Early Somatosensory Processing and Crossmodal Influences

by

Elizabeth Carmelina del Rosso

A thesis
presented to the University of Waterloo
in fulfillment of the
thesis requirement for the degree of
Master of Science
in
Kinesiology

Waterloo, Ontario, Canada, 2021

Authors Declaration

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

I understand that my thesis may be made electronically available to the public.

Abstract

Sensory stimuli from distinct modalities are continuously linked together by the brain to create a cohesive percept of the surrounding environment—a process known as multisensory integration. Furthermore, sensory information from one modality has been shown to alter the processing of another modality. This phenomenon, now referred to as crossmodal sensory integration, has led to an abundance of research, with many studies reporting enhanced cortical responses when stimuli from different modalities (i.e., visual) occur in close temporal proximity to the onset of a tactile stimulus.

Due to current COVID-19 pandemic, a time-frequency analysis (event-related spectral perturbation) of two related datasets (Faerman & Staines, 2019; Popovich & Staines, 2014) was performed in the current work. In both studies, participants were asked to attend only to crossmodal stimuli and to determine the amplitude of both the visually presented horizontal bars and vibrotactile stimuli, while electroencephalography (EEG) was recorded. Conditions involved several blocks of randomized trials with different temporal latencies between the onset of visual and tactile stimuli (i.e., 0-100ms, 100-200ms, 200-300ms). In addition, participants applied a force graded motor response using a pressure sensitive bulb, meant to represent the summation of both stimulus amplitudes. Researchers found that P50 amplitude was greatest in conditions where visual stimuli preceded tactile stimuli with later latencies of onset (0-100ms for Popovich & Staines (2014); and 200-300ms for Faerman & Staines (2019)).

Given the P50 modulation reported in the studies above, the objective of the current work was to examine excitability changes of parietal cortex using de(synchronizations) in mainly the beta, alpha, and theta frequency bands, believed to occur in response to a task where both the

timing and relevance of crossmodal (visual-tactile) events were manipulated. The rationale for this approach is supported by past studies that have demonstrated links between beta, alpha, and theta de(synchronizations) and a role in both sensorimotor integration and certain attentional processes (Barutchu et al., 2013; Lalo, Gilbertson, & Doyle, 2007; Siegel, Warden, & Miller). De(synchronizations) of neuronal activity are connected to the coupling and uncoupling of functional networks in the brain. Therefore, it is believed that repetitive and synchronous neuronal firing promotes the activation of functional networks because it increases the chances that neurons entrain each other in synchronous firing, and vice versa (Bastiaansen, Mazaheri, Jensen, 2012).

With this background information in mind, the general hypotheses were that beta band (13-30Hz) synchronization would be greatest when a visual stimulus preceded a tactile stimulus by 100ms compared to when a tactile stimulus preceded a visual stimulus by 100ms, and that both theta and alpha synchronization would be influenced by the interaction of attention and top-down/bottom-up influences, represented by the attentional demand and the temporal relationships of the sensory processing stimuli. A one-way repeated measures analysis of variance (RM-ANOVA) confirmed a strong effect of stimulus for the theta frequency at frontal site(s), with Tukey's post-hoc tests revealing a significant difference between the experimental condition where visual and tactile stimuli were presented simultaneously and the condition where tactile stimuli preceded visual stimuli by 100ms. A main effect of stimulus was also found for the alpha frequency range at central-parietal sites, with Tukey's post-hoc test revealing a significant difference when visual information preceded tactile stimuli by 100-200ms and 200-300ms.

It is quite possible that the crossmodal nature of the task used in both experiments is driving, at least in part, the alpha-theta synchronizations discussed, perhaps in a similar manner to the modulations of specific ERP components (i.e., P50, P100) reported in previous studies; however further research must be conducted to provide clarity.

Acknowledgements

This thesis was made possible by the following people:

1) Dr. Richard Staines: Thank you for all the support and guidance you have extended to me during the completion of my master's program at Waterloo. It was a pleasure learning and growing under your supervision.

2) To my committee members, Dr. Sean Meehan and Dr. Ewa Niechwiej-Szwedo: thank you your helpful suggestions throughout this process, and for encouraging me to think more critically.

3) To my peers, who were always available to answer my questions in a timely manner.

4) To my parents, thank you for emphasizing the value of education.

Table of Contents

List of Figures

List of Abbreviations

A1	Primary Auditory Cortex
ANOVA	Analysis of Variance
BOLD	Blood Oxygen Level Dependent
CL	Caudolateral
CNV	Contingent Negative Variation
cTBS	Continuous Theta Burst Stimulation
ECoG	Electrocorticography
EEG	Electroencephalography
ERP	Event Related Potential
ERSP	Event-related Spectral Perturbation
FEF	Frontal Eye Fields
FMRI	Functional Magnetic Resonance Imaging
HZ	Hertz
LGN	Lateral Geniculate Nucleus
MAEP	Middle-latency Evoked Potential
MEG	Magnetoencephalography
MFG	Middle Frontal Gyrus
MM	Medio-medial
MMN	Mismatch Negativity
PFC	Prefrontal Cortex
RM-ANOVA	Repeated Measures Analysis of Variance
S1	Primary Somatosensory Cortex
S2	Secondary Somatosensory Cortex
SEP	Somatosensory Evoked Potential
STFT	Short-time Fourier Transform
TRN	Thalamic Reticular Nucleus (TRN)
V1	Primary Visual Cortex
VPL	Ventral Posterior Lateral Nucleus
VPM	Ventral Posterior Medial Nucleus

