presented first in a cross-modal pair of audio-visual stimuli (Yuan et al., 2016). For example, when the visual stimulus preceded the auditory stimulus beta and gamma power were weaker when stimuli were perceived as occurring simultaneously than when perceived as non-simultaneous. The opposite pattern occurred when the auditory stimulus preceded the visual stimulus; beta and gamma power was stronger when the stimuli were perceived as simultaneous compared to non-simultaneous (Yuan et al., 2016). Yet, other research did not find a difference in oscillatory power for the delta to low beta frequency ranges (1 to 25 Hz) between simultaneous and non-simultaneous perception for auditory leading and visual leading audio-visual stimuli across the whole scalp (Ikumi et al., 2019). These mixed findings may be due to changes in neural activity occurring between the pre-stimulus and response periods during the task. Although the evidence indicates we can predict simultaneity perception based on pre-stimulus activity, it is unlikely that the brain decides about simultaneity before the presentation of multisensory stimuli. Therefore, examining neural activity in the post-stimulus phase (i.e., during and immediately following stimulus presentation) allows us to understand the influence of multisensory stimuli on the perception of simultaneity. Post-stimulus periods are challenging to measure given the differences in the timing of stimuli across multiple SOAs, which may contribute to the limited research in this area. Further to measuring post-stimulus activity, it is also important to measure functional connectivity between unisensory and multisensory regions to understand the role these connections play in the perception of simultaneity.

1.6.2 Functional connectivity

Functional connectivity underlying multisensory integration has been examined between different neural regions and frequency bands. When processing audio-visual and visual-tactile stimuli, connectivity has been shown to increase in the visual cortex, somatosensory cortex, parietal lobe and frontal regions across theta, alpha and beta frequencies (Keil & Senkowski, 2018). Connectivity recorded during an audio-visual simultaneity judgment task showed that individuals with narrow TBWs have more distributed connectivity across distal brain regions, whereas individuals with wider TBWs have greater connectivity within more local regions (Johnston et al., 2022). These results indicate that more precise multisensory integration is facilitated by activation of distributed connectivity throughout various regions in the brain (Johnston et al., 2022). Pre-stimulus functional

connectivity recorded during an audio-visual simultaneity judgment task showed connectivity between auditory and visual regions was stronger in the beta-high frequency (21-28 Hz) when individuals perceived stimuli as simultaneous compared to non-simultaneous (Jiang et al., 2023). Broadly, these findings indicate functional connectivity between sensory, parietal, and frontal areas across frequency bands contributes to binding multisensory stimuli and the perception of simultaneity for audio-visual stimuli. However, there is minimal research examining functional connectivity with visual-tactile stimuli in the simultaneity judgment task, therefore it is unclear if connectivity between unisensory (i.e., visual/occipital, somatosensory/central) and multisensory (i.e., parietal) regions contributes to temporal binding and the perception of simultaneity for visual-tactile stimuli. In this thesis, I have defined unisensory areas for visual and tactile stimuli as the occipital and central regions, respectively. There is a focus on visual-tactile information, specifically, in this thesis as these modalities are essential for motor control. The occipital area (electrode Oz according to the 10-20 system for EEG electrode placement) registers visual signals from the visual cortex and the central area (electrode C5) registers tactile signals from the somatosensory cortex. The multisensory area is in the parietal region (electrode P5) where multisensory signals from the superior temporal sulcus and the temporal parietal junction would be registered. Chapter three aims to address the aforementioned gap by examining functional connectivity between unisensory and multisensory regions during the post-stimulus period in the simultaneity judgment task.

1.7 Sensorimotor synchronization: Linking sensory integration and motor control

Sensorimotor synchronization refers to our ability to temporally align our actions with incoming sensory information in our environment (Iversen & Balasubramaniam, 2016; Mates et al., 1994). It is likely that we perform actions in synchrony with sensory stimuli without too much thought, consider listening to a song on the radio and tapping your foot along to the

beat, or clapping in time to music at a concert. These actions are performed by anticipating the timing of the multisensory stimuli, then integrating the multisensory stimuli and synchronizing the appropriate action with the multisensory information. There are several models that aid our understanding of how the process of temporally aligning movement with integrated multisensory information occurs, that is, sensorimotor synchronization. The linear phase correction model proposes that the central nervous system (CNS) continuously adjusts the timing of movement execution to reduce the temporal discrepancy between movement and the sensory cue, which then improves temporal accuracy of the action (Schulze & Vorberg, 2002). The maximum likelihood estimation (MLE) model extends the linear phase correction model as it explains that sensory cues are assigned a weight according to their reliability. A cross-modal cue has a combined weighting of each unisensory cue, which results in a multisensory estimate that has a higher precision than the unisensory estimate (Ernst & Banks, 2002; Ernst & Bülthoff, 2004; Nolte et al., 2004). This multisensory estimate is used by the CNS as the cue to phase shift the execution of the action towards. The MLE model is extended by causal inference and Bayesian causal inference models, which propose that the brain combines multisensory cues with prior knowledge and assigns a probability about whether these cues arise from a common cause (Ernst & Bülthoff, 2004; Körding et al., 2007; Parise et al., 2012). Multisensory stimuli with high probabilities are then used by the CNS to make further adjustments to the synchronization of movement execution (Wolpert, 2007). We can measure temporal adjustments to movement synchrony using sensorimotor synchronization tasks involving repetitive finger-tapping (Aschersleben, 2002).

Temporal adjustments in sensorimotor synchronization tasks are represented by the 'asynchrony', which is the time difference (in ms) between stimulus presentation and the execution of the movement and is used as a metric to assess sensorimotor synchronization performance (Aschersleben, 2002). Traditionally, sensorimotor synchronization performance has been examined in the auditory domain with individuals from expert (e.g., dancers,

musicians) and non-expert populations who are required to tap their finger in time with repeated auditory stimuli (Jin et al., 2019; Krause et al., 2010; Mates et al., 1994; Repp, 2005, 2010; Repp & Doggett, 2007; Repp & Su, 2013). Typically, expert musicians and dancers have lower sensorimotor synchronization variability than non-experts. There has been growing interest in examining sensorimotor synchronization performance with cross-modal stimuli that pairs auditory information with a second sensory modality, such as audio-visual and audio-tactile (Armstrong & Issartel, 2014; Elliott et al., 2010; Jin et al., 2019). With the dominance of auditory stimuli in this research area, very little research has focused on characterizing visual-tactile sensorimotor synchronization (Elliott et al., 2010). Characterizing sensorimotor synchronization with visual-tactile information will illuminate whether the CNS assigns higher reliability estimates to tactile, visual, or visual-tactile cues, and employs these estimates to adjust movement synchrony (reduce asynchrony). Understanding visual-tactile sensory reliability estimates would allow us to understand fundamental mechanisms used to enhance temporal accuracy of movement synchrony in these modalities. Further, visual-tactile sensorimotor synchronization performance might be influenced by an individuals' TBW, such that individuals with wider TBWs may have longer asynchronies. Although there is some evidence that sensorimotor synchronization performance is improved (i.e., shorter asynchronies) when moving in synchrony with crossmodal cues rather than unimodal, and performance may be related to the size of the TBW (Elliott et al., 2010), further evidence is needed to establish whether reliability estimates are sensory-modality specific.

1.8 Chapter overview

Chapter two contains a published research paper that investigates the size of the visual-tactile TBW with unimodal and cross-modal stimuli. In this study, we used visual-visual, tactile-tactile and visual-tactile stimuli in a simultaneity judgement task to measure the
width of the TBW for unimodal and cross-modal pairs of visual-tactile stimuli. As we are also interested in visual-tactile integration in ASD, we examined the relationship between the TBW and the severity of autistic traits, sensory sensitivity, and the frequency of unusual sensory experiences.

Chapter three contains an experimental study using EEG to measure functional connectivity during a visual-tactile simultaneity judgment task. In this study, we recorded EEG during a visual-tactile simultaneity judgment task to measure functional connectivity *during* and immediately following stimulus presentation across frequencies ranging from 4-30 Hz. We measured functional connectivity between unisensory and multisensory regions to investigate whether connections between these regions contribute to the perception of simultaneity, and therefore the binding of visual-tactile information.

Chapter four contains a published research paper that investigates visual-tactile sensorimotor synchronization and the relationship between synchronization and the TBW across two experiments. Experiment 1 examines unimodal and cross-modal visual-tactile sensorimotor synchronization variability, and the relationship between sensorimotor synchronization variability and the width of the visual-tactile TBW. Based on findings from Experiment 1, Experiment 2 examines sensorimotor synchronization temporal error with tactile-leading versus visual-leading visual-tactile stimuli presented inside and outside of the TBW. Further, we examined the relationship between sensorimotor synchronization temporal error with visual-tactile stimuli and the width of the visual-tactile TBW.

Finally, in chapter five, I provide a General Discussion of the main findings from this thesis, including the contribution these findings make to the broader field of multisensory research and directions for future research. As the research in this thesis shows a relationship between the TBW and motor execution, it is hoped that these findings might lead to establishing research paradigms and interventions in clinical populations where both sensory and motor deficits are core features of the conditions, such as in ASD.

1.9 Conclusion

The simultaneity judgment task has been used widely to measure the width of the TBW, particularly with audio-visual stimuli. It has been established that the width of the TBW is influenced by stimulus complexity and location, age and neurodiversity. Although less is known about the visual-tactile TBW, recent results point to similarities between the visual-tactile and audio-visual TBW. These similarities are evidenced by larger TBWs in clinical populations for both pairs of multisensory stimuli and the relationship between the width of the TBW and individual alpha frequency. However, many gaps in the research on the visual-tactile TBW remain. I aim to address these gaps in the chapters outlined previously. It is my aim to fundamentally characterize the width of the visual-tactile TBW, measure the connections between neural regions activated during the visual-tactile simultaneity task, and examine the relationship between the width of the visual-tactile TBW and autistic traits. Further, as sensory and motor processes are tightly coupled, this thesis will examine unisensory and multisensory sensorimotor synchronization performance.

1.10 References

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Chapter 2: Investigating the Role of Leading Sensory Modality and Autistic Traits in the Visual-Tactile Temporal Binding Window

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Note: Appendices have been included in this chapter for the Autism Quotient, Glasgow Sensory Questionnaire and Multi-Modality Unusual Sensory Experiences Questionnaire. These Appendices were not included in the published version of the article, but have been included here to provide additional context for this chapter.

2.0 Abstract

Our ability to integrate multisensory information depends on processes occurring during the temporal binding window. There is limited research investigating the temporal binding window for visual-tactile integration and its relationship with autistic traits, sensory sensitivity, and unusual sensory experiences. We measured the temporal binding window for visual-tactile integration in 27 neurotypical participants who completed a simultaneity judgement task and three questionnaires: the Autism Quotient, the Glasgow Sensory Questionnaire, and the Multi-Modality Unusual Sensory Experiences Questionnaire. The average width of the visual-leading visual-tactile (VT) temporal binding window was 123 ms, significantly narrower than the tactile-leading visual-tactile (TV) window (193 ms). When comparing cross-modal (visualtactile) stimuli with unimodal (visual-visual or tactile-tactile), the temporal binding window was significantly larger for cross-modal stimuli (VT: 123 ms; TV: 193 ms) than unimodal pairs of stimuli (visual: 38 ms; tactile 42 ms). We did not find evidence to support a relationship between the size of the temporal binding window and autistic traits, sensory sensitivities, or unusual sensory perceptual experiences in this neurotypical population. Our results indicate that the leading sense presented in a multisensory pair influences the width of the temporal binding window. When tactile stimuli precede visual stimuli it may be difficult to determine the temporal boundaries of the stimuli, which leads to a delay in shifting attention from tactile to visual stimuli. This ambiguity in determining temporal boundaries of stimuli likely influences our ability to decide on whether stimuli are simultaneous or non-simultaneous, which in turn leads to wider temporal binding windows.

2.1 Introduction

Our brains continually receive a steady stream of multisensory information throughout our waking lives. Timely integration of this multisensory information is crucial for forming accurate representations of the world, which in turn, contribute to our perceptions about causes of events in our environment. The integration of multisensory information is facilitated by binding mechanisms, namely, the temporal binding window (TBW) for multisensory integration. The TBW represents a brief period in which multisensory information is integrated across, or rather 'bound' together, and unified into a perceptual event (Ernst & Bülthoff, 2004; Spence & Squire, 2003; Vroomen & Keetels, 2010). For example, when you step your feet into a pool, the sight of the water and the sensation of water on your feet binds together into a single percept, allowing for more precise attribution of the cause of the sensation 'wetness'. In this example, the TBW allows a more precise causal attribution of the wet sensation being caused by the foot entering the water. With repeated experience over time, the predictive relationship between the visual (sight of water) and tactile (feeling of water) information could potentially bias our perception towards the timing of one or the other stimulus, depending on its strength and predictive ability.

The width of the TBW is essential for *accurately* attributing multisensory information to the relevant event in the environment. For example, the size of the TBW is generally wider in clinical populations, such as Autism Spectrum Disorder (ASD) and schizophrenia (Foss-Feig et al., 2010; Noel et al., 2018c; Stevenson et al., 2014b; Zhou et al., 2018; Zhou et al., 2021b), than neurotypical populations, and this wider window has been associated with some of the symptoms experienced in these conditions (Stevenson et al., 2017; Stevenson et al., 2014a; Zhou et al., 2021b). Typically, the width of the TBW is measured using a simultaneity judgement task (Hillock-Dunn & Wallace, 2012; Hillock et al., 2011; Powers et al., 2009; Spence & Squire, 2003; Stevenson et al., 2012a; Stevenson & Wallace, 2013; Stevenson et al., 2013; Stevenson et al., 2012b). In this task, two sensory stimuli are presented

simultaneously on some trials, and with varying stimulus onset asynchronies on other trials. Participants then report whether they perceive the stimuli as simultaneous; this perception of simultaneity is taken as an indicator of the TBW for multisensory integration.

The TBW has been well-characterized for audio-visual integration. Previous research has examined the width of the TBW for simple audio-visual stimuli (e.g., visual flash/auditory beep, sound/vision of a tool (e.g., visual flash/auditory beep, sound/vision of a tool - Hillock et al., 2011; Stevenson et al., 2012a; Stevenson & Wallace, 2013; Stevenson et al., 2012b) and more complex stimuli (e.g., watching and listening to speech sounds - Opoku-Baah & Wallace, 2021; Stevenson & Wallace, 2013). When comparing the width of the TBW between different complexities of audio-visual stimuli, it is generally found that, the TBW for complex stimuli is significantly wider than for simple stimuli (Stevenson & Wallace, 2013). Also, the width of the TBW can vary between different types of complex stimuli. For example, when comparing relatively complex stimuli, the TBW for speech sounds was wider than the TBW for melodies played on musical instruments (Ikeda & Morishita, 2020). In contrast, for similar simple stimuli, such as a flash/beep and the sound of a tool, there is typically no difference in the width of the TBW (Stevenson & Wallace, 2013). Hence, the audio-visual TBW is malleable depending on the type of stimuli. While the audio-visual TBW has been well-researched, less is known about the integration of visual-tactile (VT) information.

Few studies have aimed to characterize the TBW for visual-tactile integration using the simultaneity judgement task. A single study examining the development of visual-tactile integration over time found that children (< 13 yrs) had significantly wider TBWs than young adults (Chen et al., 2018). A further study using simple visual-tactile stimuli aimed to measure the width of the TBW in adults showed the width of the whole visual-tactile TBW was on average 211 ms and 196 ms across two experiments (Costantini et al., 2016). A further study showed slight differences in the width of the TBW depending on which sensory

modality was presented first (Migliorati et al., 2020). When visual stimuli preceded tactile stimuli, the width of the TBW was slightly narrower (average 169 ms) than when tactile stimuli preceded visual stimuli (average 176 ms). This study also examined the underlying neurophysiological mechanisms associated with the visual-tactile TBW. Results showed that individuals with higher frequency alpha oscillations (7-12 Hz) had narrower TBWs compared to individuals with lower frequency alpha oscillations (Migliorati et al., 2020). Although these studies provide some insight into the visual-tactile TBW, no study has compared differences in the width of the TBW between unimodal (visual, tactile) and cross-modal (visual-tactile) stimuli. Comparing widths of TBWs between unimodal and cross-modal stimuli is important for advancing our understanding of multisensory integration because it allows us to investigate and contrast how the brain processes information from multiple *versus* single senses. Therefore, the first aim of our study is to compare the width of the TBW for unimodal and cross-modal visual-tactile stimuli.

A second aim of our study is to examine whether the width of the TBW for visualtactile integration is related to autistic traits, sensory sensitivity, and unusual sensory experiences in a neurotypical population. Neurotypical individuals show variations in autistic traits, sensory sensitivities and unusual sensory experiences on a continuum (Baron-Cohen et al., 2001; Mitchell et al., 2017; Robertson & Simmons, 2013) allowing investigation of associations that could inform our understanding of autism. Generally, neurotypical individuals with high autistic traits show wider audio-visual TBWs than neurotypical individuals with low autistic traits (Kawakami et al., 2020; Zhou et al., 2021a). Although autistic individuals typically show wider audio-visual TBWs than neurotypical controls (Feldman et al., 2018; Feldman et al., 2020; Foss-Feig et al., 2010; Noel et al., 2018c; Stevenson et al., 2016; Stevenson et al., 2014a; Stevenson et al., 2014b; Zhou et al., 2018), there are conflicting findings (Ainsworth & Bertone, 2022; Turi et al., 2016; Weiland et al., 2023). The wider audio-visual TBWs in ASD have also been associated with difficulties in speech processing and social communication (Stevenson et al., 2014a; Zhou et al., 2021a), thus indicating that the width of the TBW likely selectively influences various cognitive and perceptual abilities. Despite this interest in researching the audio-visual TBW in ASD, less is known about the visual-tactile TBW in ASD. Further, it is unclear if the width of the window is associated with other characteristics of ASD, such as sensory sensitivity and unusual sensory experiences.

In the current study, we have three hypotheses. First, we hypothesize that the visualtactile TBW will be longer for cross-modal stimuli (visual-tactile (VT) and tactile-visual (TV)) than for unimodal stimuli (visual-visual (VV) and tactile-tactile (TT)). Second, we hypothesize that the visual-leading visual-tactile TBW (VT-TBW) will be narrower than the tactile-leading visual-tactile TBW (TV-TBW). Third, we hypothesize that wider visual-tactile TBWs will be related to higher autistic traits, greater sensory sensitivity, and increased occurrences of unusual sensory experiences.

2.2 Material and methods

2.2.1 Participants

Twenty-eight participants were recruited for the study from an undergraduate University population. All participants recruited for the study received points towards their course as compensation. One participant was excluded from further analysis due to an unreliable fit of their data. From visual inspection of the data, the participant did not perceive stimuli as non-simultaneous at longer SOAs in the VT-TBW condition, which meant that we were unable to attain a reliable estimate of their TBW. Therefore, 27 participants were included in the analysis (M = 21.0, SD = 2.6, 17 females). Twenty-one participants were right-handed, and all participants reported having no known neurological conditions and gave written informed consent prior to testing. The study was approved by Curtin University Human Research Ethics Committee (HRE2018-0257). Participants completed a demographics questionnaire, the simultaneity judgement task, the Autism Quotient (AQ), the Glasgow Sensory Questionnaire (GSQ) and the Multi-Modality Unusual Sensory Experiences Questionnaire (MUSEQ).

2.2.2 Stimuli

Two visual stimuli and two tactile stimuli were used in the experiment. The visual stimuli were two 5 mm green light emitting diodes (LED's; 10,000 mcd) that were inserted into individual frosted Perspex blocks 10 cm apart. The Perspex blocks were used to prevent the lights from blending together to ensure that participants perceived two individual lights and not one light and to reduce the brightness of the lights. The Perspex blocks were fixed to a custom-made black stand placed in the centre of the computer monitor. The tactile stimuli were two 10 x 3.4 mm button-type (vibration amplitude 0.75g at 3 V) shaftless vibration motors (Pololu Corporation, Las Vegas, NV; Pololu item #1636) attached to the index and middle fingers on the right hand with an elastic fabric band. As this vibration motor likely oscillates well above 100 Hz, we expect that both Meissner and Pacinian receptors are involved in the perception of the vibration ((Birznieks et al., 2019). The visual and tactile stimuli were sent direct from the computer via a parallel port connection. The experiment was programmed in Matlab version 2015b and instructions for the task were displayed on a 19" Dell LCD computer monitor (60 Hz refresh rate) using Psychoolbox (version 3.0.8).