1.0 Introduction

The brain has traditionally been thought of as a collection of unisensory parts that can be studied in isolation (Kayser & Logothetis, 2007). Furthermore, only higher association areas—including the superior temporal sulcus, the intra-parietal sulcus, and specific regions in the frontal lobe—were thought to be responsible for the merging of sensory information (Calvert, 2001; Kayser & Logothetis, 2007). That said, more recent research has provided contrasting evidence, positing that crossmodal interactions can occur in brain areas deemed 'unisensory,' as well as at the earliest stages of sensory cortical processing (Kayser & Logothetis, 2007). For example, it is well known that the higher-order ventral visual pathway processes visual information; however, more recently this pathway has also been found to be responsive to tactile inputs that carry shape and spatial information, even in the absence of a visual stimulus (Yau et al., 2015).

Crossmodal or multisensory integration itself can be broadly defined as the merging of sensory inputs into a cohesive whole, which ultimately allows for more efficient navigation of the surrounding environment (Yau et al., 2015). Several functional magnetic resonance imaging (fMRI) and electroencephalography (EEG) studies have been able to demonstrate that combined sensory input can facilitate behaviour by speeding up reaction times (Hershenson, 1962), or by enhancing the ability to detect obscure stimuli in the surrounding environment (Frens & Van Opstal, 1995). Notably, these crossmodal effects appear to be modulated by attention (Adams et al., 2019; Staines et al., 2014); however, the extent of attentional contributions remains unclear. Therefore, the proposed study will evaluate the neural correlates using a time-frequency analysis

(event-related spectral perturbation—ERSP) of two datasets to assess excitability changes of parietal cortex when the temporal onset of visual-tactile stimuli is manipulated. Findings could have important clinical implications for individuals who display increased distractibility as well as problems inhibiting cortical responses to irrelevant stimuli, such as individuals with lesions to the prefrontal cortex (PFC).

<center>**2.0 Literature Review**</center>

2.1 Neuroanatomy

2.1.1 Somatosensory Cortex

Somatosensory cortex is a brain region important for receiving sensory information (i.e., pain and touch) from various regions of the body and processing this information to guide movement. Somatosensory cortex is located in the parietal lobe and is divided into two parts: primary somatosensory cortex (S1) and secondary somatosensory cortex (S2). The location of S1 is the postcentral gyrus, while S2 is located in the superior limb of the posterior part of the lateral fissure (Lundy-Ekman, 2018).

2.1.2 Projection of Fibers: Primary Somatosensory Cortex (S1)

S1, a somatotopically organized region of the cerebral cortex, receives projection fibres from two specific thalamic nuclei: the ventral posterior lateral (VPL) nucleus and the ventral posterior medial (VPM) nucleus. Both thalamic nuclei receive fibres from the contralateral half of the body via the medial, trigeminal, and spinal lemnisci. The integration of sensory feedback from both cutaneous afferents as well as from muscles, occurs as a result of the thalamus taking in incoming sensory information and then projecting that to layer IV of the cerebral cortex. This information is then sent to other layers of the cerebral cortex. The primary role of S1 is to discriminate/detect the shape, texture, size, motion, and position of objects (Lundy-Ekman, 2018).

<center>3</center>

2.1.3 Secondary Somatosensory Cortex (S2)

Secondary somatosensory cortex receives bilateral fibres from the body. It is believed that many of the fibres in this region come from S1. S2 appears to play an important role in stereognosis, as well as in the memory of both spatial and tactile environments (Lundy-Ekman, 2018).

As will be discussed in greater detail later on in this proposal, several studies have provided evidence demonstrating that S1 is sensitive to attentional contributions and appears to be upregulated by the relevance of stimuli to behavior (Johansen-Berg et al., 2000; Meehan & Staines, 2007; Staines et al. 2002). Additionally, S1 also appears to be modulated by stimuli presented in other modalities. For example, a study by Taylor-Clarke et al. (2002) reported modulation of cortical excitability in S1 during a tactile acuity task when a visual stimulus was present.

2.1.4 Prefrontal Cortex

The PFC occupies over 10% of brain volume, and plays an important role in various neural functions, specifically executive functions. Executive functions refer to higher-level cognitive processes that include attention, cognitive inhibition, cognitive flexibility, and working memory. Notably, many studies have examined the PFC in relation to attention. For example, one study by Knight (1994) reported deficiencies in both attention and memory functions in subjects with PFC damage within 20-500ms after exposure to sensory stimulation. Another study by Adams et al. (2019) examined the role of the PFC in relation to the relevancy-based gating of

visual-tactile information, by temporarily inhibiting this region of the brain using continuous

theta burst stimulation (cTBS) during a sensory selection task. Researchers reported that

somatosensory-evoked N70 ERP was modulated by task relevance only before application of

cTBS to the PFC (Adams et al., 2019), providing further evidence into the role of the PFC and

attentional functions.

2.1.6 Thalamus

The thalamus appears to play an important role in sensory integration. For example,

many studies have highlighted the role of certain thalamic nuclei (i.e., reticular nucleus) in

assisting with the communication/interaction between different sensory streams. Past studies by

Crabtree et al. 1998; Isaac 2002; Zikopoulos & Barbas 2006, have all demonstrated that

somatosensory and motor related thalamic nuclei can both send and receive information from

converging regions of the thalamic reticular nucleus (TRN), allowing them to modulate each

other.

Notably, there has been a relatively recent shift in how thalamocortical processing is

understood, specifically with respect to the role of glutamatergic pathways. The textbook

understanding of thalamocortical organization consists of input that reaches the cortex through

thalamic relay, which is then processed sequentially through sensory, sensorimotor, and motor

areas (Alitto & Usrey, 2003). This information eventually reaches a 'top level' region, at which

point a message is sent from the cortex to the brainstem or spinal motor region for the purpose of

producing a behavioural effect (Alitto & Usrey, 2003). More recent studies have suggested that

thalamic relays have an ongoing and important role in cortical processing through transthalamic

corticocortical pathways (Sherman, 2016). This view has further promoted the identification of 'first order' and 'higher order' thalamic nuclei, which are classified based on the origin of their driving inputs, with first order nuclei representing the initial relay of information from a subcortical source (i.e., retina to cortex), and higher order nuclei representing information relay between one cortical area to another via a cortico-thalamo-cortical route (Bickford, 2016). A study by Saalmann et al. (2012) demonstrates this point. In this study, researchers utilized diffusion tensor imaging and simultaneously recorded spikes and field potentials from interrelated pulvino-cortical regions, while monkeys completed a visuospatial attention task. Researchers found that the pulvinar played an essential role in the transmission and synchronization of information between interrelated cortical regions, which appeared to be modulated according to attentional allocation (Saalmann et al., 2012; Sherman, 2016). These findings are important as they provide evidence in support of the notion that transthalamic pathways act as an avenue for various cortical regions to cooperate for cognitive functions, including but not limited to, attention.

2.1.7 Primary Visual Cortex

The primary visual cortex (also referred to as V1/striate cortex) is located in the occipital lobe, stretching into the calcarine sulcus. V1 is crucial for conscious processing of visual stimuli such as depth perception. Essentially, information leaving the retina is transmitted through the optic nerve (which shortly becomes the optic tract) to a thalamic nucleus referred to as the lateral geniculate nucleus (LGN). This information then proceeds through a track called the optic radiation, which bends around the wall of the lateral ventricle in each cerebral hemisphere and extends back to the occipital lobe. Axons that are part of the optic radiation terminate in V1 in a

retinotopic manner. Projections to V1 from the thalamus travel through three separate pathways. The first pathway emerges from magnocellular cells (also referred to as M cells, which are large neurons in the retina). The second pathway arises from smaller neurons referred to as parvocellular (or P) cells. Lastly, the third pathway travels to V1 from small neurons referred to as koniocellular (or K cells). Each of these neurons are preferentially responsive to only certain types of stimuli. For example, P cells are important for color vision as well as spatial resolution (i.e., color, size, and shape). M cells are important for movement detection, such as the speed or direction of an object in motion, while the purpose of K cells remains unclear though there is speculation that these cells are involved in some aspects of color vision. Interestingly, neurons in V1 are organized into columns of neurons with related functional properties. What this means is that neurons in a one column may only be responsive to stimuli that are in a specific orientation (i.e., upright) perceived by the contralateral eye. Other neurons could also be responsive to stimuli in an upright position, but only when the origin is the ipsilateral eye perception (Vanderah & Gould, 2015).

Notably, there are areas of the occipital lobe that exist around V1 called the extrastriate cortex. V1 is functionally connected to these extrastriate areas via two pathways: the ventral stream (the 'what' pathway) and the dorsal stream (the 'where' pathway). The ventral stream is a path that extends along the ventral portion of the brain, passing from V1 to the extrastriate areas and on the inferior part of the temporal lobe. It is proposed that this pathway is important for transmitting information about object recognition and form. The dorsal stream extends from V1 to extrastriate areas and then to the posterior parietal lobe. This stream is thought to be important for determining the spatial relationships between objects and for motion perception (Vanderah & Gould, 2015).

Several past studies have been able to demonstrate that unimodal sensory perceptions, including but not limited to vision, are enhanced in multisensory contexts. Although multimodal integration is mainly carried out by dedicated multisensory brain regions (i.e., superior colliculus or association cortices) multisensory interactions also take place in primary sensory cortices. For example, one study found that certain sounds can modulate the responses of layer 2/3 (L2/3) neurons of the mouse V1 (Ayzenshtat, Jackson, & Yuste, 2016). An extension of the latter study found that sound modulation was contingent on the tuning properties (direction selectivity as well as orientation) and the response amplitude of V1 L2/3 neurons (McClure & Polack, 2019). More specifically, sounds increased the response of neurons highly sensitive to cue orientation and direction, while in a unimodal context their activity was minimal (this is in line with the principle of inverse effectiveness discussed in greater detail in the paragraph below). Furthermore, sound had the opposite effect on neurons untuned for the orientation/direction of the visual cue (McClure & Polack, 2019). Together, these findings demonstrate that visual stimuli shown with auditory stimuli employ a neuronal population better tuned to visual orientation and direction than when presented independently (McClure & Polack, 2019).