2.2.3 Questionnaires

The Autism Quotient (AQ) (Appendix A), the Glasgow Sensory Questionnaire (GSQ) (Appendix B) and the Multi-Modality Unusual Sensory Experiences Questionnaire (MUSEQ) (Appendix C) were administered to participants following the simultaneity judgement task. The AQ is a 50-item self-report scale that measures autistic traits (Baron-Cohen et al., 2001). The AQ consists of five subscales - social skills, attention switching, attention to detail, communication, and imagination - and includes four response options

('definitely agree'. 'slightly agree', 'slightly disagree', and 'definitely disagree') (Baron-Cohen et al., 2001; Woodbury-Smith et al., 2005). Scores ranging from 0-25 indicate few autistic traits, scores from 26-32 indicate some autistic traits, and scores from 33-50 indicate significant autistic traits. The GSQ is a 42-item self-report scale that measures hyper- and hypo- sensory sensitivity typically associated with Autism Spectrum Disorder (Robertson & Simmons, 2013). The GSQ measures sensory sensitivity across seven different modalities, including vision, audition, gustation, olfaction, tactile, vestibular and proprioception. All items in the GSQ are on a 5-point Likert scale measuring the frequency of sensory sensitivities ('never' [0], 'rarely' [1], 'sometimes' [2], 'often' [3], and 'always' [4]). Scores range from 0-168; higher scores indicate greater hyper- or hypo- sensory sensitivity for each modality and overall. The MUSEQ is a 43-item self-report scale that measures unusual sensory experiences across six different sensory modalities, including vision, audition, gustation, olfaction, bodily sensations, and sensed presence (Mitchell et al., 2017). All items in the MUSEQ are on a 5-point Likert scale and measure the regularity of unusual sensory experiences occurring ('never' [0], 'hardly ever' [1], 'rarely' [2], 'occasionally' [3], and 'frequently' [4]).

2.2.4 Procedure

In the simultaneity judgement task, participants were presented with two sensory stimuli, either two lights (visual condition), two vibrations (tactile condition), or a light and a vibration (visual-tactile condition). The beginning of each trial started with the sensory type written on the screen to instruct participants which stimuli to attend to, e.g., "Visual stimuli", "Tactile stimuli", or "Both stimuli" (see Figure 2.1). Stimuli were presented either together (i.e., simultaneously) or at various stimulus onset asynchronies (SOAs) ranging from +/- 25 to 250 ms, increasing in 25 ms increments. The direction of the SOA (positive or negative) indicates one stimulus preceding the other. For the visual-tactile condition, positive SOAs indicate the tactile stimulus preceded the visual stimulus (i.e., tactile-leading, TV-TBW),

whereas negative SOAs indicate the visual stimulus preceded the tactile stimulus (i.e., visualleading, VT-TBW). For all SOAs in the visual-tactile condition, the stimuli were the right light and the vibration motor on the index finger. In the visual-visual (VV) condition, positive SOAs indicate the light on the right side of the custom-made stand preceded the light on the left side, and for negative SOAs the left light preceded the right light. For the tactile-tactile (TT) condition, positive SOAs indicate the vibration motor on the middle finger preceded the vibration motor on the index finger, and for negative SOAs the motor on the index finger preceded the middle finger. There was a 1-s interval between the presentation of the second stimulus and the question "Were the stimuli simultaneous?" appearing on the screen. Participants responded 'yes' by pressing the left mouse button or 'no' by pressing the right mouse button with their left-hand. After the participant responded, the next trial started automatically. There were 630 trials in total, presented in randomised order: 210 trials each for the visual condition, tactile condition, and visual-tactile condition. The order of stimuli was different for each participant. There were two designated breaks throughout the stimuli presentation, lasting a minimum of 10 sec. Participants completed 12 practice trials before commencing the experiment. The simultaneity judgement task was completed in a dimly lit room.



Figure 2.1: Graphical representation of the trials for visual ('Light'), tactile ('Vibration'), and visual-tactile ('Both') stimuli presented in the simultaneity judgement task. Stimuli were presented at these SOAs: +/- 0, 25, 50, 75, 100, 125, 150, 175, 200, 225, 250 ms.

2.2.5 Data analysis

Measuring the Temporal Binding Window

The percentage of simultaneity responses (i.e., 'yes', 'no') were averaged for each participant at each SOA and fitted with a model-free line, such that a curve was fit to each participant (Zychaluk & Foster, 2009). The model-free function is a parameter free method that has no assumptions about the shape of the data; this function is an alternative to a Gaussian or sigmoid function, which are commonly used methods for fitting the rate of perceived simultaneity data (Costantini et al., 2016; Hillock-Dunn & Wallace, 2012; Hillock et al., 2011; Migliorati et al., 2020; Moro & Steeves, 2018; Noel et al., 2016; Noel et al., 2017a; Powers et al., 2009; Stevenson et al., 2018; Stevenson et al., 2014a; Stevenson & Wallace, 2013; Venskus et al., 2021). To estimate the width of the TBW for each participant, we measured the halfway point between 0% and the maximal peak of simultaneity perception on the y-axis, and where this halfway point intersects the model-free fit on the x-axis: this is referred to as the "half-width window" (see Figure 2.2). Half-width windows for positive and negative SOAs were calculated for visual, tactile and visual-tactile conditions.



Figure 2.2. Graphical representation with example data from one participant showing how the model-free line was fitted to the subject-level data for each participant.

Comparing the TBW Across SOAs and Stimulus Modalities

Within-modality analysis was conducted using paired samples t-tests to compare the width of the half-width window on the positive and negative SOAs within visual only, tactile only and visual-tactile conditions. Between-modality analysis was conducted using Linear Mixed Models (LMM), with participants as the random-effect, to compare differences in the width of the half-width window between VV, TT, and visual-tactile (VT and TV) conditions. Bonferroni corrections for multiple comparisons were applied to the LMM. For visual and tactile only conditions, the negative SOAs were included in the LMM. There was no need to include positive SOAs in the model for visual and tactile only conditions as it was not hypothesized that there would be a significant difference between the widths of the windows for positive and negative SOAs) and TV (positive SOAs) stimuli were included in the model as it was hypothesized that VT-TBW would be narrower than the TV-TBW. The gamlj mixed function in RStudio (gamlj package version 2.6.5 (Gallucci, 2019); RStudio version 3.5.2 (RStudioTeam)) was used to conduct the LMM, with the half-width window and sensory modality as the fixed factors and participants as the random factor.

Correlations Between the TBWs and Questionnaires

Spearman's rank-order correlation coefficient was calculated between the VT-TBW and the TV-TBW to examine whether wider TBWs in the visual-leading condition were associated with wider windows in the tactile-leading condition. Correlations between unimodal (VV and TT) and cross-modal (VT and TV) TBWs were also performed to examine whether wider windows for unimodal stimuli were related to wider cross-modal windows. Further, Spearman's rank-order correlation coefficient was calculated between the crossmodal TBWs (VT and TV) and total scores on the questionnaires (AQ, GSQ and MUSEQ), and between each of the questionnaires (i.e., AQ and GSQ, AQ and MUSEQ, GSQ and MUSEQ).

2.3 Results

When examining differences within sensory modalities (visual-visual, tactile-tactile and visual-tactile) between negative and positive SOAs, the paired-samples t-test showed a small, but statistically reliable, 6 ms mean difference between the VV-TBWs for negative SOAs (left light precedes right light; M = 38 ms, SD = 14 ms) and positive SOAs (right light precedes left light; M = 32 ms, SD = 15 ms), (t(26) = 3.82, p < 0.001) (see Figure 2.3 for group averages of perceived simultaneity). The total width of the VV-TBW was 70 ms. There was no mean difference between the TT-TBWs for negative SOAs (index finger vibration preceded middle finger vibration; M = 42 ms, SD = 24 ms) and positive SOAs (middle finger vibration preceded index finger vibration; M = 42 ms, SD = 26 ms), (t(26) < 0.001, p > 0.99). The total width of the TT-TBW was 84 ms. There was a significant 69 ms mean difference between the visual-tactile TBW for negative SOAs (VT; M = 123 ms, SD = 51 ms) and positive SOAs (TV; M = 193 ms, SD = 54 ms), (t(26) = -9.36, p < 0.001). The total width of the TBW for visual-tactile stimuli (VT and TV negative and positive SOAs) was 316 ms.

When comparing the TBW between VV, TT and visual-tactile (VT and TV) stimuli, results from the LMM showed a main effect of sensory modality, (F(3, 78) = 186.67, p<0.001). *Post-hoc* tests showed that the VT-TBW was significantly wider than the VV-TBW (p < 0.001) and the TT-TBW (p < 0.001), and that the mean width of the TV-TBW was significantly wider than the TT-TBW (p < 0.001) and the VV-TBW (p < 0.001). When comparing cross-modal stimuli (VT versus TV), the mean width of the TV-TBW was significantly wider than the VT-TBW (p < 0.001). There was no significant mean difference between the width of the VV-TBW and the TT-TBW (p > 0.99).



Figure 2.3: Combined group averaged data of perceived simultaneity with the model-free line fitted to the data. Left: Visual-visual. Middle: Tactile-tactile. Right: Visual-tactile. Error bars represent standard error.

2.3.1 Correlations

Temporal binding windows

The Spearman correlations showed a significant positive correlation between the VT-TBW and the TV-TBW, (r = 0.78, p < 0.001) (see Figure 2.4), the left and right leading visual TBWs (r = 0.77, p < 0.0001), and the index and middle finger leading tactile TBWs (r = .89, p < 0.001). Thus, individuals with wider VT-TBW had wider TV-TBWs. When examining the relationship between the unimodal and cross-modal TBWs, there were significant positive correlations between the VT-TBW and the TT-TBW (r = 0.76, p = < 0.001), the VT-TBW and the VV-TBW (r = 0.47, p = 0.01), the TV-TBW and the TT-TBW (r = 0.56, p = < 0.001), the TV-TBW and the VV-TBW (r = 0.46, p = 0.02) (See Figure 2.5).



Figure 2.4: Scatterplot shows significant positive correlation between the visual-leading visual-tactile TBW and the tactile-leading visual-tactile TBW.



Figure 2.5: Scatterplot shows significant positive correlations between the unimodal (VV and TT) and cross-modal (VT and TV) TBWs.

Questionnaires

The AQ mean total score for the group was 17.07 (SD = 5.90), the GSQ was 49.96 (SD = 12.37), and the MUSEQ was 43.07 (SD = 19.02). These total scores are within a typical range for a neurotypical population. There were no correlations between the unimodal or cross-modal TBWs and total scores on the AQ, GSQ and MUSEQ (see Table 2.1) and relevant subscales on the GSQ and MUSEQ (see Table 2.2).

Table 2.1.

	AQ		GSQ		MUSEQ		
	r	р	r	р	r	р	
VT-TBW	-0.04	0.85	0.13	0.53	0.23	0.25	
TV-TBW	-0.02	0.91	0.09	0.64	0.36	0.07	
VV-TBW	0.03	0.88	0.26	0.18	0.36	0.06	
TT-TBW	0.13	0.52	0.27	0.17	0.19	0.35	

Correlations between the unimodal and cross-modal visual-tactile TBWs, and the total scores on the AQ, GSQ and the MUSEQ.

Abbreviations: AQ, Autism Quotient; GSQ, Glasgow Sensory Questionnaire; MUSEQ, Multi-Modality Unusual Sensory Experiences Questionnaire; T, tactile; TBW, temporal binding window; V, visual.

Table 2.2.

Correlations between the Visual-Tactile TBW and subscales on the GSQ and MUSEQ

	GSQ: visual		GSQ: tactile		MUSEQ: visual		MUSEQ: bodily sens.	
	r	р	r	р	R	р	r	р
VT-TBW	0.07	0.71	-	-	0.30	0.13	-	-
TV-TBW	-	-	-0.19	0.35	-	-	0.04	0.85

Abbreviations: GSQ, Glasgow Sensory Questionnaire; MUSEQ, Multi-Modality Unusual Sensory Experiences Questionnaire; T, tactile; TBW, temporal binding window; V, visual.

As there were no associations between the size of the visual-tactile TBWs and autistic traits, sensory sensitivity, and unusual sensory experiences as expected, we followed-up the results from the Spearman correlations with Bayes factor correlations using the BayesFactor package in Rstudio (v0.9.2+). This analysis allowed us to determine the evidence for the null hypothesis. Bayes factor correlations showed only anecdotal evidence in favour of the absence of a relationship between the AQ and the visual-tactile TBWs (VT: BF01 = 2.38; TV: BF01 = 2.37). Similarly, there was no evidence in favour of the null hypothesis when analysing the relationship between the GSQ and the visual-tactile TBWs (VT: BF01: 1.32,

TV: BF01: 1.96). However, there was moderate evidence for the absence of a relationship between the MUSEQ and the visual-tactile TBWs (VT: BF01 = 9.47; TV: BF01 = 7.24).

Since the GSQ and MUSEQ include visual- and tactile-related subscales, and we were primarily interested in visual-tactile information, we examined the relationship between the visual-tactile TBW and the subscales. There were no correlations between the size of the VT-TBW and the visual subscales on the GSQ and MUSEQ, nor between the TV-TBW and the tactile subscale on the GSQ and bodily sensation subscale on the MUSEQ (see Table 2.2). As sensory sensitivity forms part of the diagnostic criteria for ASD (APA, 2013), we performed a correlation between the AQ and GSQ to examine the relationship between autistic traits and sensory sensitivity in our neurotypical sample. Results from the correlation showed a significant positive relationship between total scores on the AQ and GSQ (r = 0.49, p = 0.01) (See Figure 2.6). However, there was no correlation between total scores on the AQ and MUSEQ (r = -0.24, p = 0.22), or the GSQ and MUSEQ (r = 0.06, p = 0.78).



Figure 2.6: Scatterplot shows significant positive correlation between the total scores on the Glasgow Sensory Questionnaire (GSQ) and the Autism Quotient (AQ).

2.4 Discussion

The first aim of our study was to compare the width of the TBW between unimodal visual and tactile stimuli, and cross-modal visual-tactile stimuli. Our first hypothesis that the

cross-modal visual-tactile TBWs would be wider than unimodal (VV and TT) windows was supported. The width of the VV-TBW and TT-TBW was significantly smaller than the visualtactile windows (both VT and TV), indicating that unimodal stimuli are integrated across a shorter period than cross-modal stimuli and that temporal acuity is more precise for single sensory binding. The non-significant difference between unimodal visual and tactile stimuli is consistent with previous literature with auditory and visual stimuli (Giurgola et al., 2022). When comparing TBWs within the unimodal conditions between the positive and negative SOAs, we found a significant difference in the VV condition, but not in the TT condition. When comparing the width of the VV-TBW between positive SOAs and negative SOAs, we found that when the left light preceded the right light the TBW was longer than when the right light preceded the left light. Since the two visual stimuli were horizontally positioned approximately 10 cm apart, we believe this significant difference between the positive and negative SOAs may be attributed to differences in visual hemifield processing bias (Karim & Kojima, 2010).

Our second hypothesis that the VT-TBW was narrower than the TV-TBW was supported as there was a significant difference between the widths of the windows. On average, the VT-TBW was 69 ms narrower than the TV-TBW. Thus, indicating that individuals' perception of simultaneity was more accurate when the visual stimulus preceded the tactile than when the tactile stimulus preceded the visual. These results are consistent with previous research that found the VT-TBW was narrower than the TV-TBW, although these results were non-significant (Migliorati et al., 2020). Similar results in the audio-visual domain also show differences in the width of the TBW based on the leading sense, with narrower windows found for the auditory-leading side of the audio-visual window than the visual-leading side (Giurgola et al., 2022). Our results, combined with previous literature (Cecere et al., 2016; Cecere et al., 2017; Hirsh & Sherrick, 1961), indicate that the width of the multisensory TBW is influenced by the type of sensory modality that is presented first in

a cross-modal pair. This influence of the leading sense means that the process of multisensory integration may be more efficient if specific modalities that initiate narrower windows are perceived first.

In addition to identifying significant differences in the widths of the VT-TBW and TV-TBW, we also found a significant relationship between the width of the VT-TBW and the width of the TV-TBW, such that individuals with a wider VT-TBW also had a wider TV-TBW. This trend persisted between unimodal and cross-modal stimuli as individuals with wider VT-TBW and TV-TBWs also had wider VV-TBW and TT-TBWs. There may be various factors that contribute to this relationship between wider windows between different leading-sense pairs of cross-modal stimuli, and between unimodal and cross-modal stimuli. One factor to consider is that some individuals may have a 'general' wider window, meaning that the width of their TBW will be wider regardless of the leading sense, the modality of the multisensory stimuli, or whether only unisensory stimuli are presented. A second factor is that the width of the TBW may rely on the individuals' global temporal acuity, such that reduced temporal acuity may be related to wider cross-modal and unimodal TBWs.

Of interest, the group data for the TV percentage of perceived simultaneity (Figure 2.3, right) shows wider (i.e., longer) TBWs than for VT. Yet, there are no differences in simultaneity perception between VV and TT unimodal conditions. These differences in simultaneity perception indicate that there is something unique about how visual-tactile stimuli are bound together that is different to respective unimodal stimuli. Various factors may contribute to these differences in simultaneity perception. One factor could be that visual stimuli may be more easily discriminable than tactile stimuli, which makes it easier to rapidly process the onset and offset of the stimuli and allows us to quickly shift our attention away from the visual stimulus to the tactile stimulus. Whereas the onset and offset of the tactile stimulus may not be perceived as precisely as the visual stimulus, which results in a delay in shifting attention to and from the tactile stimulus when it is presented first in a visual-tactile

pair, introducing variability in our estimates. A second related factor may be that temporal acuity is not as reliable when a tactile stimulus is presented first in a cross-modal pair, which then leads to difficulty determining whether stimuli are simultaneous or non-simultaneous. This ambiguity in determining simultaneity likely influences the decision-making process associated with simultaneous versus non-simultaneous responses. It seems that our ability to detect, discriminate and decide changes in the timing of cross-modal stimuli in the environment is influenced by the modality of the first stimulus. Further research using the visual-tactile simultaneity judgement task needs to consider the role attention plays in detecting, discriminating, and deciding on simultaneity perception to understand differences in between the size of the VT- and TV-TBWs.

There was insufficient evidence to support our third hypothesis that wider visualtactile TBWs would be related to higher autistic traits, greater sensory sensitivity, and increased occurrences of unusual sensory experiences. We may not have found sufficient evidence for our hypothesis due to a limited range of AQ, GSQ and MUSEQ scores in our sample and a relatively small sample to detect a modest correlation. In support of this idea, results from the Bayesian correlations showed only very weak evidence for the absence of an effect between the width of the TBW and autistic traits, sensory sensitivity, and unusual sensory experiences. However, it is not so surprising that we did not find sufficient evidence to support our hypothesis, as previous research also did not find an association between the width of audio-visual TBW and AQ scores in a neurotypical population (Donohue et al., 2012; Zhou et al., 2021c). Despite not finding a relationship between the width of the visualtactile TBWs and autistic and sensory traits in our sample, the relationship between these factors still warrants further investigation in a neurodiverse sample, such as ASD and schizophrenia. It is important that the visual-tactile TBW is examined in conditions such as ASD and schizophrenia as the audio-visual window, sensory difficulties and multisensory integration in general, has been shown to be atypical in these populations (Beker et al., 2017;

Brandwein et al., 2015; Brandwein et al., 2012; Brock et al., 2002; Cascio et al., 2012; De Boer-Schellekens et al., 2013; Foss-Feig et al., 2010; Greenfield et al., 2015; Iarocci & McDonald, 2006; Noel et al., 2018c; Russo et al., 2010; Stevenson et al., 2016; Stevenson et al., 2014a; Stevenson et al., 2014b; Zhou et al., 2018). If we can establish whether individuals with these conditions have atypical visual-tactile TBWs, as has been established in the audiovisual domain, it would enable us to understand if there is an issue with specific sensory modalities or with the mechanisms facilitating the multisensory integration process. In support of this idea, we found a positive correlation between total scores on the AQ and the GSQ, thus providing some evidence for the relationship between autistic traits and sensory sensitivity in this neurotypical sample, albeit just not for the visual-tactile TBW in this instance.

Our study shows that the width of the TBW is vastly wider for VT stimuli compared to unisensory VV and TT stimuli. Further, the sensory modality of the stimulus presented first in a visual-tactile pair influences the size of the TBW. The narrower VT-TBW compared to the TV-TBW indicates that the onset and offset of visual stimuli are more easily detectable than tactile stimuli, which allows us to rapidly shift our attention from the visual stimulus to the tactile stimulus. Whereas, when tactile stimuli are presented first it may be difficult to precisely determine the temporal boundaries of the stimuli, which leads to difficulty determining and deciding on whether stimuli are simultaneous or non-simultaneous. Although we did not find a relationship between the width of the visual-tactile TBWs and autistic traits, sensory sensitivity, and unusual sensory experiences, this may be due to the neurotypical sample, limited range of scores and the sample size. Replicating this study in a neurodiverse sample would be informative in determining whether the sensory difficulties experienced in clinical populations may be due to the TBW for visual-tactile integration.