2.2 Functional Criteria for Sensory Integration

As mentioned previously, multisensory integration can be defined as a high level of cognitive combination, where distinct sensory information is combined to form a coherent percept (Kayser & Logothetis, 2007). It can also, however, be defined in terms of specific neuronal activity (Kayser & Logothetis, 2007). Past research on the superior colliculus has laid the framework upon which a series of principles have been developed in order to determine whether something constitutes sensory convergence at the neural level (Kayser & Logothetis, 2007). The superior colliculus is a subcortical convergence region for sensory information that plays an important role in orienting the eyes towards salient objects in space. Generally speaking, sensory convergence is said to have occurred if a neuronal response is elicited when stimuli from different sensory modalities are presented in isolation, or if activity elicited by one stimulus is enhanced or depressed by a stimulus from another modality (Kayser & Logothetis, 2007). Based on this understanding, several principles have been derived. The first principle concerns the spatial arrangement of sensory stimuli; here, neurons will respond to stimulation only if it occurs within that neuron's receptive field (i.e., visual responses limited to stimuli within a confined region of the visual field) (Kayser & Logothetis, 2007). Much is the same for multisensory neurons that contain receptive fields of several, overlapping modalities. Essentially, only stimuli that fall within this overlap will create an enhanced neuronal response—defined as the principle of spatial coincidence (Stein & Wallace, 1996). The second principle is the principle of temporal coincidence, which states that only stimuli occurring in close proximity to each other will create an enhanced neuronal response, and that the opposite is true for stimuli separated in time (Stein & Wallace, 1996). The third and final principle is that of inverse effectiveness, which posits that

9

stimuli that independently evoke strong neuronal responses often yield little crossmodal

interaction and vice versa (Stein & Wallace, 1996).

2.3. Anatomical Evidence for Early Convergence

Studies have demonstrated that all types of anatomical connections including feed-forward, feed-back, and lateral can provide crossmodal inputs into early sensory cortices (Kayser & Logothetis, 2007). Research has identified cross-connections between distinct sensory streams, including projections from auditory areas to the primary and secondary visual cortex in the macaque monkey (Murray et al., 2005). Furthermore, the caudal auditory belt receives input from somatosensory areas, including the granular insula, retroinsula, as well as higher somatosensory areas (Smiley et al., 2007). Subcortical nuclei also appear to have an important role in relaying crossmodal signals to sensory cortices (Kayser & Logothetis, 2007). For example, the vast majority of intralaminar nuclei (i.e., limitans nucleus), forebrain structures, as well as koniocellular matrix neurons, extend diffusely to sensory cortices (Kayser & Logothetis, 2007). Lastly, the thalamus has been shown to play an important role in the interaction of different sensory streams. As mentioned earlier, numerous studies (i.e., Crabtree et al.,1998; Yingling & Skinner, 1976; Zikopoulos & Barbas, 2006) have demonstrated that somatosensory as well as motor related thalamic nuclei send and receive information from converging areas in the TRN, allowing them to modulate each other. It is important to note, however, that although anatomical studies have provided some evidence regarding several prospective routes for crossmodal input to early sensory cortices, no explicit association has been made between a specific connection and a specific functional finding (Kayser & Logothetis, 2007).

2.4 Assessing Event Related Potentials at Early Stages of Processing

2.4.1 Electroencephalography

EEG records cortical voltage changes that result from ionic currents within neurons, via electrodes that are placed on the scalp. These recordings can be divided into two categories: 1) the spontaneous or background EEG; and 2) event-related potentials (ERPs). Often, the focus is on analyzing specific ERPs of interest (i.e., P50, P100) time-locked to a particular event (i.e., motor, cognitive, sensory) and any corresponding changes in the waveforms generated. More specifically, ERPs are thought to reflect the summed activity of postsynaptic potentials, which is the result of many cortical pyramidal neurons with comparable orientation firing at the same time during information processing (Peterson et al., 1995; Sur & Sinha, 2009). Changes in ERPs can be quantified based on their polarity, shape, amplitude, latency, and spatial distribution on the scalp. All these characteristics, apart from peak polarity, are highly variable among individuals and can be affected by factors including subject fatigue, attention, habituation, and differences in electrode placement. Lastly, ERPs can be divided into two categories: 1) the early components (or exogenous components) that tend to peak within the first 100ms after stimulus presentation, and are referred to as sensory ERPs since they are largely dependent on the physical characteristics of the stimulus presented; and 2) the later components (or endogenous components), which are thought to reflect information processing (i.e. the process by which the participant evaluates the stimulus), and thus are typically referred to as cognitive ERPs. Unlike earlier components, the activity of late ERP components varies based on the level of attention, stimulus significance, and task relevance (Sur & Sinha, 2009).