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Appendix A

The Adult Autism Spectrum Quotient (AQ)

Ages 16+

SPECIMEN, FOR RESEARCH USE ONLY.

For full details, please see:

S. Baron-Cohen, S. Wheelwright, R. Skinner, J. Martin and E. Clubley, (2001) <u>The Autism Spectrum Quotient (AQ) : Evidence from Asperger Syndrome/High Functioning</u> <u>Autism, Males and Females, Scientists and Mathematicians</u> Journal of Autism and Developmental Disorders 31:5-17

Name:	Sex:
Date of birth:	Today's Date

How to fill out the questionnaire

Below are a list of statements. Please read each statement <u>very carefully</u> and rate how strongly you agree or disagree with it by circling your answer.

DO NOT MISS ANY STATEMENT OUT.

Examples

E1. I am willing to take risks.	definitely	slightly	slightly	definitely
	agree	agree	disagree	disagree
E2. I like playing board games.	definitely	slightly	slightly	definitely
	agree	agree	disagree	disagree
E3. I find learning to play musical instruments easy.	definitely	slightly	slightly	definitely
	agree	agree	disagree	disagree
E4. I am fascinated by other cultures.	definitely	slightly	slightly	definitely
	agree	agree	disagree	disagree

1. I prefer to do things with others rather than on	definitely	slightly	slightly	definitely
my own.	agree	agree	disagree	disagree
	definitely		aliabelu	مامطنية مارر
2. I prefer to do things the same way over and over	dennitely	slightly	slightly	definitely
250m	agree	agree	disagree	disagree
3. If I try to imagine something, I find it very easy	definitely	slightly	slightly	definitely
to create a picture in my mind.	agree	agree	disagree	disagree
4. I frequently get so strongly absorbed in one	definitely	slightly	slightly	definitely
thing that I lose sight of other things.	agree	agree	disagree	disagree
	agree	agree	uisagree	uisagiee
5. I often notice small sounds when others do not.	definitely	slightly	slightly	definitely
	agree	agree	disagree	disagree
6. I usually notice car number plates or similar	definitely	slightly	slightly	definitely
strings of information.	agree	agree	disagree	disagree
7. Other people frequently tell me that what I've	definitely	slightly	slightly	definitely
said is impolite, even though I think it is polite.	agree	agree	disagree	disagree
	ugree	ugree	usugree	uisugree
8. When I'm reading a story, I can easily imagine	definitely	slightly	slightly	definitely
what the characters might look like.	agree	agree	disagree	disagree
9. I am fascinated by dates.	definitely	slightly	slightly	definitely
	agree	agree	disagree	disagree
10. In a social group, I can easily keep track of	definitely	slightly	slightly	definitely
several different people's conversations.	agree	agree	disagree	disagree
		-	-	-
11. I find social situations easy.	definitely	slightly	slightly	definitely
	agree	agree	disagree	disagree
12. I tend to notice details that others do not.	definitely	slightly	slightly	definitely
	agree	agree	disagree	disagree

13. I would rather go to a library than a party.	definitely	slightly	slightly	definitely
	agree	agree	disagree	disagree
14. I find making up stories easy.	definitely	slightly	slightly	definitely
	agree	agree	disagree	disagree
		U	Ū	U
15. I find myself drawn more strongly to people	definitely	slightly	slightly	definitely
than to things.	agroo	agroo	dicagraa	disagraa
	agree	agree	uisagiee	uisagiee
16. I tend to have very strong interests which I get	definitely	slightly	slightly	definitely
upset about if I can't pursue.	agroo	agroo	dicagraa	disagraa
	agree	agree	uisagiee	uisagiee
17 Loniov social chit-shat	definitely	slightly	slightly	definitely
	Gennitely	Singhtiy	diagana	diseases
	agree	agree	disagree	disagree
18. When I talk, it isn't always easy for others to get	definitely	slightly	slightly	definitely
a word in edgeways.	agree	agree	disagree	disagree
19. I am fascinated by numbers.	definitely	slightly	slightly	definitely
	agree	agree	disagree	disagree
20. When I'm reading a story, I find it difficult to	definitely	slightly	slightly	definitely
work out the characters' intentions.	agree	agree	disagree	disagree
21. I don't particularly enjoy reading fiction.	definitely	slightly	slightly	definitely
	agree	agree	disagree	disagree
22. I find it hard to make new friends.	definitelv	slightly	slightly	definitelv
	, agree	agree	disagree	, disagree
	-0.00	20,00		31505100
	J-£	-11.1.1.1	-11.1.1	-l- <i>f</i> , ., .
23. I notice patterns in things all the time.	definitely	slightly	slightly	definitely
	agree	agree	disagree	disagree

24. I would rather go to the theatre than a museum.	definitely	slightly	slightly	definitely
	agree	agree	disagree	disagree
25. It does not upset me if my daily routine is	definitely	slightly	slightly	definitely
disturbed.	agree	agree	disagree	disagree
	al a fina ita a la c	-1	-11-1-1-1	d a fina ita a lu c
26. I frequently find that I don't know how to keep a	definitely	slightly	slightly	definitely
	agree	agree	disagree	disagree
27. I find it easy to "read between the lines" when	definitely	slightly	slightly	definitely
someone is talking to me.	agree	agree	disagree	disagree
28. I usually concentrate more on the whole picture,	definitely	slightly	slightly	definitely
rather than the small details.	agree	agree	disagree	disagree
29. I am not very good at remembering phone	definitely	slightly	slightly	definitely
numbers.	agree	agree	disagree	disagree
30. I don't usually notice small changes in a	definitely	slightly	slightly	definitely
situation, or a person's appearance.	agree	agree	disagree	disagree
31. I know how to tell if someone listening to me is	definitely	slightly	slightly	definitely
getting bored.	agree	agree	disagree	disagree
32. I find it easy to do more than one thing at once.	definitely	slightly	slightly	definitely
	agree	agree	disagree	disagree
33. When I talk on the phone, I'm not sure when it's	definitely	slightly	slightly	definitely
my turn to speak.	agree	agree	disagree	disagree
34. I enjoy doing things spontaneously.	definitely	slightly	slightly	definitely
	agree	agree	disagree	disagree
35. I am often the last to understand the point of a	definitely	slightly	slightly	definitely
joke.	agree	agree	disagree	disagree

36. I find it easy to work out what someone is	definitely	slightly	slightly	definitely
thinking or feeling just by looking at their face.	agree	agree	disagree	disagree
37. If there is an interruption, I can switch back to	definitely	slightly	slightly	definitely
what I was doing very quickly.	agree	agree	disagraa	disagraa
	agree	agree	uisagree	uisagree
38. I am good at social chit-chat.	definitely	slightly	slightly	definitely
	agree	agree	disagree	disagree
39. People often tell me that I keep going on and on	definitely	slightly	slightly	definitely
about the same thing.	agree	agree	disagree	disagree
	agree	ugice	uisagree	uisagree
		-1	-1	d - Constants
40. When I was young, I used to enjoy playing games involving pretending with other children	definitely	slightly	slightly	definitely
games involving pretending with other children.	agree	agree	disagree	disagree
41. I like to collect information about categories of	definitely	slightly	slightly	definitely
things (e.g. types of car, types of bird, types of	agree	agree	disagree	disagree
train, types of plant, etc.).				
42. I find it difficult to imagine what it would be like	definitely	slightly	slightly	definitely
to be someone else.	agree	agree	disagree	disagree
		-	-	-
43 Llike to plan any activities L participate in	definitely	slightly	slightly	definitely
carefully.			diagana	diagana
	agree	agree	uisagree	uisagree
44. I enjoy social occasions.	definitely	slightly	slightly	definitely
	agree	agree	disagree	disagree
45. I find it difficult to work out people's intentions.	definitelv	slightly	slightly	definitely
	, agree	agree	disagree	disagree
	agree	agree	uisagiee	uisagiee
46. New situations make me anxious.	definitely	slightly	slightly	definitely
	agree	agree	disagree	disagree
47 Leniov meeting new people	definitely	slightly	slightly	definitely
				diagana
	agree	agree	disagree	uisagree

48. I am a good diplomat.	definitely	slightly	slightly	definitely
	agree	agree	disagree	disagree
49. I am not very good at remembering people's	definitely	slightly	slightly	definitely
date of birth.	agree	agree	disagree	disagree
50. I find it very easy to play games with children	definitely	slightly	slightly	definitely
that involve pretending.	agree	agree	disagree	disagree

Developed by:

The Autism Research Centre

University of Cambridge

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Appendix B

SAMPLE QUESTIONS (please read to make sure you know how to answer the questionnaire but do not answer these sample questions).

These sample questions (and answers) have been included to make it as easy as possible for you to fill out the questionnaire.

A. Do you find it difficult to concentrate on visual information (for example, reading a book) when there are noises in the background?

In this question, an example is given which helps to explain the question further. Examples are only given to help prompt you (if needed).

Sample answer to question A:

If I experience problems (most of the time) in concentrating while watching a movie when there is background noise, I would answer 'Often'. This would be regardless of whether I experienced the exact issue detailed by the example.

Never Sometimes Often Always Rarely

B. Do you find it difficult to look people in the eyes?

It can be hard to answer questions like this as the amount that eye contact (or something else) is a problem for you is likely to have varied throughout your life-time. For this reason, we ask that you choose the option that corresponds best with your experience over the last 12 months.

Sample answer to B:

If I found it difficult to have eve contact with someone all of the time at the age of 7, but as an adult I find it easy most of the time, I would answer 'Rarely'.

Never	Rarely	Sometimes	Often	Always
-------	--------	-----------	-------	--------

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1.	Do you	dislike	the	physical	sensation	you	get	when	people	hug you	?
----	--------	---------	-----	----------	-----------	-----	-----	------	--------	---------	---

	Never	Rarely	Sometimes	Often	Always
2.	Do you gag when yo	ou are eating certai	in foods, perhaps fee	ling as if you ar	e going to be sick)?
	Never	Rarely	Sometimes	Often	Always
3.	Do you find it diffic example, picking up	ult to manipulate y small objects or t	your hands when cor ransferring objects f	npleting a delica rom one hand to	te task (for the other)?
	Never	Rarely	Sometimes	Often	Always
4.	Do you ever run you	ur hand around the	outside of an object	before picking i	it up?
	Never	Rarely	Sometimes	Often	Always
5.	Do you stand very c more than 3 metres/	lose (for example, 9 feet away) when	less than 1 metre/3 you are talking to se	feet away) or ve omeone?	ry far (for example,
	Never	Rarely	Sometimes	Often	Always
6.	Do you find certain	noises/pitches of s	ound annoying?		
	Never	Rarely	Sometimes	Often	Always
7.	Do you smell your f	food before you ea	t it?		
	Never	Rarely	Sometimes	Often	Always
8.	Do bright lights eve	r hurt your eyes/ca	use a headache?		
	Never	Rarely	Sometimes	Often	Always
9.	Do you like to lister	to the same piece	of music/part of a D	VD over and ov	/er again?
	Never	Rarely	Sometimes	Often	Always
10	Do you feel ill/dizzy	/peculiar if you ha	ave to reach up high	or bend down lo	w for something?
	Never	Rarely	Sometimes	Often	Always
11	Do you find yoursel	f fascinated by sm	all particles (for exa	mple, little 'bits'	' of dust in the air)?
	Never	Rarely	Sometimes	Often	Always
12	Do you like to spin	yourself round and	l round?		
	Never	Rarely	Sometimes	Often	Always

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Do you	ever feel ill just	t from smelling a	certain odour?
--------------------------	--------------------	-------------------	----------------

	Never	Rarely	Sometimes	Often	Always			
14. Do	you find it diffic	ult to hear what p	eople are saying?					
	Never	Rarely	Sometimes	Often	Always			
15. Do	15. Do you dislike having a haircut (for example, because little bits of hair go down your back)?							
	Never	Rarely	Sometimes	Often	Always			
16. Do	you notice that y	you have hurt your	self but did not feel	any pain?				
	Never	Rarely	Sometimes	Often	Always			
17. Are	e you ever told by	y others that you w	vear too much perfu	ne/after-shave?				
	Never	Rarely	Sometimes	Often	Always			
18. Do app	lights ever seem pearing to turn on	to flicker when yo and off very quic	ou look at them? ('I kly instead of appea	'lickering' in thi ring constant).	s question means			
	Never	Rarely	Sometimes	Often	Always			
19. Do you like lining objects up?								
	Never	Rarely	Sometimes	Often	Always			
20. Do	you rock yourse	lf backwards and i	forwards?					
	Never	Rarely	Sometimes	Often	Always			
21. Do Sho	you find it diffic op")?	ult to go into a str	ong-smelling shop (:	for example "Lu	sh" and "The Body			
	Never	Rarely	Sometimes	Often	Always			
22. Do	you cut the labe	ls out of your cloth	ies?					
	Never	Rarely	Sometimes	Often	Always			
23. Do	you hate the fee	l or texture of cert	ain foods in your mo	outh?				
	Never	Rarely	Sometimes	Often	Always			
24. Do	you avoid going	to restaurants bec	ause you can smell a	a certain odour?				
	Never	Rarely	Sometimes	Often	Always			

25. Do you dislike loud noises?

	Never	Rarely	Sometimes	Often	Always				
26. Do yo	ou use the tip of	your tongue to ta	ste your food before	eating it?					
	Never	Rarely	Sometimes	Often	Always				
27. Does	27. Does your body ever feel 'numb' - like you can't feel anything against your skin?								
	Never	Rarely	Sometimes	Often	Always				
28. Do you think you have a weak sense of taste? One example of this would be if most food taste of 'nothing'?									
	Never	Rarely	Sometimes	Often	Always				
29. Do yo hungi	ou find that you ry/tired/thirsty)?	are unaware of yo	our body's signals (fo	or example, don	't often feel				
	Never	Rarely	Sometimes	Often	Always				
30. Do yo	ou ever feel dizz	zy/ill when playing	g fast-paced sports, f	or example basl	cetball or football?				
	Never	Rarely	Sometimes	Often	Always				
31. Do yo	ou react very str	ongly when you h	ear an unexpected s	ound?					
	Never	Rarely	Sometimes	Often	Always				
32. Do yo	ou dislike walki	ng on uneven surf	aces?						
	Never	Rarely	Sometimes	Often	Always				
33. Do yo	ou really like lis	tening to certain s	ounds (for example,	the sound of pa	per rustling)?				
	Never	Rarely	Sometimes	Often	Always				
34. Do yo	ou like to run ab	out – perhaps up a	and down in straight	lines or round i	n circles?				
	Never	Rarely	Sometimes	Often	Always				
35. Do yo you li	35. Do you chew and lick objects that aren't food (for example pen lids or bottle tops) because you like the way they feel in your mouth?								
	Never	Rarely	Sometimes	Often	Always				
36. Do yo	ou enjoy wearin	g very strong perf	umes/after-shaves?						
	Never	Rarely	Sometimes	Often	Always				

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37.	37. Do you find that you position your body in a way that is different to most people (for example, lie on your back on a sofa with your legs straight up in the air at a 90° angle)?								
	Never	Rarely	Sometimes	Often	Always				
38.	38. Do you find it difficult to tie your shoelaces or button up your clothes?								
	Never	Rarely	Sometimes	Often	Always				
39. Do you find that you are able to go outside without a coat or a jacket when other people think that it is too cold?									
	Never	Rarely	Sometimes	Often	Always				
40.	Do you eat the same	foods most of the	time?						
	Never	Rarely	Sometimes	Often	Always				
41.	41. Do you like to wear something/hold something (for example, a hat or a pencil) so that you know where your body 'ends'?								
	Never	Rarely	Sometimes	Often	Always				
42.	Do you flick your fin	gers in front of yo	ur eyes?						
	Never	Rarely	Sometimes	Often	Always				

Appendix C

Multi-Modality Unusual Sensory Experiences Questionnaire (MUSEQ) (Mitchell et al, 2017)

We now know that both healthy people and people with medical or psychological conditions report having strange or unusual experiences. These experiences range from being very subtle to quite obvious. We want to find out more. Please answer <u>all</u> questions by **placing a tick or cross (** \checkmark or X) in the most appropriate response box. There are no right/wrong answers and your responses are kept confidential.

SECTION	A: AUD	ITORY
---------	--------	-------

There have been times when	Never (Never happened)	Hardly Ever (Once or twice in my life)	Rarely (Once or twice a year)	Occasionally (A few times a year)	Frequently (At least monthly)
My ears have played tricks on me					
Sounds were louder than they normally would be					
I thought of a song and could almost hear it with distinct clarity					
I was in a crowd or with other people and heard my name being called, only to find that I was mistaken					
I have heard my phone ring then found that it wasn't ringing at all					
I could hear sounds, music, or noises that other people could not hear					
I have heard a person's voice and then found that no-one was there					

Please continue to next page \rightarrow

Please answer <u>all</u> questions by placing a tick or response box

cross (\checkmark or X) in the most appropriate

SECTION B: VISUAL

There have been times when	Never (Never happened)	Hardly Ever (Once or twice in my life)	Rarely (Once or twice a year)	Occasionally (A few times a year)	Frequently (At least monthly)
My eyes have played tricks on me					
I found that lights or colours seem brighter or more intense than they normally would be					
I thought of people, objects, or landscapes, and could almost see their image in front of my eyes					
I have looked at a patterned object (e.g., wallpaper, curtains, tiled floor) and a figure or face has emerged					
I have seen lights, flashes, or other shapes that other people could not see					
I looked at an object and it transformed itself before my eyes into something else					
I saw a brief image of an object, animal, or person pass me by in my peripheral vision, but when I looked there was nothing there					
I saw people, faces, or animals, and then found that nothing was there					

Please continue to next page \rightarrow

Please answer <u>all</u> questions by **placing a tick** response box or cross (\checkmark or X) in the most appropriate

SECTION C: SMELL

There have been times when	<i>Never</i> (Never happened)	Hardly Ever (Once or twice in my life)	Rarely (Once or twice a year)	Occasionally (A few times a year)	Frequently (At least monthly)
My nose (sense of smell) has played tricks on me					
I thought that everyday smells were unusually strong					
I thought of a smell and I could almost smell it for real					
Common smells seemed unusually different					
I noticed the smell of smoke, burning, or gas when there was nothing there					
I have suddenly been struck by an unpleasant or disgusting smell that no-one else could smell					
I have suddenly been struck by a very pleasant smell that no- one else could smell					
I have been struck with the smell of odd things which I interpreted as death, colours, or ghosts					

Please continue to next page \rightarrow

Please answer all questions by placing a tick or cross (✓ or X) in the most appropriate response box

SECTION D: TASTE

There have been times when	Never (Never happened)	Hardly Ever (Once or twice in my life)	Rarely (Once or twice a year)	Occasionally (A few times a year)	Frequently (At least monthly)
My sense of taste has played tricks on me					
I thought that food or drink tasted stronger than it normally would					
I thought of a taste and found that I could taste it in my mouth as if it was real					
I ate the same food as another person and thought it tasted off, but the other person did not seem to think so					
I have consumed food or drink and it tasted like something completely different					
I had nothing in my mouth but I suddenly tasted something very confusing which faded very quickly					
I had nothing in my mouth but I suddenly tasted something unpleasant which was really persistent					
I had nothing in my mouth but I suddenly tasted something very pleasant which was really persistent					

Please continue to next page \rightarrow

Please answer all questions by placing a tick or cross (✓ or X) in the most appropriate response box

SECTION E: BODY SENSATIONS

There have been times when	Never (Never happened)	Hardly Ever (Once or twice in my life)	Rarely (Once or twice a year)	Occasionally (A few times a year)	Frequently (At least monthly)
My body senses have played tricks on me					
I found my skin to be more sensitive to cold, heat, or touch than usual					
I thought of a touch or other sensations on my skin and almost felt it on my skin					
I have experienced the sensation that my body (or part of my body) was different in shape or size					
I could feel burning, tingling, scraping, or heat on my skin, although there was nothing causing it					
I have felt things moving or crawling on or under my skin					
I have experienced the sensation that something was pressing on my skin, or that I was holding an object in my hand, but then found there was nothing there					
I have felt someone or something touching me, but when I turned to look there was nothing there					

Please continue to next page \rightarrow

Please answer <u>all</u> questions by **placing a tick or response box** cross (✓ or X) in the most appropriate

SECTION F: SENSED PRESENCE

There have been times when	Never (Never happened)	Hardly Ever (Once or twice in my life)	Rarely (Once or twice a year)	Occasionally (A few times a year)	Frequently (At least monthly)
I felt the presence of someone, even though I could not see them (e.g., behind me, or in another room)					
I have felt an unseen evil presence around me					
I have felt an unseen angelic presence around me					
I have felt the presence of a relative or friend who has passed away					

Chapter 3: Functional Connectivity is Stronger Between Unisensory and Multisensory Regions for Non-Simultaneous Judgements of Visual-Tactile Stimuli

3.0 Abstract

Multisensory integration is an automatic process that occurs across unisensory and multisensory areas of the brain. Although multisensory integration is often quantified using the simultaneity judgment task, which measures the temporal binding window for multisensory integration, little is known about the neural processes associated with the task. In 26 participants, we used electroencephalography to measure functional connectivity between parietal - occipital, parietal - central, and central - occipital regions during the simultaneity judgment task. Our aim was to compare patterns of connectivity between simultaneous and non-simultaneous perception, which is crucial for calculating the temporal binding window. Further, participants completed three questionnaires — Autism Quotient, the Glasgow Sensory Experiences Questionnaire and the Multi-Modality Unusual Sensory Experiences Questionnaire — to examine the relationship between the temporal binding window and autistic traits, sensory sensitivity and unusual sensory experiences. Results show functional connectivity in the beta frequency was stronger between parietal-occipital, parietal-central and central-occipital regions when individuals perceived visual-tactile stimuli as non-simultaneous than simultaneous, however; was only stronger in the theta and alpha frequencies for parietal-central and central-occipital regions. Stronger connectivity in the theta and alpha frequencies is likely associated with detecting and encoding changes in temporal dynamics between cross-modal, and in the beta frequency stronger connectivity is likely related to a violation of expectancy for simultaneous stimuli. We found minimal evidence supporting a relationship between the width of the window and autistic traits, sensory sensitivity and unusual sensory experiences. Overall, our findings demonstrate that functional connectivity between unisensory and multisensory neural regions occurring during (and immediately following) stimulus presentation is important for the perception of simultaneity.

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3.1 Introduction

Our perceptual experience is shaped by the integration of various sensory inputs, such as visual, auditory, and tactile information, which are processed, integrated, and interpreted by the brain. The formation of our perceptual experience is largely facilitated by the temporal binding window (TBW) for multisensory integration. The TBW is a period in which multisensory stimuli are bound together (i.e., integrated) into a single percept and attributed to an event in the environment (Vroomen & Keetels, 2010). When TBWs are wider (i.e., multisensory integration occurs over a longer period), there is more opportunity for irrelevant information to be bound together with relevant information (Wallace & Stevenson, 2014), which in turn can distort our perceptual experiences and make it difficult to effectively interact with the environment (Iarocci & McDonald, 2006). In clinical populations, wider TBWs have been associated with social and communication differences in autism spectrum disorder (ASD), and hallucinations in schizophrenia (Stevenson et al., 2017; Stevenson et al., 2014a; Zhou et al., 2021b). In both clinical and non-clinical populations, the TBW for multisensory integration is typically measured using the simultaneity judgment task. In this task, participants are presented with two stimuli from different modalities, either simultaneously or at varying stimulus onset asynchronies (SOAs), and they are asked to judge whether the stimuli occurred simultaneously. The width of the TBW is taken from the timepoint at which participants display ambiguity in their judgments about whether stimuli are simultaneous or non-simultaneous.

Behavioural studies have used the simultaneity judgment task to measure the audiovisual, visual-tactile and olfaction-gustation TBWs (Chen et al., 2018; Costantini et al., 2016; Gotow & Kobayakawa, 2023; Hillock et al., 2011; Ikeda & Morishita, 2020; Migliorati et al., 2020; Opoku-Baah & Wallace, 2021; Stevenson et al., 2012a; Stevenson & Wallace, 2013; Stevenson et al., 2012b). To understand mechanisms underlying the TBW, electroencephalography (EEG) research has primarily focused on the neural activity that occurs *prior* to the onset of the first stimulus in cross-modal simultaneity judgment tasks, that is, the activity that occurs prior to multisensory binding. Simultaneity perception, which refers to the ability to distinguish between simultaneous and non-simultaneous stimuli, has been associated with pre-stimulus individual alpha frequency and pre-stimulus alpha power, such that individuals with faster alpha oscillations and stronger alpha power can more easily distinguish between simultaneous and non-simultaneous audio-visual and visual-tactile stimuli (Bastiaansen et al., 2020; Migliorati et al., 2020). Whereas individuals with slower pre-stimulus alpha oscillations and weaker pre-stimulus alpha power perceive stimuli as occurring simultaneously at longer SOAs. Simultaneity perception of audio-visual stimuli is also influenced by pre-stimulus beta (14 - 28 Hz) and gamma (55 - 80 Hz) oscillatory power (Bastiaansen et al., 2020; Ikumi et al., 2019; Yuan et al., 2016). In the beta (14-28 Hz) and gamma (55-80 Hz) frequency bands, pre-stimulus power across parietal-occipital areas was stronger when audio-visual stimuli were perceived as occurring simultaneously than nonsimultaneously, and weaker when visual-auditory stimuli were perceived as simultaneous rather than non-simultaneous (Yuan et al., 2016). Similarly, functional connectivity measured during an audio-visual simultaneity judgment task showed stronger pre-stimulus connectivity across auditory and visual regions in the beta-high frequency (21-28 Hz) when stimuli were perceived as occurring simultaneously than non-simultaneously, but this pattern of connectivity was not replicated for visual-auditory stimuli (Jiang et al., 2023). This prestimulus research is important as it shows that the state of the brain prior to stimulus onset influences whether individuals perceive stimuli as occurring simultaneously or nonsimultaneously. However, given that judgments about simultaneity can only be made after presentation of the stimuli, the perception of simultaneity is more likely to be influenced by neural activity occurring during and immediately following stimulus presentation.

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An additional factor influencing the perception of simultaneity, and consequently the duration of temporal binding, is the neural activity that occurs either *during* or immediately after stimulus presentation. When recording neural activity with EEG during an audio-visual simultaneity judgment task, individuals with narrower audio-visual TBWs showed stronger connectivity across distributed populations of neurons in various regions of the brain, particularly in the temporal and frontal regions, than in localized populations of neurons (Johnston et al., 2022). By comparison, individuals with wider TBWs – who integrate multisensory information across a longer period - showed stronger connectivity in localized populations of neurons than in distributed populations of neurons. Thus, efficient integration of multisensory information involves strong connections between various neural regions activated during the simultaneity judgment task with audio-visual stimuli. However, it is unclear whether specific areas associated with the processing of unisensory and multisensory stimuli during the simultaneity judgment task show increased functionally connectivity, particularly for visual-tactile information. Gaining an understanding about the connectivity patterns between neural regions associated with the processing of visual-tactile stimuli during, and immediately following, stimulus presentation in the simultaneity judgment will improve our understanding about multisensory integration in general. This understanding will further aid exploring multisensory integration differences between neurotypical and neurodivergent populations, (e.g., ASD and schizophrenia).

In the current study, we examine functional connectivity between somatosensory (tactile), occipital (visual) and parietal (multisensory) regions *during* temporal binding in a visual-tactile simultaneity judgment task. Our study focuses on connections between neural regions associated with unisensory and multisensory processing of visual and tactile information As multisensory interactions and the transfer of sensory information between cortices induces changes in oscillatory activity in the theta, alpha and beta frequencies (Bauer

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et al., 2020; Göschl et al., 2015; Senkowski et al., 2008), we have focused on functional connectivity within these frequency bands. We hypothesise that functional connectivity between parietal-occipital, parietal-central and central-occipital regions will be stronger when individuals perceive visual-tactile stimuli as simultaneous than non-simultaneous in the simultaneity judgment task. Further, to investigate the relationship between the width of the visual-tactile TBW and autistic traits, sensory sensitivity, and unusual sensory experiences, we hypothesise that wider TBWs will be related to the severity of autistic traits, higher sensory sensitivities and increased unusual sensory experiences.

3.2 Method

3.2.1 Participants

Twenty-six participants were recruited from Curtin University undergraduate student population to participate in the study (M = 20.88 years old, SD = 3.14, 20 female). All volunteers received credit points towards their course as compensation for their participation in the study. We determined our sample size based on previous research investigating multisensory interactions with EEG (Bastiaansen et al., 2020; Göschl et al., 2015; Hipp et al., 2011; Ikumi et al., 2019; Migliorati et al., 2020; Wang et al., 2019), exceeding the typically observed sample sizes in comparable studies within this research area. All participants were right-handed, reported an absence of colour blindness and had no known neurological condition. Written informed consent was obtained from the participants prior to conducting the experiments. The study was approved by Curtin University Human Research Ethics Committee (HRE2018-0257). Participants completed a demographics questionnaire, the simultaneity judgment task, and three questionnaires: the Autism Quotient (AQ), Glasgow Sensory Questionnaire (GSQ) and the Multi-modality Unusual Sensory Experiences Questionnaire (MUSEQ).

3.2.2 Materials

<u>Stimuli</u>

One visual stimulus and one tactile stimulus were used in the experiment. The visual stimulus was a 5 mm green light emitting diode (LED; 10,000 mcd) and the tactile stimulus was a 10 x 3.4 mm shaftless vibration motors (Pololu Corporation, Las Vegas, NV; Pololu item #1636). The visual and tactile stimuli were placed beside each other on the participants right index finger under a semi-transparent fabric elastic band that was secured with micropore tape. The participant's hand was then placed onto a raised piece of foam with the index finger resting at a similar level to the instruction on the computer monitor. This placement of the hand on the foam aimed to reduce excessive eye muscle activity from the participant moving their eyes between the monitor and the stimuli on their finger. Both the visual and tactile stimuli were presented for 50 ms duration in each trial. Timing triggers for presentation of the stimuli were sent direct from the computer via a parallel port connection. The experiment was programmed in MATLAB version 2015b and instructions for the task were displayed on a 19" Dell LCD computer monitor (60 Hz refresh rate) using Psychtoolbox (version 3.0.8).

Questionnaires

The Autism Quotient (AQ), the Glasgow Sensory Questionnaire (GSQ) and the Multi-Modality Unusual Sensory Experiences Questionnaire (MUSEQ) were transferred into electronic format in Inquisit (version 6) and were administered to participants following the simultaneity judgment task. The AQ is a 50-item self-report scale measuring the severity of autistic traits (Baron-Cohen et al., 2001). The AQ consists of five subscales - social skills, attention switching, attention to detail, communication, and imagination – and includes four response options from 'definitely agree' to 'definitely disagree' (Baron-Cohen et al., 2001; Woodbury-Smith et al., 2005). AQ scores range from 0 to 50 and are in three ranges: 0-25 indicates few autistic traits, 26-32 indicates some autistic traits, and 33-50 indicates significant autistic traits. The GSQ is a 42-item self-report scale that measures hyper- and hypo- sensory sensitivity typically associated with Autism Spectrum Disorder (Robertson & Simmons, 2013). The GSQ measures the frequency of hyper- and hypo-sensory sensitivity and consists of seven sensory sub-scales: vision, audition, gustation, olfaction, tactile, vestibular and proprioception. All items in the GSQ are on a 5-point Likert scale and range from 0 ('never') to 4 ('always'). GSQ scores range from 0-168 with higher scores indicating greater hyper- or hypo- sensory sensitivity overall and for each sensory modality. The MUSEQ is a 43-item self-report scale that measures the regularity of unusual sensory experiences occurring and consists of six sensory sub-scales including, vision, audition, gustation, olfaction, bodily sensations, and sensed presence (Mitchell et al., 2017). All items in the MUSEQ are on a 5-point Likert scale and range from 0 ('never') to 4 ('frequently'). The total score on the MUSEQ ranges from 0 to 172, and subscale scores are between 0-32 for vision, olfaction, gustation and bodily sensations, 0-28 for audition, and 0-16 for sensed presence. Higher scores on the MUSEQ indicate increased occurrences of unusual sensory experiences.

3.2.3 Procedure

In the simultaneity judgment task, participants were presented with two sensory stimuli, one light as the visual stimulus and one vibration as the tactile stimulus. Participants were instructed to attend to both stimuli: the words "Both stimuli" were presented on the screen at the beginning of each trial, prior to stimulus onset (see Figure 3.1 for trial design) to prompt participants to attend to both stimuli. Stimuli were presented either together (i.e., simultaneously) or at various stimulus onset asynchronies (SOAs) ranging from +/- 25, 50, 75, 100, 125 and 150 ms. Positive SOAs indicate that the visual stimulus preceded the tactile stimulus ("visual-tactile"), and negative SOAs indicate that the tactile stimulus preceded the

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visual stimulus ("tactile-visual"). There were four target positive SOAs: 0, 50, 75 and 100 ms, three non-target positive SOAs: 25, 125 and 150 ms, and six non-target negative SOAs: 25, 50, 75, 100, 125 and 150 ms. "Target" SOAs refer to the SOAs we wanted to obtain enough stimuli for EEG analysis. The "non-target" visual-tactile and tactile-visual SOAs were used to reduce the likelihood of participants learning which trials were simultaneous and non-simultaneous, which may have happened if they had repeated exposure to only a few SOAs. The visual-tactile target positive SOAs were the primary interest for this study as our previous research shows that the width of the VT-TBW is reliably narrower for each participant than the TV-TBW (Huntley et al., 2023); higher variability in the size of the TV-TBW precludes it from group-level analysis with EEG. The target SOAs are based on our previous findings that show at SOA 0 ms individuals perceive visual-tactile stimuli occurring simultaneously for approximately 90% of trials and at SOA 100 ms individuals perceive the stimuli as occurring simultaneously for approximately 50% of the trials. Following presentation of the cross-modal stimuli in each trial, participants were asked "Were the stimuli simultaneous?", and participants responded either 'yes' by pressing the left mouse button or 'no' by pressing the right mouse button. After the participant responded, the next trial started automatically. There were 410 trials in total presented in random order: 80 trials presented for each target SOA and 10 trials presented for each non-target SOA. There was one designated break during the task, lasting a minimum of 10 sec. Participants completed practice trials before commencing the experiment. The practice trials and experimental task were completed in a dimly lit room. Following completion of the simultaneity judgment task, participants completed the three questionnaires: AQ, GSQ and MUSEQ.

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Figure 3.1: Graphical representation of the trial design for visual-tactile stimuli presented in the simultaneity judgment task. Green circle represents the green LED used as the visual stimulus and the white star represents the vibration motor that was used as the tactile stimulus. Stimuli were presented at these SOAs: +/- 0, 25, 50, 75, 100, 125, 150 ms.

3.3 Electroencephalography (EEG) processing

3.3.1 EEG acquisition and pre-processing

EEG data were recorded continuously throughout the simultaneity judgment task using a 64-channel Biosemi Active Two EEG system and ActiView (version 7.07). Data were sampled at 2,048 Hz with a DC-100 Hz online filter. The 64-channel electrodes were positioned on the scalp in accordance with the 10-20 system and additional electrodes were placed adjacent to the outer canthi of both eyes and on the left infraorbital region to record eye muscle activity. The EEG data were pre-processed offline using MATLAB (version 2018b) and EEGLAB (version 14.1.2, Delorme & Makeig, 2004), with Cz as the reference electrode. Prior to filtering the data, electrode channels recorded from the outer canthi of both eyes and on the left infraorbital region were removed from the dataset. Each data set was visually inspected to identify channels that showed excessive noise or drift, which was not typical of neural activity, and these channels were interpolated. A high-pass filter of 0.5 Hz and a low-pass filter of 45 Hz were applied to the data and then subsequently down-sampled to 256 Hz. The epoch length was initially set to -1600 ms to 2500 ms relative to the onset of the first stimulus and baseline amplitudes were corrected based on the 100 ms period preceding the onset of the first (visual) stimulus. After baseline correction, data were timelocked to the second (tactile stimulus) in the cross-modal pair. Independent components analysis was performed using adaptive mixture independent component analysis (AMICA, version 1.5, Palmer et al., 2012), and components were visually inspected for each participant. Components that were identified as artifacts, such as eye blinks and muscle activity, were subtracted from each participant's data. Artifact rejection was determined by removing activity that was less than -75 mV or exceeded 75 mV, and Surface Laplacian was applied to the pre-processed EEG data to minimise the impact of volume conduction contaminating the signal (Carvalhaes & de Barros, 2015; Perrin et al., 1989).

3.3.2 Time-frequency decomposition

After pre-processing, time-frequency decomposition was performed on the EEG signal to extract information about both the temporal and spectral characteristics of the signal in preparation for connectivity analysis. The data for time-frequency decomposition were organised based on experimental condition with SOA and response type (either 'yes' for simultaneous and 'no' for non-simultaneous) used as sorting variables. Morlet wavelet convolution was performed for time-frequency decomposition with a frequency range of 1-50 Hz, 30 frequencies, and a cycle range of 4-13 cycles (increasing in frequency) in MATLAB. Trials were split by the target SOA – SOA0, SOA50, SOA75 and SOA100 – and then split by response into 'yes' for simultaneous and 'no' for non-simultaneous. Data were converted to FieldTrip format using the FieldTrip toolbox (version 2019; Oostenveld et al., 2011) to calculate debiased weighted phase lag index (dWPLI).

3.4 Data Analysis

3.4.1 Measuring the temporal binding window

The percentage of simultaneity responses (i.e., 'yes', 'no' to the question 'were the stimuli simultaneous?') were averaged for each participant at each SOA and fitted with a

model-free line across all SOAs using the modelfree package in RStudio (Model-Free Estimation of a Psychometric Function, version 1.2) (Zychaluk & Foster, 2009). The modelfree function is a parameter free method that has no assumptions about the shape of the data. This function is an alternative to a Gaussian or sigmoid function, which are commonly used methods for fitting the rate of perceived simultaneity data in simultaneity judgment tasks (Costantini et al., 2016; Hillock-Dunn & Wallace, 2012; Hillock et al., 2011; Migliorati et al., 2020; Moro & Steeves, 2018; Noel et al., 2016; Noel et al., 2017a; Powers et al., 2009; Stevenson et al., 2018; Stevenson et al., 2014a; Stevenson & Wallace, 2013; Venskus et al., 2021). To estimate the width of the TBW for each participant, we measured the halfway point between 0% (no perceived simultaneity) and the maximal peak of simultaneity perception on the y-axis and where this half-way point intersects the model-free fitted line on the x-axis. The distance (in ms) between where this halfway point on the y-axis intersects with the model-free fitted line on the x-axis is taken as the width of the TBW.

3.4.2 Correlations between the TBW and questionnaires

Spearman's rank-order correlation coefficient was calculated between the width of the visual leading visual-tactile TBW and the three questionnaires (AQ, GSQ and MUSEQ). These correlations were conducted to investigate the relationship between the length of time multisensory information is integrated across and autistic traits, sensory sensitivity and unusual sensory experiences. Spearman correlations were also calculated between the questionnaires, AQ and GSQ, AQ and MUSEQ, and the GSQ and MUSEQ.

3.4.3 Debiased weighted phase lag index (dWPLI)

Debiased weighted phase lag index (dWPLI) is a functional connectivity measure that is an extension of previous phase synchronization methods, imaginary component of the coherency (IMC) (Nolte et al., 2004), and phase lag index (PLI, Stam et al., 2007). These methods measure synchronization between neural regions while reducing the potential for capturing spurious connectivity. We used the dWPLI method for measuring connectivity over other methods of phase synchronization (i.e., weighted PLI and PLI) as it is robust against volume conduction and is not limited by sample size (Vinck et al., 2011). Using FieldTrip in MATLAB, dWPLI was averaged across frequency ranges from 2 to 30 Hz in steps of 1 Hz, and across a time range of 0 to 400 ms, in steps of 5 ms, from the onset of the second stimulus. Then, dWPLI was calculated between all channel pairs (4,489 electrode pairs), across SOAs (SOA50, SOA75, SOA100), response ('yes' = simultaneous, 'no' = nonsimultaneous perception) and time-ranges (0-100 ms, 100-200 ms, 200-300 ms and 300-400 ms) in four frequency bands: theta (4-7 Hz), alpha (7-11 Hz), beta-low (12-20 Hz) and betahigh (20-30 Hz) (see Figure 3.2). dWPLI values range from -1 to +1, with 1 indicating maximum connectivity; negative values typically occur to due reduced sampling and therefore were corrected to zero values prior to statistical analysis (Yusuf et al., 2021). We analysed dWPLI between P5-Oz, C5-Oz, C5-P5 as these electrode pairs are the most relevant for our study measuring connectivity between unisensory areas and between unisensory and multisensory areas. Note, due to insufficient non-simultaneous responses at SOA0 across participants (likely due to the perception of simultaneity being at maximum), we have only presented results for simultaneous responses at SOA0 in Figures 3.4-3.6 and did not include SOA0 in the statistical analysis.