2.4.2 Strengths & Limitations of EEG

With all that said, EEG is advantageous in that it provides excellent temporal resolution, and therefore, provides insight into the speed of neural activity/processing in response to different stimuli from one millisecond to the next (Brang et al., 2015; Starke et al., 2017). Secondly, the use of ERPs allows the researcher to be able to determine which stage(s) of processing are modulated in response to certain experimental manipulations (i.e., stimulus onset time), given that they provide a constant measure of processing between stimuli and participant response (Luck, 2005). Thirdly, even when no outward behavioral change is evident, ERPs continue to provide a measure of stimulus processing (Luck, 2005). Lastly, there is no measurable conduction delay between neural activity and potentials that are recorded from the scalp, and this is due to two factors in particular: 1) the tissue that the ERPs are produced in; and 2) the nature of the electrical activity (Nunez & Srinivasan, 2006).

With that said, it is worth noting that EEG does have its limitations. The first, and perhaps most significant limitation, has to do with the fact that only neural activity at the cortical level is detected and thus any contribution from subcortical structures cannot be determined directly. The second limitation concerns the spatial resolution of EEG. Although EEG has excellent temporal resolution, its spatial resolution is rather limited. This places restrictions on the types of conclusions researchers can draw, since they are unable to accurately discriminate between brain regions that may all be active at a given time in response to a provoking stimulus, and thus contribute to the brain activity measured. With specific reference to ERPs, the location of ERP sources can only be estimated, which can place restrictions on the type of research questions that can be studied (i.e., research questions that rely heavily on the location of neural

activity may not be well suited when using ERPs). The last limitation concerns the presence of artifacts. Eye blinks, muscle movements (i.e., clenching of the jaw), and swallowing are common artefacts that can affect the quality of ERPs generated (Beres, 2017).

2.4.3 Time Frequency Analysis

EEG can be represented in two domains: a time domain and a frequency domain. As discussed earlier, EEG is modeled as a sequence of sine waves of varying frequencies that overlap in time, and phase angles that differ based on the stimulus present. Sine waves are defined by their frequency, phase, and magnitude. Frequency specifically refers to the number of complete oscillations occurring in a 1-second time range (units Hertz, Hz = cycles per second), while the phase of a sine wave refers to distinct time points within a cycle of the sine wave (anywhere between −180° to 180°). Lastly, magnitude is defined as the maximum height of a sine wave's peaks/valleys relative to the x-axis.

A signal presented in the 'frequency domain' is accomplished via a spectral decomposition, where a complex number is approximated for each time point in the time-domain signal. Time-frequency decomposition of EEG data may be accomplished in several ways. One of the most basic forms of time-frequency analysis is called the short-time Fourier transform (STFT), where a Fourier transform is performed in a specific time frame that shifts along the time series for the purpose of characterizing changes in power and phase of EEG signals that occur across time. It is worth noting that for all time-frequency transformations (i.e., the Hilbert transform, matching pursuits, continuous/discrete wavelet transforms) there is a trade-off between frequency and temporal resolution. For example, the greater the time window used to approximate the complex data for a specific time point is, the higher the frequency resolution but

the poorer the temporal resolution. With that said, time-frequency analysis remains useful in

being able to evaluate alterations in both power and synchronization on a higher order in relation

to the onset of task events between spatial locations over trials (Roach & Mathalon, 2008).

2.5 Functional Evidence for Sensory Convergence

Accumulating evidence from both EEG and magnetoencephalography (MEG) studies have been successful in demonstrating changes of evoked potentials in sensory areas that take place shortly after stimulus onset, and as a result of merging stimuli from different modalities (Kayser & Logothetis, 2007). One specific study by Murray et al. (2005) demonstrated that facilitative interactions between auditory-somatosensory stimuli occur in healthy adults when these stimuli are presented concurrently at the same or two different locations—a finding in line with the principle of spatial alignment discussed earlier. With respect to the behavioural data obtained, reaction times were facilitated when participants were tasked with detecting both auditory and somatosensory stimuli pairs, in comparison to all other conditions (Murray et al., 2005). Notably, this effect exceeded simple probability summation, which is important to mention as it argues against an attention-based explanation for the behavioural results obtained. Regarding the electrophysiological data, researchers reported enhanced auditory evoked responses when an additional somatosensory stimulus was applied to participants' hands, and that this crossmodal enhancement reached significance 50ms post-stimulus (note: EEG data was analyzed on a total of 8 subjects—two women and one left-handed man, mean age 25.4 years—due to the presence of significant artifacts) (Murray et al., 2005). Source localization of the ERPs clarified the origin of all spatial configurations, which included the superior temporal gyrus in the hemisphere contralateral to the hand stimulation, as well as around posterior auditory cortices—a finding in line with two principles of sensory integration mentioned earlier being the principle of inverse effectiveness and the principle of temporal coincidence (Murray et al., 2005; Stein & Wallace, 1996). Taken together, these findings have important implications regarding the current

16

understanding of multisensory interactions, as well as spatial representations. First, the fact that reaction times did not differ between stimulus pairs for both the aligned and misaligned configurations, provides new insight concerning the temporal synchrony and spatial alignment of bisensory inputs, specifically that auditory-somatosensory multisensory interactions for the aligned and misaligned stimulus configurations seem to share a common spatiotemporal neural mechanism (Murray et al., 2005). The latter is better supported by the electrophysiological data, particularly the scalp topographies, which indicate that the auditory- somatosensory interactions do not create activity in new networks, but rather regulate responses in already active generators (Murray et al., 2005). Lastly, the timing of these auditory-somatosensory interactions are in line with other studies and provide further support for a model of multisensory interactions, by being able to demonstrate that early stages of sensory processing have access to information from additional sensory modalities.