Linear mixed models (LMM) were conducted using the lme4 function in the lmerTest package (version 1.1-33, Bates et al., 2015) in R (R version 4.3.2; RStudioTeam). Results from the LMMs are reported as F-values, obtained using the "anova" function with Satterthwaite method applied for correcting degrees of freedom. LMMs were conducted to analyse the effect of dWPLI on response ('yes' or 'no'), time-range (0-100 ms, 100-200 ms, 200-300 ms, 300-400 ms) and SOA (50, 75, 100), with response, time-range and SOA as the

fixed factors and participants as the random factor. LMMs were performed for each electrode pair (P5-Oz, C5-Oz, C5-P5) and frequency band (theta, alpha, beta-low and beta-high).



Figure 3.2: The left image shows the timing of stimuli presentation for SOA50, SOA75 and SOA100 relative to the onset of the tactile stimulus. For statistical analysis, data were time-locked to the tactile stimulus, which is depicted in this figure as the tactile stimuli are all aligned at 0 ms. Green circles and arrows show the onset and duration of the visual stimulus. Black star shows the onset and duration of the tactile stimulus. The incremental shading for 0-100, 100-200, 200-300 and 300-400 ms shows the time-ranges that were examined in the connectivity analysis. The right image shows the three electrode pairs used for connectivity analysis (P5-Oz, C5-Oz and C5-P5).

3.5 Results

3.5.1 Behavioural data

The visual-tactile TBW was significantly narrower (VT; M = 93 ms, SD = 33 ms) than the tactile-visual TBW (TV; M = 129 ms, SD = 48 ms), (t(25) = 17.1, p < 0.001 (See Figure 3.3). However, for 17 participants, the mean width of their TV-TBW was set at the maximum SOA tested in our experiment of 150 ms and their width may extend beyond 150 ms. So, these results may underestimate the difference between VT and TV TBWs. Furthermore, for 3 participants, the uniformity of the response data limited the applicability of the model-free fitting, resulting in an estimated TV-TBW of 0 ms.



Figure 3.3: Combined group averaged data of perceived simultaneity for visual-tactile (black) and tactile-visual (red) stimuli with model-free line fitted to the data. Error bars represent standard error.

3.5.2 Connectivity using dWPLI

Parietal - Central (P5-C5). There were significant response by SOA interactions for all frequencies (Table 3.1), thus indicating that the simultaneity of stimuli could be determined when stimuli were presented at SOAs of 50, 75 and 100. Specifically, at SOA50, dWPLI connectivity was stronger when individuals perceived visual-tactile stimuli as non-simultaneous compared to simultaneous for all frequency bands. At SOA75, dWPLI connectivity was stronger when individuals perceived visual-tactile stimuli as non-simultaneous compared to simultaneous for theta, beta-low, and beta-high. While at SOA100, theta connectivity was increased for non-simultaneous perception (see Figure 3.4).
Table 3.1.

		Theta	
	df	F	р
Response	1, 575	48.346	< 0.001*
Time	3, 575	1.265	0.285
SOA	2, 575	11.564	< 0.001*
Response:Time	3, 575	0.983	0.400
Response:SOA	2, 575	13.179	< 0.001*
Time:SOA	6, 575	0.857	0.526
Response:Time:SOA	6, 575	0.802	0.568

Parietal – Central ANOVA tables for theta, alpha, beta-low and beta-high frequencies.

	Alpha		
	df	F	р
Response	1, 575	22.064	< 0.001*
Time	3, 575	1.024	0.381
SOA	2, 575	1.941	0.144
Response:Time	3, 575	1.805	0.145
Response:SOA	2, 575	9.286	0.0001*
Time:SOA	6, 575	0.791	0.577
Response:Time:SOA	6, 575	1.607	0.142

	Beta-low		
	df	F	р
Response	1, 575	47.463	< 0.001*
Time	3, 575	1.742	0.157
SOA	2, 575	3.154	0.043*
Response:Time	3, 575	1.237	0.295
Response:SOA	2, 575	6.5082	0.001*
Time:SOA	6, 575	0.7860	0.581
Response:Time:SOA	6, 575	1.0475	0.393

	Beta-high		
	df	F	р
Response	1,600	52.6354	< 0.001*
Time	3,600	0.2011	0.895
SOA	2,600	7.3139	< 0.001*
Response:Time	3,600	0.3936	0.757
Response:SOA	2,600	8.7380	< 0.001*
Time:SOA	6,600	1.5625	0.155
Response:Time:SOA	6,600	1.2865	0.261



Figure 3.4: Parietal-Central dWPLI values for 'yes' (simultaneous) and 'no' (non-simultaneous) responses by SOA across theta, alpha, beta-low and beta-high frequencies. The electrode pair – C5 and P5 – represents the tactile and multisensory areas of the cortex, respectively. Error bars represent the standard error of the model estimates.

Parietal – Occipital (P5-Oz). There was a significant response by SOA interaction for beta-high and main effects for response, time and SOA for beta-low (see Table 3.2), thus indicating that activity in the beta-high frequency contributes to the accuracy of perceiving stimuli as non-simultaneous when they occur at SOA50. In both cases, dWPLI was generally stronger for non-simultaneous perception than simultaneous perception across all time-ranges, with the largest difference for beta-high at SOA50. For theta and alpha, there were only main effects of time, with dWPLI decreasing in strength from 0 ms to 400 ms for all SOAs (Figure 3.5).

Table 3.2.

	Theta			
	df	F	р	
Response	1, 575	2.3309	0.127	
Time	3, 575	19.752	< 0.001*	
SOA	2, 575	0.638	0.529	
Response:Time	3, 575	0.343	0.794	
Response:SOA	2, 575	0.643	0.526	
Time:SOA	6, 575	0.204	0.975	
Response:Time:SOA	6, 575	0.373	0.896	

Parietal – Occipital ANOVA tables for theta, alpha, beta-low and beta-high frequencies.

	Alpha		
	df	F	р
Response	1, 575	2.079	0.149
Time	3, 575	19.454	< 0.001*
SOA	2, 575	0.356	0.700
Response:Time	3, 575	0.496	0.685
Response:SOA	2, 575	0.530	0.589
Time:SOA	6, 575	0.544	0.775
Response:Time:SOA	6, 575	0.514	0.798

	Beta-low		
	df	F	р
Response	1, 575	12.492	0.0004*
Time	3, 575	4.587	0.003*
SOA	2, 575	4.074	0.017*
Response:Time	3, 575	0.346	0.791
Response:SOA	2, 575	1.190	0.304
Time:SOA	6, 575	1.394	0.214
Response:Time:SOA	6, 575	0.780	0.585

	Beta-high		
	df	F	р
Response	1, 575	59.046	< 0.001*
Time	3, 575	0.351	0.7887
SOA	2, 575	5.629	0.003*
Response:Time	3, 575	1.023	0.382
Response:SOA	2, 575	4.750	0.009*
Time:SOA	6, 575	0.684	0.662
Response:Time:SOA	6, 575	0.576	0.749



Figure 3.5: Parietal-Occipital dWPLI values for 'yes' (simultaneous) and 'no' (non-simultaneous) responses by SOA across theta, alpha, beta-low and beta-high frequencies. The electrode pair -P5 and Oz - represents the multisensory and visual areas of the cortex, respectively. Error bars represent the standard error of the model estimates.

Central - Occipital (Oz-C5). There were significant response by SOA interactions for all frequencies (Table 3.3), and an additional time by SOA interaction in the alpha frequency. Broadly, these results indicated that connectivity was stronger for non-simultaneous perception at SOA50 and SOA75, but not SOA100 (Table 3.3). In the theta, alpha and beta-low frequencies there were main effects of response, and an additional main effect of SOA in the theta frequency, thus indicating connectivity was stronger for non-simultaneous perception across these frequencies, particularly at SOA50 and SOA75 in the theta frequency. For beta-high, the main effect of time reflects stronger connectivity for non-simultaneous

perception at early time-points (0-200 ms) followed by a decrease in connectivity strength over time (see Figure 3.6).

Table 3.3.

Central–Occipital ANOVA tables for theta, alpha, beta-low and beta-high frequencies.

		Theta	
	df	F	р
Response	1, 575	67.371	< 0.001*
Time	3, 575	0.680	0.564
SOA	2, 575	14.250	< 0.001*
Response:Time	3, 575	0.164	0.920
Response:SOA	2, 575	8.620	0.0002*
Time:SOA	6, 575	0.649	0.690
Response:Time:SOA	6, 575	0.672	0.672

	Alpha		
	df	F	р
Response	1, 575	40.523	< 0.001*
Time	3, 575	1.047	0.371
SOA	2, 575	2.386	0.092
Response:Time	3, 575	0.553	0.646
Response:SOA	2, 575	5.958	0.002*
Time:SOA	6, 575	2.216	0.040*
Response:Time:SOA	6, 575	1.384	0.218

	Beta-low		
	df	F	р
Response	1, 575	59.244	< 0.001*
Time	3, 575	2.494	0.059*
SOA	2, 575	1.484	0.227
Response:Time	3, 575	1.074	0.359
Response:SOA	2, 575	3.576	0.028*
Time:SOA	6, 575	0.973	0.442
Response:Time:SOA	6, 575	1.462	0.189

	Beta-high		
	df	F	р
Response	1, 575	40.360	< 0.001*
Time	3, 575	0.382	0.766
SOA	2, 575	1.940	0.144
Response:Time	3, 575	0.852	0.465
Response:SOA	2, 575	3.243	0.039*
Time:SOA	6, 575	0.420	0.865
Response:Time:SOA	6, 575	0.576	0.749



Figure 3.6: Central – Occipital dWPLI values for 'yes' (simultaneous) and 'no' (non-simultaneous) responses by SOA across theta, alpha, beta-low and beta-high frequencies. The electrode pair – C5 and Oz – represents the visual and tactile areas of the cortex, respectively. Error bars represent the standard error of the model estimates.

3.5.3 Correlations with questionnaires and the TBW

The mean score for the group on the AQ was 12.2 (SD = 5.1), the GSQ was 50.2 (SD = 16.6), and the MUSEQ was 52.6 (SD = 29.4). All scores on the questionnaires were within a typical range for a non-clinical sample. The Spearman rank-order correlation coefficients were significant between the AQ and GSQ, $\rho = 0.61$ (p < 0.001), and the MUSEQ and GSQ, $\rho = 0.69$ (p < 0.001). The AQ and MUSEQ was also correlated, but less strongly $\rho = 0.39$ (p = 0.05) (see Figure 3.7). We failed to find significant correlations between the VT-TBW and the AQ $\rho = -0.20$ ([CI -0.54, 0.21], p = 0.34), GSQ $\rho = -0.24$ ([CI -0.57, 0.17], p = 0.25) and the MUSEQ $\rho = -0.12$ ([CI -0.49, 0.28], p = 0.55).



Figure 3.7: Scatterplots show correlations between the AQ and GSQ*, AQ and MUSEQ and the GSQ and MUSEQ*. *Denotes significant correlations.

3.6 Discussion

Our study measured functional connectivity between neural regions associated with unisensory and multisensory processing to understand differences in the strength of connectivity between simultaneous and non-simultaneous judgements of visual-tactile stimuli pairs. Generally, our results show stronger functional connectivity between central-occipital and parietal-central regions when individuals perceive visual-tactile stimuli as nonsimultaneous compared to simultaneous across theta, alpha and beta frequencies, but for parietal-occipital this effect was only observed in the beta frequencies. The strength of connectivity was largely similar across regions, SOAs and time-ranges, which suggests temporal binding of multisensory stimuli occurs automatically, thus giving rise to the perception of simultaneity. This pattern of results for all sites was opposite to what we predicted, and is in contrast to previous research that shows pre-stimulus connectivity was stronger for simultaneous than non-simultaneous responses (Jiang et al., 2023).

It is likely that stronger connectivity for non-simultaneous responses in the theta and alpha frequencies for central-occipital and parietal-central reflects the detection and encoding of temporal differences of each stimulus in the cross-modal pair (Kayser et al., 2012) and the shifting of attention between multisensory stimuli (Keil & Senkowski, 2018; Keller et al., 2017). For example, at SOA50 the visual stimulus is presented for a duration of 50ms, and then the tactile stimulus is presented for 50 ms. This timing of stimuli is difficult within the constraints of our perceptual system. Since these stimuli are presented immediately following each other, greater attention to, and encoding of, the temporal onset and offset of the stimuli is required to make a judgment on whether the stimuli occurred simultaneously or non-simultaneously. The increase in attention and encoding of temporal differences between stimuli is reflected by increased connectivity for non-simultaneous perception as these stimuli are actually occurring non-simultaneously. Supporting this idea, connectivity was strongest primarily at SOA50 and SOA75, which attention and encoding of the temporal differences are most crucial due to the ambiguity of judging simultaneity at these short SOAs compared to longer SOAs (e.g., SOA100), when it is arguably easier to correctly identify stimuli as simultaneous or non-simultaneous. Activity in the theta and alpha frequency connecting parietal and occipital areas to a central site likely plays a specific role in maintaining attention (Keller et al., 2017), explaining why we observe stronger connectivity between these regions than for parietal-occipital connectivity.

In the beta frequency (12-30 Hz), stronger connectivity for non-simultaneous responses likely reflects a violation of expectation and the feed forward/back of information about this violation. That is, the brain has been conditioned across trials to expect multiple stimuli in the environment to occur simultaneously due to two stimuli being presented in each trial within close temporal proximity, so when stimuli are perceived as non-simultaneous, potentially an expectancy/prediction is violated. Beta oscillations have been suggested to facilitate both feed-forward and feedback flow of information (Alais et al., 2010; Keil & Senkowski, 2018), and are involved in making predictions about our environment, and updating predictions with new information following violations of expectancy of simultaneous cross-modal stimuli is transferred between unisensory and multisensory regions

to update expectations of stimulus-simultaneity in the current environment for future predictions. These findings in the theta, alpha and beta frequencies are supported by previous research showing synchronization of neural oscillations (i.e., functional connectivity) in different frequency bands across unisensory and multisensory brain regions are involved in processing multisensory information (Alais et al., 2010; Hipp et al., 2011; Keil & Senkowski, 2018; Senkowski et al., 2008; Wang et al., 2019).

Our results extend previous functional connectivity research as we have shown that connectivity between visual and tactile regions *during* stimulus presentation in the simultaneity judgment task is important for determining whether stimuli occur simultaneously and whether they are subsequently integrated into multisensory percepts. Our findings add to the research examining pre-stimulus activity and functional connectivity across alpha and beta frequencies in the simultaneity judgment task (Bastiaansen et al., 2020; Hipp et al., 2011; Jiang et al., 2023; Johnston et al., 2022; Migliorati et al., 2020; Yuan et al., 2016) by demonstrating that neural activity occurring *during* and immediately following stimulus presentation contributes to the perception of simultaneity. Our results build upon previous research measuring visual-tactile connectivity across large-scale brain networks (Wang et al., 2019) as we have demonstrated that functional connectivity is strongest between unisensory and multisensory areas when neural resources are needed to discriminate the separation of visual-tactile stimuli and encode the timing differences between the stimuli.

We also hypothesised that the width of the VT-TBW would be related to higher autistic traits, greater sensory sensitivity and increased frequency of unusual sensory experiences. The lack of evidence in favour of this hypothesis was likely due to the limited range of scores on the AQ, GSQ and MUSEQ in our neurotypical sample, which is also consistent with our previous findings (Huntley et al., 2023). However, associations between constructs measured by the questionnaires showed greater sensory sensitivity was related to

higher autistic traits and increased frequency of unusual sensory experiences, but higher autistic traits were not related to the frequency of unusual sensory experiences. It is not surprising that autistic traits were associated with sensory sensitivity as this relationship has been established previously (Robertson & Simmons, 2013) and sensory sensitivity forms part of the diagnosis for ASD (APA, 2013). The relationship between higher sensory sensitivity and increased frequency of unusual sensory experiences is somewhat novel and indicates that sensory pathways facilitating hyper vigilance in sensory sensitivity might also underlie the occurrence of unusual sensory experiences.

3.6.1 Limitations and future directions

Functional connectivity measures, such as dWPLI, are limited to measuring nondirectional connectivity between two neural regions. The benefit of using directional connectivity measures is that they indicate the direction of information flow between neural regions - that is, whether the signal travels from point A to point B or vice versa. Examining the direction of information flow during presentation of cross-modal stimuli (and immediately after) in the simultaneity judgment task would aid in understanding the neural mechanisms associated with the task specifically and multisensory integration more broadly. Further, as multisensory integration involves various cortical and sub-cortical regions, measuring connectivity between two regions at a time (i.e., bivariate connectivity) may result in missing some key information. Measuring connectivity between more than two neural regions (i.e., multivariate connectivity; occipital – central – frontal connectivity) is especially important for multisensory integration as the combined signals from unisensory regions (i.e., parietal and occipital) may be sent to high-order areas for processing and there may be contributions from other regions that perceive, process and integrate unimodal stimuli or the combined multisensory signal. Therefore, future research may benefit from using effective connectivity measures with EEG data, such as Granger Causality and Transfer Entropy that

can measure the direction of connectivity between multiple neural regions to determine cause-effect relationships and further our understanding about neural mechanisms underlying the TBW (Cao et al., 2022; Chiarion et al., 2023).

Further, it is important for future research to consider specific aspects of the experimental protocol that are used to measure the width of the TBW. Specifically, there are two important factors to consider, 1) SOAs need to be long enough to capture width of the TV-TBW sufficiently, and 2) including unimodal trials (in addition to cross-modal trials) likely influences the width of the cross-modal TBW. Our findings, combined with our prior research (Huntley et al., 2023) indicate the SOAs need to be > 250 ms to obtain the full width of the TV-TBW, particularly when participants have no prior experience judging pairs of unimodal stimuli. When participants are not exposed to unimodal stimuli (i.e., tactile-tactile) there is limited opportunity to form representations of the stimuli, which likely assist in facilitating efficient integration. Therefore, when designing experiments using the simultaneity judgment task, it is important to consider whether to measure the TBW with prior experience (i.e., including unimodal trials) or without prior experience (i.e., excluding unimodal trials) as the inclusion of unimodal trials seems to influence the width of the TBW. For example, including unimodal trials provides an opportunity for participants to judge the simultaneity of two unimodal stimuli, which forms their prior experience for other trials when they are required to judge the simultaneity of multisensory stimuli. In the current study, we observed large differences between the widths of the curves on the percentage of simultaneity for TV-TBW and VT-TBW, which is in contrast to our previous study that showed a similar pattern of percentage of simultaneity for both VT-TBWs and TV-TBWs (Huntley et al., 2023). In short, including tactile-tactile trials sharpens the temporal precision of tactile-visual judgements of synchronicity, which results in narrower TV-TBWs. The inclusion of visualvisual trials seems to have little effect on the temporal accuracy used to decide on the

simultaneity of visual-tactile stimuli as the curves for the percentage of simultaneity in both studies.

3.6.2 Conclusion

Functional connectivity between unisensory (central, occipital) and multisensory (parietal) regions was stronger when individuals perceived cross-modal stimuli as nonsimultaneous compared to simultaneous. Stronger connectivity between unisensory and multisensory areas in the theta and alpha frequencies was likely associated with processing the temporal dynamics of the cross-modal stimuli. Whereas stronger connectivity in the beta frequency reflected violations of expectancy in the timing of stimuli and the feed forward/back of information flow between unisensory and multisensory regions. Our study provides a foundation for future research to investigate visual-tactile connectivity in the simultaneity judgment task in clinical populations, such as ASD and schizophrenia, to determine whether connectivity *during* the task contributes to the wider TBWs typically found in these populations.

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Chapter 4: Tactile Cues are More Intrinsically Linked to Motor Timing than Visual Cues in Visual-Tactile Sensorimotor Synchronization.

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4.0 Abstract

Many tasks require precise synchronization with external sensory stimuli, such as driving a car. This study investigates whether combined visual-tactile information provides additional benefits to movement synchrony over separate visual and tactile stimuli and explores the relationship with the temporal binding window for multisensory integration. In Experiment 1, participants completed a sensorimotor synchronization task to examine movement variability and a simultaneity judgment task to measure the temporal binding window. Results showed similar synchronization variability between visual-tactile and tactile only stimuli, but significantly lower than visual only. In Experiment 2, participants completed a visual-tactile sensorimotor synchronization task with cross-modal stimuli presented inside (stimulus onset asynchrony 80 ms) and outside (stimulus onset asynchrony 400 ms) the temporal binding window to examine temporal accuracy of movement execution. Participants synchronized their movement with the first stimulus in the cross-modal pair, either the visual or tactile stimulus. Results showed significantly greater temporal accuracy when only one stimulus was presented inside the window and the second stimulus was outside the window than when both stimuli were presented inside the window, with movement execution being more accurate when attending to the tactile stimulus. Overall, these findings indicate there may be a modality-specific benefit to sensorimotor synchronization performance, such that tactile cues are weighted more strongly than visual information as tactile information is more intrinsically linked to motor timing than visual information. Further, our findings indicate that the visualtactile temporal binding window is related to the temporal accuracy of movement execution.

4.1 Introduction

Navigating through our sensory-filled environment often involves little conscious effort. Yet, what is occurring in our brains is a complex interplay between sensory and motor processes. This sensory and motor interplay occurs within a millisecond time range (Mauk & Buonomano, 2004), such that, sensory information is integrated and actions are performed almost in synchrony (Mates et al., 1994; Roy et al., 2017). For sensory and motor processes to occur almost in synchrony, there is a reliance on temporal processing to facilitate the rapid integration of sensory information, and execute well-timed movements in response to external sensory cues (Mauk & Buonomano, 2004). The temporal nature of these sensorimotor processes has been investigated using sensorimotor synchronization tasks, which measure our ability to perform rhythmic actions in synchrony with external sensory stimuli (Iversen & Balasubramaniam, 2016; Mates et al., 1994).

Sensorimotor synchronization is an important skill that involves simultaneously anticipating the temporal pattern of external sensory information, integrating this sensory information, and performing coordinated actions in time with this information (Mates et al., 1994). For example, when driving a car, the driver monitors traffic conditions while performing coordinated actions with their arms and legs in response to changes in external sensory cues, such as when the traffic light changes color and the driver responds by accelerating, slowing down, or stopping the vehicle. Also, when walking with a friend, your walking pattern often falls into line with theirs or when listening to music you tap your foot along to the beat of a song – these are all ways we intrinsically synchronize our actions to external sensory stimuli. In an experimental setting, sensorimotor synchronization is typically measured using tasks that require participants to press a button with their finger (i.e., finger-tap) in time with external sensory stimuli (Aschersleben, 2002).

Several models have been proposed to understand the processes involved in sensorimotor synchronization. The linear phase correction model highlights the importance of adjustments ("corrections") made by the central nervous system (CNS) to the timing ("phase") of movement execution (Schulze & Vorberg, 2002). These adjustments to the timing of movement execution reduce temporal discrepancies between the presentation of the sensory cue and movement execution, thereby improving the temporal accuracy of the response. In sensorimotor synchronization, the timing discrepancy between the presentation of the sensory cue and the response is known as the asynchrony. If the response (i.e., finger tap) occurs after the sensory stimulus, the asynchrony is positive, but it can negative if the response precedes the external stimulus (Repp, 2005). Therefore, according to the linear phase correction model, the CNS corrects the phase of movement execution to reduce the time difference or asynchrony between stimulus and response in sensorimotor synchronization tasks. While the linear phase correction model explains the timing of our actions in relation to sensory cues, the maximum likelihood estimate (MLE) model explains how the reliability of the sensory cues themselves can affect integration.

In the MLE model, weights are assigned to each cross-modal cue, which results in a multisensory estimate that may be more precise than any unisensory estimate alone (Alais & Burr, 2004; Ernst & Banks, 2002). Therefore, this weighted multisensory estimate with higher precision may bias movement synchronization towards the cross-modal cue with the highest reliability. A highly reliable sensory cue would be consistent and accurate in predicting the appropriate timing for the motor response to occur, increasing the chances of success in a task. In the case of sensorimotor synchronization with cross-modal cues, movement synchrony would be more closely aligned with the sensory cue (or combined multisensory cue) that has the highest weight as this cue provides the most reliable sensory

estimate of the appropriate time to act. As an extension of the MLE model, causal inference models are also relevant in the context of our study.

In addition to MLE models that focus on the weight of the reliability of sensory cues, the causal inference model proposes that the brain uses the current available multisensory information in combination with prior knowledge about the sensory stimuli to make predictions about the common cause of the cues (Körding et al., 2007; Parise et al., 2012). In the context of sensorimotor synchronization, information from previous trials would inform the individual about the timing of the multisensory cues and that the sensory stimuli originated from a common cause (Elliott et al., 2010, 2014). This prior knowledge would have to be weighted based on the result of the action. In other words, feedback about the success (or the lack of) would be important to form priors. This prior knowledge can then be used to reduce uncertainty associated with differences in the timing of sensory cues, improving the asynchrony between the multisensory cues and movement execution. Bayesian causal inference models offer an extension to the original causal inference model in that they consider the likelihood of the causal sources of multiple sensory cues given the prior knowledge and the available sensory information, and assign a probability to the likelihoods of the sources (Körding et al., 2007).

Sensorimotor synchronization with unisensory auditory stimuli has been wellestablished in different populations (Krause et al., 2010; Repp, 2005, 2010; Repp & Doggett, 2007; Repp & Su, 2013). Increasingly, research has explored the effect of unisensory auditory, visual and tactile stimuli on sensorimotor synchronization and multisensory crossmodal combinations of these stimuli (Armstrong & Issartel, 2014; Elliott et al., 2010; Jin et al., 2019; Roy et al., 2017; Wing et al., 2010). As our environment contains an abundance of sensory information, using multisensory stimuli in experimental protocols allows for a more realistic and in-depth understanding about the influence of sensory information on the

accuracy of movement execution (Shams & Seitz, 2008). Previous research shows that participants are typically less variable when synchronizing their actions with multisensory stimuli including audio-visual, audio-tactile and visual-tactile modalities, than respective unisensory stimuli alone (i.e., auditory, visual, or tactile stimuli) (Armstrong & Issartel, 2014; Elliott et al., 2010; Jin et al., 2019; Roy et al., 2017; Wing et al., 2010). However, this multisensory benefit may be dependent upon sensory modality. For example, when synchronizing movement with simultaneously presented audio-tactile stimuli, sensorimotor synchronization variability has been shown to be similar between multisensory stimuli and auditory alone, with variability only increasing marginally with tactile alone stimuli (Elliott et al., 2010; Roy et al., 2017). Similarly, when synchronizing movement with simultaneously presented visual-tactile stimuli there was no difference in variability between multisensory stimuli and tactile alone, with variability only increasing with visual alone stimuli (Elliott et al., 2010). Although this reduction in sensorimotor synchronization variability with multisensory stimuli, compared to unisensory stimuli, may be small and dependent on sensory modality, it is still a consistent finding, and therefore indicates that multisensory information improves the temporal precision of motor execution. However, to our knowledge, the only study to examine visual-tactile sensorimotor synchronization used a relatively small sample (n = 6) (Elliott et al., 2010). Hence, further investigation is required to characterize sensorimotor synchronization with visual-tactile stimuli. Due to the crucial role visual-tactile information plays in motor control and the limited research on visual-tactile sensorimotor synchronization, the aim of Experiment 1 in the current study is to characterize sensorimotor synchronization with visual-tactile stimuli.

Further evidence for a unique multisensory effect on sensorimotor synchronization performance can be gleaned from studies that apply temporal jitter to one stimulus in a crossmodal pair. Typically, when temporal jitter is applied to one stimulus in a cross-modal pair,

variability of sensorimotor synchronization increases; this effect is consistent across different cross-modal pairs of stimuli (audio-tactile, audio-visual, visual tactile) and a range of temporal jitter from 20 ms to 160 ms (Elliott et al., 2010; Roy et al., 2017; Wing et al., 2010). As temporal jitter increases, the variability of sensorimotor synchronization also increases, i.e., variability was higher when temporal offsets were longer (Elliott et al., 2010; Roy et al., 2017; Wing et al., 2010). These results indicate that presenting cross-modal stimuli nonsimultaneously influences variability of movement execution in sensorimotor synchronization tasks. A potential explanation for this increase in variability in sensorimotor synchronization is the length of an individual's temporal binding window (TBW) for multisensory integration. The TBW is the time range in which sensory information from multiple modalities is integrated into a single concept, which is then attributed to a concurrent perceptual event (Ernst & Bülthoff, 2004; Stein & Stanford, 2008; Wallace & Stevenson, 2014; Wallace et al., 2020). We can think of the TBW in terms of the causal inference model such that when multisensory stimuli are received within the TBW, they are attributed to the same cause. Since sensory information within the window is perceived as occurring simultaneously yet is received at different times across the brain, movement execution may be phase shifted towards the presentation of the later stimulus that is still within the TBW. The degree to which the movement is temporally shifted towards to later stimulus is likely dependent upon the relative reliability weighting between sensory cues. Hence, sensorimotor synchronization variability may increase (or decrease) depending on the modality of the stimulus that is temporally jittered within the TBW, and the weighting assigned to the sensory modality.

Despite the suggestion in previous literature that the TBW influences sensorimotor synchronization performance (Elliott et al., 2010; Repp, 2005; Roy et al., 2017), only one study to date has examined sensorimotor synchronization performance when stimuli are presented inside and outside the TBW (Elliott et al., 2014). Further, no studies have used the simultaneity judgment task to measure the TBW to establish a relationship between the window and sensorimotor synchronization performance. It is relevant to use the simultaneity judgment task as it is an established method for measuring the TBW (Chen et al., 2018; Hillock-Dunn & Wallace, 2012; Hillock et al., 2011; Powers et al., 2009; Stevenson et al., 2012a; Stevenson & Wallace, 2013; Stevenson et al., 2013; Stevenson et al., 2012b). Therefore, the aim of Experiment 2 in the current study is to, 1) investigate whether sensorimotor synchronization performance is differentially influenced by the presentation of stimuli either inside and outside of the TBW, and 2) examine the relationship between sensorimotor synchronization performance and the length of the TBW.

In Experiment 1, our first hypothesis was that sensorimotor synchronization variability would be lower with cross-modal visual-tactile stimuli than with respective unimodal stimuli. We analysed standard deviation to examine variability as we were interested in determining whether individuals showed enhanced precision in their tapping ability when synchronizing their tap with either a) unimodal or bimodal stimuli, and b) visual or tactile sensory stimuli. Our second hypothesis was that higher sensorimotor synchronization variability would be related to a longer TBW. In Experiment 2, our first hypothesis was that sensorimotor synchronization temporal error would be higher when cross-modal stimuli were presented inside the TBW with a stimulus onset asynchrony (SOA) of 80 ms, than when one stimulus in the cross-modal pair was presented inside the TBW and the second outside the TBW, with an SOA of 400 ms. We examined mean asynchrony to investigate whether there were differences in sensorimotor synchronization accuracy when cross-modal sensory stimuli were presented both inside the TBW and when the second stimulus in the cross-modal pair was presented outside of the TBW, and whether the sensory modality influenced the accuracy of sensorimotor synchronization ability. Our second hypothesis was that sensorimotor synchronization temporal error would be lower when

TBWs were narrower, compared to when TBWs were wider. In both experiments, we expect that the size of the TBW will be related to sensorimotor synchronization performance. A smaller TBW indicates multisensory stimuli are bound efficiently and are more likely to represent a 'true' perception about events in the environment, whereas a larger (wider) TBW indicates multisensory stimuli are bound over a longer period. When stimuli are bound together over a longer period, there is more opportunity for irrelevant information to be bound with relevant information, which likely distorts the 'true' cause of the stimuli and potentially inaccurately representing perceptual events in the environment (Wallace & Stevenson, 2014). Without an accurate perception of events in the environment it would be difficult to accurately synchronize movement with external sensory stimuli (Iarocci & McDonald, 2006).

Experiment 1

4.2 Method

4.2.1 Participants

Thirty-one participants were recruited for the study from an undergraduate University population. All participants recruited for the study received points towards their course as compensation for participating in the study. For Task 1 (sensorimotor synchronization task), all 31 participants were included in the data analysis (M = 20.77, SD = 2.31, range 18 - 28 years old, 20 female). In Task 2 (simultaneity judgment task), seven participants were excluded from the analysis due to poor fit of their data. From visual inspection of the data, these participants were unable to discriminate between simultaneous and non-simultaneous stimuli across the range of SOAs, which meant that we were unable to attain a reliable estimate of their TBW. Therefore, 24 participants were included in the data analysis (M = 20.83, SD = 2.50, 14 female). Our sample size was guided by previous literature (Armstrong

& Issartel, 2014; Elliott et al., 2010, 2014; Lagarde & Kelso, 2006; Wing et al., 2010), and exceeds those commonly seen in similar studies in this area of research. All participants were right-hand dominant and free from any neurological conditions. The study was approved by Curtin University Human Research Ethics Committee. Experiments in this study were conducted in accordance with the Declaration of Helsinki. All participants gave written informed consent prior to testing and completed a demographics questionnaire.

4.2.2 Stimuli

Instructions for the tasks were displayed on a 19" Dell LCD computer monitor (60 Hz refresh rate). The experiment was programmed in MATLAB version 2015b, and the instructions and stimulus triggers were programmed using Psychtoolbox (version 3.0.8). The visual stimuli were two 5 mm green light emitting diodes (LED's) (10,000 mcd) inside two frosted Perspex blocks fixed to a black stand placed in the centre of the computer monitor. The tactile stimuli were two 10 x 3.4mm shaftless vibration motors (Pololu Corporation, Las Vegas, NV; Pololu item #1636) attached to the index finger and middle finger on the left hand (non-dominant) with elastic fabric bands. In Task 1, the LED on the right-side of the board and the vibration motor on the left index finger was used, and each stimulus were presented for 64 ms. In the Task 2, left and right LED's were presented, and the second vibration motor attached to the left middle finger was used, and each stimulus was presented for 50 ms. Participants completed all tasks in a dimly lit room. In both tasks, participants were approximately 60 cm from the visual stimuli, which were in front of the computer monitor and in central view. For the tactile stimuli, participants were instructed to place their hand on the desk in front of them and were allowed to place the hand in a comfortable position.

Experimental procedures

4.2.3 Task 1: Sensorimotor Synchronization

Participants were instructed to keep their right index finger resting on the right arrow key on a computer keyboard and tap their finger in synchrony with the sensory stimuli: either a visual stimulus, tactile stimulus, or a visual-tactile stimulus, and to continue tapping at the same pace when the stimuli disappeared. We used a computer keyboard to record the timing of the finger tapping, as previous research has shown that using PsychToolbox in MATLAB accurately records the timing of responses from key-presses (Navracsics & Darzhinova, 2020), and that keyboards only introduce minor jitter in the millisecond range, therefore recording reaction time with good accuracy (Anwyl-Irvine et al., 2021; De Clercq et al., 2003). The sensorimotor synchronization task consisted of 480 trials for each ISI (total of 960 trials). For both the 600 ms ISI and 1200 ms ISI, there were 480 trials; 240 sensory trials (80 visual, 80 tactile, 80 visuo-tactile) and 240 non-sensory trials in which no sensory stimuli were presented. As shown in Figure 4.1, the sensory and non-sensory trials were presented in one of six possible combinations. Within each combination, 20 sensory trials (either visual, tactile or visual-tactile) were followed by 20 non-sensory trials, and this pattern was repeated three times. The combination order of the sensory condition and the ISI was pseudorandomized between participants to reduce potential order effects. In the non-sensory trials, the sensory stimuli were suppressed so that the computer monitor only displayed a black screen and no tactile or visual stimuli were presented. We opted to suppress the sensory stimuli, rather than simply presenting a black screen, to maintain the exact timing of the sensory trials. These non-sensory trials were used as a wash-out period between sensory trials in a different modality to avoid any carry over effects associated with the timing of stimuli in any given modality. Participants were instructed to continue tapping during the wash-out period to maintain the rhythmic pattern of the stimuli for when the sensory trials next

commenced. There were two blocks of trials at different inter-stimulus intervals (ISIs) – 600 ms and 1200 ms – to observe any differences in sensorimotor synchronization variability between sub- and supra-second timing intervals. Participants wore industrial passive headphones to prevent the sound of the key press being used as feedback about their timing. Practice blocks were completed prior to each experimental block and were in the same combination order as the experimental blocks. Each practice block consisted of 60 sensory and 60 "wash out" (non-sensory) trials.



Figure 4.1: Graphical representation of the trial design for Task 1 – Sensorimotor synchronization. Green circles represent the green LED (visual stimulus), the white star represents the vibration motor (tactile stimulus), and the black square represents the blank screen presented during wash-out trials. Trials were presented at either 600 ms ISI or 1200 ms ISI; the 600 ms and 1200 ms ISIs were presented in separate blocks, counterbalanced between participants. Pictured here is Combination 1 (of six possible combinations that were pseudo-randomised between participants) which follows: 20 visual trials, 20 wash-out trials, 20 tactile trials, 20 wash-out trials, 20 wash-out, repeat x 3; (3) tactile, wash-out, visual, wash-out, visual-tactile, wash-out, visual-tactile, wash-out, visual-tactile, wash-out, visual, wash-out,

4.2.4 Task 2: Simultaneity judgment task

Participants completed a simultaneity judgment task with visual and tactile stimuli. The beginning of each trial started with the sensory type written on the screen, e.g., "Visual stimuli", "Tactile stimuli", or "Both stimuli" (see Figure 4.2). In the "Visual stimuli" condition both (left and right) LEDs were presented in each trial, in the "Tactile stimuli" condition both (index and middle finger) vibration motors were presented in each trial, and in the "Both stimuli" condition one LED and one vibration motor were presented (right LED and index finger) in each trial. The two sensory stimuli were presented either together (i.e., simultaneously) or at varying SOAs from +/- 25 ms to 250 ms, increasing incrementally in 25 ms steps. When stimuli were presented at negative SOAs it means one stimulus preceded the other, e.g., when SOAs were negative the visual stimulus preceded the tactile stimulus, and when SOAs were positive SOAs the tactile stimulus preceded the visual stimulus. Following the presentation of either visual stimuli, tactile stimulu or both stimuli (cross-modal stimuli), the question "Were the stimuli simultaneous?" appeared on the screen, and participants responded "yes" by clicking the left mouse button or "no" by clicking the right mouse button. Participants were instructed to respond as quickly as possible following the second stimulus. There were 10 trials for each condition (+/- SOA x sensory pair), totaling 630 trials. Participants completed 12 practice trials in pseudorandomized order before commencing the experiment. The order of the sensorimotor synchronization task and simultaneity judgment task were counterbalanced between participants.



Figure 4.2: Graphical representation of the trials for visual ("light"), tactile ("vibration") and visual-tactile ("both") stimuli presented in the simultaneity judgment task. Stimuli were presented at these SOAs: +/- 0, 25, 50, 75, 100, 125, 150, 175, 200, 225, 250 ms.
4.3 Data analysis

In Task 1, the time between stimulus presentation and the finger-tap is referred to as the asynchrony, and the standard deviation of the asynchrony is used as the measure of sensorimotor synchronization ability (Repp, 2005; Repp & Su, 2013). Asynchrony standard deviation was calculated across all trials for each participant. As such, the asynchrony standard deviation (SD) was included in the statistical analysis for Task 1, in which Linear Mixed Models (LMM) were conducted using the gamlj mixed function in RStudio (gamlj package version 2.6.5 (Gallucci, 2019); RStudio version 3.5.2 (RStudioTeam)) to test main effects and interactions. Post-hoc tests were conducted using the estimated marginal means (part of the gamlj package in RStudio), with the Holm method used to correct for multiple comparisons (Holm, 1979), and Satterthwaite method to correct the degrees of freedom. In Task 1, the effect of stimulus type (visual, tactile, visual-tactile) and time (ISI; 600 ms, 1200 ms) on sensorimotor synchronization was analysed using LMMs, with stimulus type and time as the fixed factors and participants as the random factor.

In Task 2, the percentage of simultaneous responses (i.e., responding "yes" to "were the stimuli simultaneous?" after each trial) were averaged for each participant at each SOA and fitted with a model-free line was fitted to each participants data across SOAs using the modelfree package in RStudio (Model-Free Estimation of a Psychometric Function, version 1.2) (Zychaluk & Foster, 2009). The modelfree function is a parameter free method that has no assumptions about the shape of the data. This function provides an alternative to commonly used methods, such as Gaussian or sigmoid functions, which are commonly used to fit data for the perception of simultaneity (Costantini et al., 2016; Hillock-Dunn & Wallace, 2012; Hillock et al., 2011; Migliorati et al., 2020; Moro & Steeves, 2018; Noel et al., 2016; Noel et al., 2017a; Powers et al., 2009; Stevenson et al., 2018; Stevenson et al., 2014a; Stevenson & Wallace, 2013; Venskus et al., 2021). For each participant, we estimated

the width of the TBW by identifying the half-way point between 0% and the maximal peak of simultaneity perception on the y-axis, and where this half-way point intersects the model-free fit on the x-axis. Only visual leading visual-tactile trials have been included in the calculation of the TBW and statistical analysis as when the data was inspected for the tactile leading visual-tactile trials it was found that a number of participants had the same width window as the longest SOA, thus indicating that the SOAs for Experiment 1 and 2 in this study were not long enough to measure the width of the TBW. Spearman's rank-order correlation coefficient was calculated to examine the relationship between the visual leading visual-tactile TBW and visual-tactile sensorimotor synchronization ability in Task 1.