Another related study, by Meehan et al. (2009), sought to determine the effects of intermodal influences on somatosensory processing in S1 using somatosensory evoked potentials (SEPs). Other objectives of this study included: examining spatiotemporal relationships between bimodal stimuli in S1 and their effects and observing any behavioural changes as a result of intermodal modulation. To address these objectives, median nerve SEPs were evoked via electrical stimulation and recorded using scalp electrodes during a task that required tracking of either vibrotactile or visual stimuli presented simultaneously. Researchers reported a reduced P27 amplitude when there was a greater spatial relationship between the vibrotactile and the visual stimuli (Meehan et al., 2009). Furthermore, increased temporal synchrony led to a greater P27 amplitude, while task-relevance was linked to greater N140 amplitude (Meehan et al., 2009). Interestingly, the P27 SEP component was found to be generated in primary somatosensory

cortex (BA 1), which is an area typically thought of as a somatosensory specific area. Lastly, tracking performance reflected early SEP amplitude changes, and temporal synchrony for vibrotactile tracking resulted in greater P50 amplitude (Meehan et al., 2009). The noted changes in the P50 component indicate multisensory features of somatosensory processing, while the noted changes in P27 amplitude are likely indicative of an intermodal mechanism of somatosensory gating, modulated by spatiotemporal properties of bimodal stimulation. Collectively, the results of this study have important implications for how early somatosensory processing is understood by revealing: first, that the presence of intermodal influence can occur as early as P27 and is associated with both the relevancy of vibrotactile stimuli as well as the spatial and temporal properties of the two modalities; and second, that alterations in P50 amplitude are associated with changes in participant vibrotactile tracking performance (Meehan et al., 2009).

Similar findings to those discussed above have also been observed in several fMRI studies. One study in particular by Kayser et al. (2007) showed that crossmodal influences on auditory cortex occurs at the earliest stages—in the primary sensory cortex. At the time, what was unknown was which auditory fields were susceptible to crossmodal influences. To gain insight into this, the researchers used fMRI on macaque monkeys to study the modulation of auditory processing by visual stimulation. Their study design included visual stimuli, which consisted of clips taken from commercially available documentaries of animal wildlife; auditory stimuli of nature sounds that matched the video clips being viewed by the monkeys; and combined audiovisual stimuli. Researchers found that both the primary (core) and nonprimary (belt) auditory fields became active merely in response to the presentation of visual scenes—a finding that highlights the presence of regions in auditory cortex that contain an overlap of both

auditory and visual representations (Kayser et al., 2007). Additionally, activation in response to combined audiovisual stimulation was greater when compared to auditory stimulation alone in the mediomedial (MM) and the caudolateral (CL) fields, as well as the primary auditory cortex (A1) (Kayser et al., 2007). Together, these results provide strong evidence that support the multisensory model by revealing that multisensory modulation of auditory processing occurs to a large extent in caudal fields but is also evident at the lowest stages of auditory cortical processing. The findings from this study also addressed a major gap in the literature at the time —the inability to systematically localize which auditory fields were susceptible to multisensory influences due to both the small size and large number of auditory fields—by using high-resolution imaging with a functional approach. Importantly, the reported finding that multisensory integration is evident in the caudal auditory cortex provides support for the notion that multisensory convergence may actually work to improve the spatial localization of external events. Given these results, future research may wish to look at subcortical exchange of multisensory information between sensory modalities, including but not limited to visual and auditory modalities. With all that said, it is important to note one limitation of this study, which is that the reported multisensory enhancement partially reflects enhanced sensory processing as a result of more focused attention.

In conclusion, given that both sensory integration and attention heighten sensitivity to stimuli in the surrounding environment, thereby enhancing perception, it makes sense that they share similar underlying mechanisms; however, further research is warranted in order to confirm or clarify the extent of attentional contributions.