4.4 Results

4.4.1 Task 1: Sensorimotor Synchronization

For asynchrony variability, results from the LMM showed main effects of stimulus type (F(2, 150) = 6.37, p = 0.002), and time (F(1, 150) = 109.97, p < 0.001), but no stimulus type * time interaction (F(2, 150) = 0.086, p = 0.92) (see Table 4.1 for group mean asynchrony and standard deviation). Post-hoc tests indicate that sensorimotor synchronization ability was more accurate when tapping in synchrony with the visual-tactile stimuli than visual alone (p = 0.003), but there was no difference in sensorimotor synchronization ability when tapping in synchrony with visual-tactile stimuli and tactile alone (p = 0.661). When comparing differences between unimodal conditions, sensorimotor synchronization ability was more accurate when tapping in synchrony with tactile stimuli alone than visual alone (p = 0.010) (see Figure 4.3). For all sensory modality conditions, the finger-tap movement preceded the sensory stimuli, consistent with previous literature (Aschersleben, 2002). Overall, mean asynchrony was lower for the 1200 ms condition than 600 ms (See Supplementary Material for LMM with mean asynchrony).

Table 4.1.

	600 ms		1,200 ms	
	М	SD	М	SD
Visual	-71.46	38.23	-56.45	46.14
Tactile	-64.99	39.04	-55.65	43.05
Visual-tactile	-68.01	36.63	-57.32	35.15
	300	•	•	ISI • 1200 • 600
	ny (ms)			:
	asynchroi	•	•	
	of mean s			
	iation (SD)			
	Standard devi 001			
		Tactile	Visual Stimulus Ty	Visual-tactile /pe

Group mean asynchrony and standard deviation for 600 ms and 1,200 ms ISI conditions

Figure 4.3: Sensorimotor synchronization asynchrony standard deviation for visual, tactile and visual-tactile conditions. Red circles represent the 1200-ms ISI condition, and the blue triangles represent the 600-ms ISI condition. Group-level data is shown in black outline, and subject-level data is shown without outline. Error bars represent 95% confidence intervals.

4.4.2 Task 2: Simultaneity judgment task (N = 24)

Results showed that mean width of the visual leading visual-tactile TBW was 149 ms (VT-TBW; SD = 55 ms) and the mean width of the tactile-leading visual-tactile TBW was 180 ms (TV-TBW; SD = 48 ms) (see Figure 4.4).



Figure 4.4: Group percentage of perceived simultaneity for visual leading visual-tactile stimuli (VT) and tactile leading visual-tactile stimuli (TV). Error bars represent the standard error of the model estimates.

There was a significant correlation between the visual leading visual-tactile TBW and sensorimotor synchronization asynchrony standard deviation (as a measure of sensorimotor synchronization ability) in the 1200 ms ISI condition, (r = -0.56, p = < 0.001), but no correlation in the 600 ms ISI condition, (r = -0.34, p = 0.100). Despite there being no correlation in the 600 ms ISI condition, Figure 4.5 shows the pattern of results is similar between the 600 ms and 1200 ms conditions. Taken together, these results indicate that greater variability in sensorimotor synchronization ability - indicating poorer movement synchrony – may rely on the engagement of similar mechanisms that are engaged when temporally binding sensory information within a specified time (i.e., the TBW).



Figure 4.5: Scatterplots showing correlations between sensorimotor synchronization ability (standard deviation asynchrony) at 600 ms and the visual leading visual-tactile TBW (top), and between sensorimotor synchronization ability at 1200 ms and the visual-tactile TBW (bottom).

Experiment 2

4.5 Method

4.5.1 Participants

Thirty-seven participants were recruited for the study from the same undergraduate University population as Experiment 1. As with Experiment 1, all participants recruited for the study received points towards their course as compensation for participating in the study. In Task 1 (sensorimotor synchronization with stimuli inside and outside the window), nine participants were excluded from the data analysis: eight due to technical issues and one due to an incomplete data set. Therefore, a total of 28 participants were included in the data analysis for Task 1 (M = 21.18, SD = 3.15, range 18 – 32 years old, 20 female). In Task 2 (simultaneity judgment task), four participants were excluded: three due to a poor fit of their data (as outlined in Experiment 1 – Task 2) and one due to an incomplete data set. Therefore, a total of 33 participants were included in the data analysis for Task 2 (M = 21.30, SD = 3.04, range 18 – 32 years old, 22 female). All participants reported normal-to-corrected vision and were free from any neurological conditions. The study was approved by Curtin University Human Research Ethics Committee. All participants gave written informed consent prior to testing and completed a demographics questionnaire.

4.5.2 Stimuli

The same stimuli were used as Experiment 1 - the visual stimulus was a green LED and the tactile stimulus was a shaftless vibration motor. The LED and the vibration motor were attached to the top third part of the left index finger with an elastic fabric band and secured with micropore tape. The stimuli were in this position for both experimental tasks.

Experimental procedures

4.5.3 Task 1: Sensorimotor synchronization with stimuli inside and outside window

Participants completed the sensorimotor synchronization task with the same visual and tactile stimuli as Experiment 1. There were two blocks of trials, one block of trials consisted of visual only and visual-tactile trials, the other block of trials consisted of tactile only and tactile-visual trials. The order of block presentation was counterbalanced across participants. At the beginning of each block of trials, participants were instructed to press the right arrow key on the computer keyboard in synchrony with the visual stimulus for the visual only and visual-tactile trials, or the tactile stimulus for the tactile only and tactile-visual trials. Within each bimodal condition, that is, visual-tactile and tactile-visual, the second stimulus in the pair was presented with a SOA of 80 ms or 400 ms. The 80 ms SOA meant that both stimuli were presented inside the TBW, and the 400 ms SOA meant that the first stimulus was presented inside the TBW and the second stimulus was presented outside the TBW. Prior to determining the inside and outside TBW SOAs (80 and 400 ms, respectively), we had previously conducted the visual-tactile simultaneity judgment task in two experiments with different groups. In these studies, the mean width of the visual-tactile

window was 149 ms (Experiment 1, Task 2 in the current manuscript) and 123 ms (Huntley et al., 2023) and the shortest width was ~80 ms. From this data we estimated that 80 ms would be inside the TBW, and 400 ms would be well outside the window. We have referred to the first stimulus in the pair as the "attended" to stimulus as the participants were instructed to tap in synchrony with this stimulus, and the second stimulus in the pair as the "irrelevant" stimuli. Note however that we did not specifically manipulate attention as we did not explicitly instruct participants to maintain attention on the first stimulus and ignore the second stimulus. The "attended" to stimulus was presented at the same time in both unimodal and cross-modal conditions and only the timing of the "irrelevant" stimulus varied as it was presented either "inside" (SOA 80 ms) or "outside" (SOA 400 ms) the TBW. Each block consisted of 60 unimodal trials (visual or tactile), followed by 60 cross-modal trials. The ISI for unimodal and cross-modal blocks was 1200 ms. Therefore, there were six conditions: visual only, tactile only visual-tactile attend (in), visual-tactile attend (out), tactile-visual attend (in) and tactile-visual attend (out). Practice blocks were completed before each experimental block, and experimental blocks were counterbalanced across participants. 4.5.4 Task 2: Simultaneity Judgment Task

Participants completed a simultaneity judgment task with cross-modal visual-tactile stimuli only. The visual and tactile stimuli used were the same as those in the "Both stimuli" condition in Experiment 1 – Task 2. Consistent with Experiment 1, when SOAs were negative the visual stimulus preceded the tactile stimulus, and when SOAs were positive the tactile stimulus preceded the visual stimulus. Positive SOAs ranged from 25 to 225 ms, and negative SOAs ranged from -25 to -250 ms, and both increased in 25 ms increments. All instructions to participants were consistent with Experiment 1 – Task 2. There were 10 trials for the 0 ms condition and each SOA, totaling 200 trials. Participants completed practice trials in pseudo-randomised order before commencing the experiment. The order of the

sensorimotor synchronization task and simultaneity judgment task were counterbalanced between participants.

4.6 Data analysis

In Task 1, the mean asynchrony of the unimodal trials was used as the baseline condition and was subtracted from the respective mean asynchrony of the cross-modal condition (e.g., visual attend/tactile irrelevant (in) mean asynchrony minus visual baseline mean asynchrony) to create an asynchrony difference score for each condition. Therefore, the difference score represents the effect of the combined cross-modal stimuli after removing the modality-specific effects on mean asynchrony. The effect of attended sensory modality (visual attend/tactile irrelevant, tactile attend/visual irrelevant) and the timing of the second stimulus (80 ms, 400 ms) on sensorimotor synchronization was analysed using LMM, with sensory modality and time as the fixed factors and participants as the random factor. LMM's were conducted to test main effects and interactions, and post-hoc tests were conducted for further analysis. Statistical software and packages used was consistent with Experiment 1.

In Task 2, the TBW was calculated for each participant using the same method as Experiment 1. Spearman's rank-order correlation coefficient was calculated to examine the relationship between the visual leading visual-tactile TBW and the mean asynchrony difference score on the sensorimotor synchronization task. Due to exclusions from Task 1 and Task 2, 26 participants were included in the correlations between sensorimotor synchronization mean asynchrony and the TBW.

4.7 Results

4.7.1 Task 1: Sensorimotor synchronization with stimuli inside and outside window

Temporal error during the sensorimotor synchronization task was measured using the mean asynchrony across trials for each condition. The mean asynchrony for each condition was assessed using a LMM with fixed effects of time (80 ms, 400 ms) and sensory modality (visual-tactile/tactile irrelevant, tactile-visual/visual irrelevant), and a time*sensory modality interaction. Results from the LMM showed a main effect of time, (F(1, 81) = 4.89, p = 0.029), no effect of sensory modality, (F(1, 81) = 2.16, p = 0.145), and no time*sensory modality interaction, (F(1, 81) = 0.001, p = 0.923). As shown in Figure 4.6, temporal error (mean asynchrony difference from baseline) was lower for the tactile attend (visual irrelevant) than the visual attend (tactile irrelevant) for stimuli presented both inside and outside the TBW although this effect was not significant. See Supplementary Material for the LMM with sensorimotor synchronization variability (standard deviation difference from baseline) and stimulus modality.



Figure 4.6: Sensorimotor synchronization mean asynchrony difference score (cross-modal minus unimodal per condition) for tactile-visual (tactile attend/visual irrelevant) and visual-tactile (visual attend/tactile irrelevant) for SOAs 80 ms and 400 ms. Error bars represent the standard error of the model estimates.

4.7.2 Task 2: Simultaneity Judgment Task

Results from the simultaneity judgment task showed that the mean width of the VT-TBW for the group was 139 ms (SD = 50 ms) and the mean width of the TV-TBW was 179 ms (SD = 87 ms) (see Figure 4.7). Caution should be exercised when interpreting the mean width of the TV-TBW in Experiment 2 as a subgroup of participants possessed a window equal to the largest SOA, which indicates that their TV-TBW is likely to be longer than we were able measure with the SOAs included in the task. Another sub-group of participants had a TV-TBW equal to 0 ms, which indicates that they were unable to distinguish between simultaneous and non-simultaneous stimuli therefore a model-free curve could not be fitted to the data.



Figure 4.7: Group percentage of perceived simultaneity for visual leading visual-tactile stimuli (VT) and tactile leading visual-tactile stimuli (TV). Error bars represent the standard error of the model estimates.

For the tactile attend condition, there was a significant correlation between the TBW and sensorimotor synchronization mean asynchrony when both stimuli were presented inside the TBW (80 ms), (r = -0.42, p = 0.04), but no correlation when the second stimulus was presented outside the TBW (400 ms), (r = 0.36, p = 0.07). Although, not statistically significant, the pattern of results for tactile attend (out) was similar to tactile attend (in), suggesting that tactile information is relied on more than visual information in both tasks (see Scatterplots – Figure 4.8). The results can be interpreted as evidence that information bound within the TBW likely influences the timing accuracy of movement execution. In the visual attend condition, there was no significant correlation between the TBW and sensorimotor

synchronization mean asynchrony inside, (r = 0.1, p = 0.65), or outside the window (r = 0.12, p = 0.56).



Figure 4.8: Top row scatterplots show correlations between sensorimotor synchronization mean asynchrony at 80 ms ISI (i.e., when both stimuli are presented within the TBW) and the visual-tactile (visual leading TBW) when participants attend to the visual and tactile stimuli. Bottom row scatterplots show correlations between sensorimotor synchronization mean asynchrony at 400 ms ISI (i.e., when one stimulus is presented within the TBW and the second stimulus is presented outside the TBW) and the visual-tactile (visual leading) TBW when participants attend to the visual and tactile stimuli.

4.8 Discussion

The aim of Experiment 1 was to characterize sensorimotor synchronization with visual-tactile stimuli by comparing variability in movement synchronization between crossmodal and unimodal stimuli. Although, we found that sensorimotor synchronization with visual-tactile stimuli was less variable than with visual stimuli alone, there was no difference between visual-tactile stimuli and tactile stimuli alone. Therefore, our hypothesis about multisensory stimuli providing a benefit to performance in sensorimotor synchronization was only partially supported. These results are reasonably consistent with previous literature, which found that there was no difference in sensorimotor synchronization variability between audio-tactile stimuli and auditory alone, but there was a difference between audio-tactile stimuli and tactile alone (Roy et al., 2017). Similarly, with visual-tactile stimuli, sensorimotor synchronization variability was comparable between visual-tactile stimuli and tactile alone, but there was a noticeable difference in variability between visual-tactile stimuli and visual alone (Elliott et al., 2010; Fig 2C). Previous research has shown differential sensorimotor synchronization effects across sensory modality. In an audio-tactile bimanual coordination task, a finger flexion was more tightly coupled with sound and finger extension with touch (Lagarde & Kelso, 2006). Our results show that when the sensory cue (tactile) is in the same modality as the action (finger-tapping) our ability to synchronize our movements with sensory information is enhanced. Supporting this idea, we have shown that the TBW for tactile-tactile stimuli is very narrow indicating that tactile information is integrated rapidly (Huntley et al., 2023), which enables faster execution of an action.

Our results are consistent with the linear phase correction and MLE models as sensorimotor synchronization to sensory cues is related to the task-type in addition to the stability of the sensory cue itself. Our results from Experiment 1- Task 1 (SMS) indicate that tactile cues are assigned a higher weight by the CNS, which increases the reliance on tactile cues for temporal regularity of incoming sensory information. As the tactile cue is more intrinsically related to motor timing than the visual cue, the CNS phase shifts the execution of the finger tap to be temporally aligned with the presentation of the tactile cue, which in turn reduces the asynchrony between action and the sensory cue. The dominance of the tactile cue in this task suggests that task-type influences the weighting of sensory cues and in the context of sensorimotor synchronization where the task is inherently automatic and predicable, tactile information contributes to motor performance more than visual information.

In Experiment 2, we aimed to examine whether cross-modal stimuli presented separately during the TBW influenced temporal error of sensorimotor synchronization. Our results showed higher temporal error (mean asynchrony) in movement execution when crossmodal stimuli were presented inside the TBW than outside the window, thus supporting our hypothesis. As with Experiment 1, the results from Experiment 2 also fit within the assumptions of the linear phase correction model, MLE model, and Bayesian causal inference. It is likely that multisensory stimuli that are perceived and integrated (bound) within the TBW are assigned a weight by the CNS according to the reliability of the sensory cue, and then attributed to a common cause. Across trials, this attribution of a common cause of the multisensory stimuli may form the participants' prior knowledge ('priors') for future trials. This prior knowledge and the reliability weighting of sensory cues enables the CNS to phase shift the action of finger tapping towards the cue with the highest reliability. In the context of our study, when cross-modal stimuli were received within the TBW, mean asynchrony difference from baseline (temporal error) was higher than when one stimulus in the cross-modal pair was inside the TBW and the other stimulus was outside the TBW. Higher mean asynchrony (difference from baseline) here refers to longer intervals between stimulus and response that are due to the presence of both stimuli, and not only the influence of one sensory modality over the other. These results indicate that cross-modal stimuli received within the TBW influences the timing of movement execution such that the action is phase shifted away from the first stimulus: this is a form of time averaging, where the temporal proximity of the stimuli can affect the temporal estimation for an action. However, as we found that temporal error was lower for the tactile-visual (tactile attend/visual irrelevant) condition than for visual-tactile (visual attend/tactile irrelevant) in both the 80 and 400 ms conditions, the degree to which the action is phase shifted may depend on the weighting of the sensory cue, which aligns with the MLE model of cue integration. In our

case, asynchrony (temporal error) was lower when the tactile cue was dominant (i.e., in the tactile-visual condition) for both 80- and 400-ms conditions.

A further aim for Experiment 1 and 2 was to examine the relationship between sensorimotor synchronization and the TBW. Results from both Experiments showed that individuals who integrate multisensory information over a longer period (i.e., have wider TBWs) are less precise at synchronizing their movements than those who integrate multisensory information over a shorter period. This finding indicates that the width of the TBW is related to anticipating the timing of sensory information. When the TBW is narrow (i.e., shorter in duration), the ability to anticipate the timing of events is more accurate. In contrast, when the window is wider, an individual may anticipate that the event they are timing their action with occurs later than it actually does, thereby delaying the execution of the action and making asynchrony more positive. Although the timing for anticipatory actions might be separable from time perception in specific conditions (Marinovic & Arnold, 2012), it is likely that anticipatory timing and other co-occurring motor processes, such as planning and preparation, are also affected by the width of the TBW.

Given the temporal nature of both tasks (simultaneity judgement task and the sensorimotor synchronization task), it is likely that the relationship between the binding window and movement execution is facilitated by temporal processing. In line with this idea, previous research shows that neural temporal processing is related to the perception of simultaneity (Roach et al., 2011), and that temporal perception plays a key role in sensory processing and motor coordination (Buonomano & Karmarkar, 2002). This inter-dependent relationship between the sensory, motor and temporal processes is important for considering a link between sensory processing difficulties and motor dysfunction in clinical populations, such as Autism Spectrum Disorder (ASD). In the context of ASD, there is likely a connection between sensory and motor function that is underpinned by temporal processing. In support

of this three-way relationship between sensory perception, motor function and temporal processing, individuals with autism experience a variety of sensory difficulties associated with processing (Beker et al., 2017; Tavassoli et al., 2014), integration (Brandwein et al., 2015; Brandwein et al., 2012; Russo et al., 2010; Stevenson et al., 2014a; Stevenson et al., 2014b), and binding (Brock et al., 2002; Foss-Feig et al., 2010; Greenfield et al., 2015; Zhou et al., 2018), as well as motor deficits (Bhat et al., 2011; Calhoun et al., 2011; Cascio et al., 2012; Fournier et al., 2010a; Fournier et al., 2010b; Rinehart et al., 2006). These motor deficits extend to sensorimotor synchronization with ASD participants showing higher sensorimotor synchronization variability compared to non-ASD participants (Morimoto et al., 2018; Murat Baldwin et al., 2021). Further, it has been suggested that individuals with autism may have deficits in temporal synchrony (Murat Baldwin et al., 2021), temporal processing and temporal perception (Allman, 2011; Allman et al., 2011; Casassus et al., 2019; Stevenson et al., 2016), and experience difficulty in detecting temporal changes in sensory stimuli (Brodeur et al., 2014; Falter et al., 2012). As individuals with ASD often have differences in cerebellum function (D'Mello & Stoodley, 2015; Mosconi et al., 2015) - a crucial neural region involved in sub- and supra-second timing mechanisms and motor control (Bijsterbosch et al., 2011; Grondin, 2010; Rao et al., 2001) - this difficulty with temporal perception and processing may be related to activity in the cerebellum. These findings in ASD further support the idea that temporal processing may aid in facilitating the relationship between multisensory integration and movement execution.

Although it was not a main aim of Experiment 1, our results inform whether sensorimotor synchronization performance was influenced by sub- and supra-second interstimulus intervals. Despite seeing a difference in sensorimotor synchronization variability between sub- and supra-second timing intervals, we believe this difference is not due to changes in activation patterns in neural regions associated with sub- and supra-second

timing intervals. Instead, the difference in variability between sub- and supra-timing intervals might be driven simply by the fact that longer intervals are likely to have higher variability than shorter intervals. If the pattern of results for sensorimotor synchronization had been different between the sub- and supra-second intervals, we could have inferred that neural regions were differentially activated, but this was not the case.

In conclusion, our results show that individuals' who take longer to integrate multisensory information are more variable, and have larger temporal errors, when synchronizing actions with external sensory cues. When there is a temporal delay between multisensory stimuli that are bound in the TBW, the timing of motor execution is affected such that longer offsets between the onset of multisensory cues interferes with the temporal precision of the action (i.e., finger tap). Further, we have shown that tactile cues are weighted more strongly than visual information as they are more intrinsically linked to motor timing and the performance of the action in sensorimotor synchronization tasks in our study. These results have implications for clinical populations, such as ASD, in which there may be a relationship between difficulties with multisensory integration and differences in motor abilities.