2.6 Early Modality-specific Somatosensory Cortical Regions (S1) and Attention

There are certainly attentional modulations that exist at early stages in somatosensory processing and play a role in crossmodal integration, as suggested by the literature (Jäncke et al., 1999; Johansen-Berg et al., 2000; Macaluso et al., 2000; Macaluso et al., 2002; Mima et al., 1998). First, to provide some context, the word 'attention' is often applied to various information selection processes in the brain given that there are many sources that can activate the attention system. These sources include the type of stimuli that are presented (i.e., 'bottom-up,' 'stimulus driven' attention, or 'saliency'), and internal cognitive processes (i.e., 'goal-directed' attention) (Berger & Bülthoff, 2009). Furthermore, attention also entails the selection of information with reference to different stimulus parameters, such as spatial location (i.e., spatial attention); a particular sensory modality; or a particular class of information (i.e., 'feature-based' attention, such as the specific shape of an object) (Berger & Bülthoff, 2009; Corbetta & Shulman, 2002). Many studies have looked at how attention might influence the integration of signals if one modality is suppressed by attention, and the consequences that this has for the sensory precept. For example, Mozolic et al. (2008), Warren et al. (1981); and Talsma et al. (2007) have all suggested that ignoring one information source/cue while paying attention to another minimizes the combining of the two cues. On the other hand, attending to both cues at the same time seems to promote their integration (Berger & Bülthoff, 2009). A study by Meehan & Staines (2007), provides insight into the effects of task-relevance on S1. Functional magnetic resonance imaging was used while vibrotactile and visuospatial stimulation were delivered simultaneously to participants ($n=10$). For each condition, participants were required to track either a visuospatial stimulus or vibrotactile stimulation. The visuospatial stimulus consisted of presentation of a dial in which the position of a needle randomly moved upon application of graded force to a force

sensing resistor, while the vibrotactile stimulation (delivered at 25 Hz) varied in intensity and was delivered to the right index finger of each participant. Further, the distractor modality emerged from either a spatially related location or a location distinct to the target guiding the movement. Researchers found that intermodal selective attention to the vibrotactile stimulus led to a reduction in the BOLD response observed in S1, in comparison to when it was a task-irrelevant distractor (Meehan & Staines, 2007). In addition to this, an increased activation volume in S1 was observed in response to a task-irrelevant vibrotactile stimulus (Meehan & Staines, 2007). A potential explanation for these patterns could be that the task demands associated with continuous tracking led to increased surround inhibition during vibrotactile tracking (Meehan & Staines, 2007). In other words, the requirement for participants to extract continuous vibrotactile information specific to their right index finger (ventral surface) in order to successfully complete the task at hand, could have possibly resulted in surround inhibition within S1 and a decreased activation in volume. A second potential explanation for these patterns could concern the role of low-level connections between sensory areas in multisensory integration. Essentially, many research studies focusing on multisensory integration have been successful in demonstrating that interactions among modality-specific sensory cortices occur via top-down feedback projections, but also via direct parallel low-level connections amidst sensory areas (Macaluso, 2006). Therefore, it could be entirely plausible that the increase in S1 volume is reflective of a complementary mechanism of intermodal selective attention that works to improve the overall speed and precision of motor output. In other words, the requirement for participants to continually track both visuospatial and vibrotactile stimulation could have placed more emphasis on quick multisensory effects/interactions, possibly moderated by low-level connections that link somatosensory as well as visual cortices (Meehan & Staines, 2007).

Notably, researchers observed an increased BOLD response in relation to the visuospatial tracking conditions in the following areas: the left inferior occipital gyrus, the superior parietal lobe and precuneus, the right lingual gyrus, the precentral gyrus, and the inferior parietal lobule. These areas may reflect top-down influences on S1 as suggested by past studies (i.e., Corbetta & Shulman, 2002; Shomstein & Yantis, 2004), where the precentral gyrus, the inferior parietal lobe, and the superior parietal lobe in particular have been shown to play an important role in the control of unimodal and intermodal visual selective attention. Lastly, it is important to make note of another significant finding in this study being that the spatial origin of the two modalities did not result in any additional effects on S1 activation (Meehan & Staines, 2007). A potential explanation for this stems from past research by Murray et al. (2005) as well as McGurk & MacDonald (1976), who both suggested that these effects are likely perceptual, and thus, mediated at higher levels of sensory processing.

A related study by Dionne et al. (2010) investigated how simultaneous bimodal (visual and vibrotactile) stimulation modulates S1 activity. This study involved a delayed sensory-to-motor task, where both stimuli were relevant to the task. Functional magnetic resonance imaging was performed while subjects completed a sensory-guided motor task and received visual, vibrotactile, or both visual and vibrotactile stimuli. Researchers were ultimately interested in whether S1 activity was modulated by the need to use both visual and vibrotactile information in order to successfully complete the task at hand. They were also interested in identifying the neural areas involved in this process. Researchers reported an increase in blood oxygenation level in S1 for the bimodal (visual and tactile) task in comparison to the unimodal task—a novel finding in the literature (Dionne et al., 2010). Additionally, whole-brain analysis displayed a common fronto-parietal network (specifically the right precentral gyrus, left middle frontal

gyrus, right medial frontal gyrus, right superior temporal gyrus, and the left parietal lobule) that was operative across both the bimodal and unimodal tasks (Dionne et al., 2010). This observed neural activation pattern provides support for the notion that these brain areas may be sensitive to the attentional as well as the motor-planning aspects of a task, rather than just the nature of the stimuli (that is, unimodal or bimodal). Interestingly, the results from this study differ from those discussed in the Meehan & Staines (2007) paper above where researchers observed a decrease in the volume of S1 activity when participants were tasked with tracking a tactile stimulus and ignoring a visual stimulus during bimodal visual and tactile stimulation. That said, it is possible that these differences may have to do with the type of task employed in the two studies (i.e., in the Dionne et al. 2010 study, both visual and tactile stimuli were relevant for task completion, which required participants to maintain focus on both stimuli rather than on just one, thereby engaging selective intermodal attention). Taken together, these results demonstrate that information from different modalities modulate early sensory processing. Notably, the main limitations of this study include: 1) poor temporal resolution of fMRI, which has an impact on the temporal nature of the reported crossmodal interactions; and 2) possible reduction in the sensitivity of the behavioral measure to observe what it was intended to measure as tasks were completed in an fMRI machine, which may have posed certain restrictions (i.e., restrictions in movement) (Dionne et al., 2010).