4.9 References

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Chapter 4: Supplementary Material

4.10 Results

4.10.1 Experiment 1 – Task 1

Mean asynchrony

Mean asynchrony was averaged across trials per condition for each participant. Mean asynchrony was analysed using a LMM with time (600 ms, 1200 ms) and stimulus type (visual, tactile and visual-tactile) as fixed effects and participants as the random effect. Results from the LMM showed a main effect of time (F(1, 2) = 3.93, p = 0.049) but no effect of stimulus type (F(1, 2) = 0.13, p = 0.877), and no time * stimulus type interaction (F(1, 2) = 0.083, p = 0.919) (see Figure 4.9). As the interaction was not significant, we did not conduct post-hoc tests.



Figure 4.9: Sensorimotor synchronization mean asynchrony for tactile, visual and visual-tactile conditions for 600 and 1200 ms ISIs. Error bars represent the standard error of the model estimates.

Standard deviation asynchrony

Sensorimotor synchronization variability was measured using the asynchrony standard deviation across trials for each condition. The standard deviation asynchrony was analysed using a LMM with time and condition as fixed effects and participants as the random effect. Results from the LMM showed a main effect of condition (F(1, 81) = 7.64, p = 0.007) but no effect of time (F(1, 81) = 2.40, p = 0.125), and no condition * time interaction (F(1, 81) = 3.66, p = 0.059) (see Figure 4.10). As the interaction did not reach significance, we did not conduct post-hoc testing.



Figure 4.10: Sensorimotor synchronization asynchrony variability (standard deviation) difference score (crossmodal minus unimodal per condition) for tactile-visual (tactile attend/visual irrelevant) and visual-tactile (visual attend/tactile irrelevant) for SOAs 80 ms and 400 ms. Error bars represent the standard error of the model estimates.

Chapter 5: General Discussion

5.1 Overall summary

It is the end of a long day. You shut down your computer, walk out the door and make your way to your car. You sit down into the driver's seat, start the engine and ease out of the carpark, on your way home. This process, from leaving work to driving off into the sunset, involves a series of complex sensorimotor processes that work in tandem to create meaningful interactions with your environment. Through this thesis, I have discussed two key aspects of sensorimotor processes, that is, the temporal binding window (TBW) for multisensory integration and sensorimotor synchronization (SMS). I have demonstrated that combining visual-tactile cues into a single percept (i.e., the TBW), and weighting these cues according to their reliability, are instrumental in executing everyday actions, such as driving your car.

In chapter two, we examined unimodal (visual-visual, tactile-tactile) and cross-modal visual-tactile TBWs (visual-tactile [VT] and tactile-visual [TV]), and the relationship between the width of the visual-tactile TBW (VT-TBW) and autistic and sensory traits (Huntley et al., 2023). We found cross-modal visual-tactile TBWs were wider than unimodal TBWs, and when comparing widths of the VT and TV TBWs we found that VT-TBWs (visual leading) were narrower than TV-TBWs (tactile leading). We infer from our results that the width of the TBW is influenced by the modality of the stimulus presented first (i.e., leading sense) in the cross-modal pair. The influence of the leading sense on the width of the TBW is likely largely dependent on the reliability weight assigned to a specific sensory modality by the central nervous system (CNS). Sensory modalities assigned higher reliabilities are preferentially used by the CNS to execute actions than sensory modalities with lower reliabilities (Alais & Burr, 2004; Ernst & Banks, 2002). Therefore, in the visual-tactile simultaneity judgment task, VT stimuli were weighted more reliably than TV stimuli, resulting in narrower (i.e., more precise) TBWs for VT stimuli than TV (see Figure 5.1).

Further, temporal acuity is likely higher for VT stimuli (due to a higher reliability estimate), which leads to more accurate perceptions and decision-making.



Figure 5.1: Left plot shows unisensory and multisensory reliability estimates for visual-visual, tactile-tactile and visual-tactile stimuli in the simultaneity judgment task (Chapter two). Right plot shows unisensory and multisensory reliability estimates for visual, tactile and visual-tactile stimuli in the sensorimotor synchronization tasks (Chapter four: Experiment 1 and 2). Plots adapted from Kayser and Shams (2015).

Regarding the correlational analysis between the width of the VT-TBW and the questionnaires, there was insufficient evidence to support the hypothesis linking wider VT-TBWs to higher autistic traits, hyper- and/or hypo-sensory sensitivity, and increased frequency of unusual sensory experiences. Since VT-TBWs across participants were not as wide as TBWs typically found in clinical populations, and scores on the questionnaires were within the normal range, it is likely that scores on the questionnaires were not extreme enough to detect a relationship between the width of the TBW and autistic traits, sensory sensitivity, and unusual sensory experiences. Perhaps the inability to establish a relationship between the aforementioned variables was limited by our sample size. Although our sample was large enough to detect effects for our primary experimental analysis, it was insufficient to detect an effect in our secondary correlational analysis. Therefore, further investigation in neurodiverse samples, such as ASD and schizophrenia, is crucial to understand whether the VT-TBW exhibits similar characteristics to the audio-visual TBW in these populations. Identifying whether wider TBWs exist for visual-tactile stimuli in clinical populations, as they do for audio-visual stimuli, is important to understand if wider TBWs are sensorymodality specific or a more global difference in multisensory integration that spans across modalities. It is important to determine whether sensory differences in ASD and schizophrenia are specific to certain sensory modalities or indicative of a global sensory deficit. Obtaining this knowledge is essential for exploring various potential underlying causes of presenting symptoms and for identifying appropriate targeted interventions in these populations.

In chapter three, we investigated functional connectivity between unisensory and multisensory neural regions that are expected to be involved in processing and integrating multisensory information during the visual-tactile simultaneity judgment task. The aim of the study was to ascertain whether connectivity between these regions contributed to simultaneity perception. Contrary to our predictions, our results showed stronger connectivity for nonsimultaneous than simultaneous responses between parietal-central and central-occipital electrodes (with a current source density spatial filter transform applied) across theta, alpha, and beta frequencies, and between parietal-occipital in the beta frequency. Our study revealed a unique relationship between simultaneity perception and functional connectivity. Stronger functional connectivity was associated with improved discrimination between the timing of stimuli, which enhanced the ability for individuals to ascertain that the stimuli were nonsimultaneous. We infer from our findings that stronger connectivity for non-simultaneous perception in the theta and alpha frequencies reflects an increase in neural resources required to encode the different temporal dynamics of each sensory stimulus. Whereas stronger connectivity in the beta frequencies may reflect a violation of expectation that the stimuli will

be simultaneous and the resulting feed-forward and feedback of sensory information between regions from trial to trial.

Previous research shows pre-stimulus activity in the alpha and beta frequencies influences simultaneity perception (Bastiaansen et al., 2020; Ikumi et al., 2019; Jiang et al., 2023; Migliorati et al., 2020; Yuan et al., 2016). However, at the pre-stimulus stage of the task primarily attention, anticipation and prediction processes are at play. Focusing solely on this pre-stimulus neural activity provides an incomplete picture as it overlooks the influence of activity occurring during and immediately following stimulus presentation that more directly reflects perception and the subsequent reporting of simultaneity. Examining neural activity during and immediately following stimulus presentation is crucial as the judgements are made on sensory input, which must be processed and integrated before determining whether stimuli occur simultaneously. Without examining activity during stimulus presentation, a core component of the task, we only know half of the story that contributes to simultaneity perception, and multisensory integration by proxy. Indeed, our findings help illuminate the missing half of the story by demonstrating that connectivity between unisensory and multisensory regions, which would be active during the task, contributes to simultaneity perception. These connectivity findings are also important for understanding the neural mechanisms underlying multisensory integration more broadly.

In chapter four, we conducted two experiments investigating unimodal and crossmodal sensorimotor synchronization (SMS), and the relationship between SMS and the VT-TBW (Huntley et al., 2024). In Experiment 1, we compared movement synchronization variability between cross-modal and unimodal stimuli. Our results showed that SMS was less variable with visual-tactile stimuli and tactile-alone stimuli than visual-alone stimuli. Therefore, the inclusion of a visual stimulus did not enhance SMS performance, indicating no meaningful advantage for cross-modal stimuli in this task. The variability of SMS is likely

influenced by sensory estimates, with higher reliability assigned to visual-tactile and tactilealone estimates of stimulus timing compared to visual-alone estimates. This pattern of results was found for both sub- and supra-second ISIs (600 ms and 1200 ms, respectively).

In Experiment 2, we examined the influence of cross-modal visual-tactile stimuli presented inside and outside the TBW on SMS temporal error. Within each cross-modal condition, that is, visual-tactile and tactile-visual, the second stimulus in the pair was presented with an SOA of 80 ms or 400 ms. The 80 ms SOA meant that both stimuli were presented inside the TBW, and the 400 ms SOA meant that the first stimulus was presented inside the TBW, and the second stimulus was presented outside the TBW. Our results showed SMS temporal error was higher when the second stimulus was presented inside the TBW compared to when the second stimulus was presented outside the TBW. These findings indicate cross-modal stimuli presented inside the TBW biases movement towards the onset of the second stimulus. Thus, indicating that sensory estimates for cross-modal stimuli presented inside the TBW (SOA 80 ms) were weighted less reliably than when one stimulus in a crossmodal pair is presented inside the TBW and the second stimulus outside the window. Sensory modality seemed to play a role in reliability estimates for both Experiment 1 and Experiment 2, with tactile-alone and tactile-leading visual-tactile stimuli weighted more reliably than visual-alone and visual-leading visual-tactile stimuli (See Figure 5.1). It is feasible that tactile information was weighted more reliably in this context due to the nature of the task. That is, finger-tapping is largely an automatic and repetitive process that utilises tactile information quite heavily, with little need for visual input to be successful in the task. Further, for both experiments, wider TBWs were associated with increased variability and larger temporal errors in SMS. These findings suggest that reduced temporal acuity and extended multisensory integration impacts the accuracy of anticipating stimulus timing, consequently

affecting the initiation of motor execution. Thus, highlighting the interdependence of sensory, motor, and temporal processes.

As mentioned throughout this thesis, the TBW and SMS tasks can be explained by various complimentary sensorimotor models, including linear phase correction (Schulze & Vorberg, 2002), maximum likelihood estimation (Alais & Burr, 2004; Ernst & Banks, 2002), causal inference (Körding et al., 2007; Parise et al., 2012), Bayesian causal inference (Elliott et al., 2014; Jagini, 2021) and predictive coding (Friston & Kiebel, 2009). These models posit that sensory estimates are derived from the probability of certain aspects of sensory information in the environment, which are weighted according to their reliability (Kayser & Shams, 2015). The reliability estimates can be updated by new information that is integrated into existing information as the likelihood. The combined findings in this thesis provide evidence that supports the idea that reliability weighting of sensory estimates differs depending on the task and the sensory modality that is most optimal for task performance at the time. For example, in the simultaneity judgment task, the VT stimuli had a higher reliability weighting than TV, whereas in the SMS tasks, the TV stimuli had higher reliability weightings, which is likely due to the nature of the task (see Figure 5.1). These results indicate that reliability estimates of sensory modalities are not fixed and are flexible depending on the task and multisensory information available in the environment. Outlined below is an example of how these models explain sensory and motor processes involved in the TBW and SMS (Figure 5.2). It is important to note that these models do not act in isolation, they all contribute to our understanding of sensorimotor integration.
Multiple theoretical	TBW and SMS	In the visual-tactile sensorimotor synchronization task unimodal and cross-modal stimuli are integrated and finger-tapping is temporally aligned with the sensory cues.
	Linear phase	The participant taps their finger in synchrony with the visual, tactile and visual-tactile stimuli. They use sensory feedback (e.g.
	model	visual information) to temporally adjust the timing of finger-
		taping to reduce error in the sensorimotor synchronization task.
	Maximum	Visual, tactile, and visual-tactile cues provide information about
	likelihood	the timing pattern of the stimuli, in which they need to
	estimation	synchronize their finger-tap. The sensory cues are assigned a
	model	weight according to their reliability estimate (e.g., in accurately
		timing their finger-tap with the sensory cue).
	Causal	Participant identifies if the visual, tactile and visual-tactile cues
	inference	share a common source. Sensory cues arising from the same
		source are combined / integrated into a perceptual whole (i.e., the
		temporal binding window). This process is useful to help the
		participant differentiate between the modality and timing of each
frameworks		stimulus in the visual-tactile, tactile-visual, visual-visual or
underlie the		tactile-tactile pair of stimuli. Each pair of stimuli form individual
temporal		percepts that are crucial for determining whether the current pair
binding window and		occurs simultaneous or non-simultaneously.
	Bayesian	The participant uses new sensory cues in subsequent repeated
sensorimotor	causal	trials to update existing sensory estimates (i.e., their 'prior
synchronization	inference	belief'). The updated estimate, known as the 'posterior' is used to
		anticipate the timing of the next stimulus to improve the temporal
		accuracy of synchronizing their finger tap with the timing of the
		sensory cues. The 'prior' is continuously updated with new
		sensory information/feedback as the block of trials continue.
		Based on the likelihood, the participant decided whether to adjust
		the timing of their finger tap to reduce error.
	Predictive	ne participant anticipates and predicts the timing and sensory
	coung	nior When the sensory information is aligned with their
		prior. when the sensory information is anglied with their predictions, the brain minimises prediction error, which
		rainforces the existing prior. When the sensory information is
		unexpected for example when a tactile trial follows a visual
		tactile trial the prediction error increases. The participant
		undates their existing prior with this new information which
		allows for more accurate predictions and motor responses as the
		task continues
	1	

Figure 5.2: This figure shows the complementary theoretical models underlying the TBW for multisensory integration and sensorimotor synchronization, as described in this thesis.

5.2 Unravelling the simultaneity judgment task

The simultaneity judgment task is commonly used to measure the TBW for

multisensory integration from development through to adulthood (Hillock-Dunn & Wallace,

2012; Hillock et al., 2011; Powers et al., 2009; Spence & Squire, 2003; Stevenson et al.,

2012a; Stevenson et al., 2012b). Yet, it is important to acknowledge that the task

encompasses more than temporal binding; it involves anticipation and prediction of incoming

sensory information, attention, memory (working memory and short-term memory), executive function, perception, sensory processing and integration, decision-making and motor response (see Figure 5.3). As these sensory, motor and cognitive functions are all involved in completing the simultaneity judgment task, it stands to reason that actually all of these functions influence the neural activity measured by EEG and the behavioural output of the task, but with varying degrees of influence. I have attempted to overcome this issue by examining functional connectivity between unisensory and multisensory regions involved in the task across a time-range where it is likely multisensory integration processes are primarily in effect. However, it is worth noting that during this time-range there are other processes (cognitive, motor etc) that occur concurrently that are likely combined within the EEG signal and influence the behavioural output.



Figure 5.3: This diagram shows the various sensory, motor and cognitive processes involved throughout the simultaneity judgment task.

5.3 Embodied cognition in sensorimotor control

Embodied cognition is an overarching theoretical framework for which we can understand models for sensorimotor control. In essence, embodied cognition proposes a shift in focus from original ideas of cognition (i.e., that cognition drives motor responses), by asserting that our cognitive functions are shaped by our body's interactions with the environment (Foglia & Wilson, 2013; Wilson & Golonka, 2013). This theory posits that our sensory systems, both internal and external, along with our motor system, actively processes information from our surroundings. Therefore, our body, rather than being passively driven by cognitive functions, actively shapes and informs cognitive processes, such as thinking, decision-making, memory, and attention. A prime example of embodied cognition is how a toddler learns through direct interaction with their environment. A toddler does not understand that pouring a bucket of water over themselves will result in getting wet. However, through the visual and tactile experience of seeing and holding the bucket, and then pouring the water over themselves, they quickly learn the cause-and-effect relationship, embodying the knowledge that the action of pouring water over themselves leads to the sensation of wetness.

In the context of this thesis, embodied cognition can be used to describe the multisensory and motor processes involved in the visual-tactile SMS task in chapter four, experiment two. In this task, visual-tactile stimuli are both presented during the TBW, or one stimulus is presented inside the window and the second stimulus is presented outside the window. The aim of the task is to synchronize the finger-tap with the timing of the visual-tactile information. When the second stimulus is presented within the TBW of the first stimulus (80ms SOA), the brain integrates these stimuli together and decides when to execute the finger-tap with the least amount of temporal error. As there is an 80 ms delay between the stimuli, the movement is inherently biased towards the timing of the second stimulus, which increases temporal error. However, when the first stimulus is inside the window and the second stimulus is outside the TBW (400 ms SOA), the brain easily discriminates between the timing of these signals and treats them as being independent because only one stimulus falls within the TBW. Resulting in the finger-tap synchronizing with the first stimulus in the cross-modal pair. The multisensory information and feedback from the motor system about

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the timing of the finger-tap relative to visual-tactile stimuli are combined with our existing knowledge about the timing and experience of sensory and motor events into an embodied representation. This embodied sensory and motor information creates an internal representation that is used to anticipate, plan and adjust the timing of future finger-taps to reduce temporal and cognitive error.

5.4 Autism and the visual-tactile TBW

While no direct relationship between the width of the VT-TBW and the severity of autistic traits, sensory sensitivity and frequency of unusual sensory experience was found in this thesis, replicating the visual-tactile simultaneity judgment task and the SMS tasks in ASD and schizophrenia warrants further investigation. As there are a multitude of sensory and motor difficulties in ASD and schizophrenia (Fournier et al., 2010a; Gowen & Hamilton, 2013; Greenfield et al., 2015; Iarocci & McDonald, 2006; Ozonoff et al., 2008; Stevenson et al., 2014a; Stevenson et al., 2014b; Zhou et al., 2018), identifying patterns of functional connectivity associated with the VT-TBW and differences in SMS performance might provide insight into the sensorimotor difficulties experienced in these clinical populations. In ASD specifically, it has been identified that neural regions closer together are hyperconnected, and more distant neural regions are hypo-connected (Guofa et al., 2017; O'Reilly et al.). Thus, examining the strength of functional connectivity associated with sensorimotor integration would be useful to understand whether connectivity between unisensory, multisensory and motor regions contribute to these sensorimotor difficulties observed in ASD. Understanding whether atypical functional connectivity between unisensory, multisensory and motor regions contribute to sensorimotor difficulties may help to identify adjustments that can be made to environments that will help individuals manage their sensorimotor difficulties, or potentially design interventions aimed at improving sensorimotor function. Further, as both the SMS and TBW tasks rely on temporal processing, performance

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on these tasks might be hindered by an individual's temporal processing ability, which has been thought to be impaired in individuals with ASD (Morimoto et al., 2018; Murat Baldwin et al., 2021; Stevenson et al., 2016; Zhou et al., 2021b).

5.5 Future directions

The studies in this thesis lay the groundwork for future investigations into the impact of cross-modal stimuli (estimates) on more complex actions, such as reaching and grasping or bimanual coordination. This further investigation should aim to identify whether the reliability estimates for specific (multi)sensory modalities vary based on the task at hand. Further, investigating connectivity between unisensory, multisensory and motor regions during multisensory motor tasks in clinical populations will highlight any differences in connectivity patterns between neurotypical and neurodiverse populations, which will be beneficial for targeted interventions. In the context of the simultaneity judgment task, we propose measuring neural oscillations at longer SOAs. This approach would offer additional support for the idea that non-simultaneous perception is stronger for SOA50 and SOA75 due to the increased challenge of separating and discriminating between the two sensory cues, which are temporally closer compared to cross-modal cues presented at SOA100.

5.6 Conclusion

This thesis has effectively measured the TBWs for visual, tactile and visual-tactile modalities using the simultaneity judgment task. In addition, it has examined functional connectivity between unisensory and multisensory neural regions to understand neural activity during and immediately following stimulus presentation in the task. Further, this thesis has examined unisensory and multisensory sensorimotor synchronization performance and manipulated the timing of cross-modal stimuli to fall either inside, or partially inside, the TBW to understand the effect of cross-modal stimuli on SMS performance. Combined results from this thesis provide novel insights into the visual-tactile TBW, its neural underpinnings, and its contribution to SMS. These processes, that form part of sensorimotor integration more broadly, are essential for our successful interaction with the environment in our everyday life – from making a cup of coffee to playing sport at an elite level. Outcomes from the simultaneity judgement task and SMS tasks can be best explained by complimentary theoretical models that propose that sensory cues are weighted according to their reliability for the task at hand. These estimated reliabilities contribute to shaping the priors that are used for future evaluations of stimulus timing, and by which new beliefs are formed following the integration of new information. While we did not observe a relationship between the width of the VT-TBW and autistic traits, sensory sensitivity, and unusual sensory experiences in our neurotypical sample, further investigation is warranted within an autistic population. It is crucial to explore whether the absence of a relationship is due to specific characteristics of our neurotypical sample, or to establish whether there is no actual relationship between the width of the VT-TBW and autistic traits, sensory sensitivity and unusual sensory experience in an autistic population.

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