With all that said, the results of both studies highlight attentional contributions in early somatosensory processing by demonstrating that there are sensorimotor requirements that exist and that determine the mechanisms of intermodal selective attention.

2.7 Attention Modulation of Primary Somatosensory Oscillations

As mentioned earlier, there is evidence to support the presence of crossmodal sensory interactions occurring early in the processing stream, in neural areas once deemed 'unimodal' (Kayser & Logothetis, 2007). Studies have shown that these crossmodal sensory interactions are heightened when stimuli are task-relevant—referred to as top-down modulation (Dionne et al., 2013; Popovich & Staines, 2014). Furthermore, if one of two (or more) simultaneously presented stimuli is considered irrelevant for task completion, it will be either suppressed or separated out of the cortical processing stream—a process referred to as sensory gating (McIlroy et al., 2003; Wasaka et al., 2005). Sensory gating can be more specifically defined as the inhibition of sensory information moving from the periphery to the cortex (McIlroy et al., 2003; Wasaka et al., 2005), which ultimately prevents higher cortical areas from becoming overwhelmed with incoming irrelevant information (Kumar et al., 2005). The PFC is often associated with gating, particularly its influence in the top-down inhibition of ascending sensory information (Knight et al., 1999; Yamaguchi & Knight, 1990). In fact, many studies have provided evidence for the role of the PFC in inhibiting task-irrelevant stimuli during behavioural tasks. One such study by Wiesman and Wilson (2020) explored the impact of directed attention on somatosensory sensory gating. Twenty-six healthy participants completed a somato-visual paired-pulse oddball paradigm (while undergoing a MEG scan) that involved attention being directed either towards or away from paired-pulse stimulation of the left median nerve. Stimuli were shown to participants in alternation, with a portion of stimuli designated as temporal oddballs for the purpose of monitoring participant behaviour and being certain that attention was actually being directed towards either the somatosensory or visual domain. The somatosensory stimulus in this experiment involved paired-pulses that were delivered using unilateral electrical stimulation to

the median nerve of the left hand, where 80 paired-pulse trials were collected with a 50ms inter-stimulus interval while the oddball somatosensory trials (8 total) were collected using an inter-stimulus interval of 1000ms. The visual stimulus included a right-lateralized circle centralized on a horizontal axis and to the right of a centrally-presented fixation crosshair. Participants completed a total of two experimental blocks (total 352 trials; 176 somatosensory trials, with 16 somatosensory oddballs), with the difference between the two blocks being the instructions participants received. For example, in the somatosensory block participants would be instructed to respond only to somatosensory oddballs, while directing attention away from the task-irrelevant visual stimuli. The opposite was true for the visual block. Notably, during this task, the participants were required to focus on the centrally-presented crosshair as well as to keep their left arm still throughout both experimental blocks. An MEG-compatible five-finger response pad was used to respond to the presence of oddball stimuli. With respect to results obtained, researchers found that attention in the direction of somatosensation considerably modified the gating of all three population-level neural oscillatory responses to the paired-pulse stimuli. Furthermore, the observed gating effect varied according to the spectro-temporal profile of the response. More precisely, sensory gating of the early theta response was greater when attention was focused towards the somatosensory domain (Wiesman & Wilson, 2020). Alternatively, gating of beta and alpha responses were lower in the same attentional state. This finding provides support for the conceptualization of the early theta component as a representation of low-level stimulus recognition, as well as feature encoding, as supported by several other past studies including those by Andersen & Lundqvist (2019), Hlushchuk & Hari (2006), and Wiesman et al. (2016). On this note, such gating is believed to be indicative of a 'filtering' mechanism that removes unnecessary/redundant stimulus information at an early stage of neural processing.

Therefore, it is likely that enhanced attention directed towards this stimulus increases the efficiency of gating. To make the point even clearer, because the stimulus properties (i.e., pulse-width and amplitude) were exactly the same for both stimulations in this experiment, further processing of these properties would be futile, and thus, this effect would only be accentuated/heightened when the timing was relevant and not the stimulus properties (Wiesman & Wilson, 2020). Furthermore, the reported finding regarding the decrease in gating of the later alpha and beta responses with focused attention suggests that these responses are very likely to be an indicator of modulatory feedback and temporal processing given that the timing of the second stimulus was more pronounced in the 'attend somatosensory' condition (Wiesman & Wilson, 2020). This point is further supported by the finding that alpha coherence between both the primary somatosensory cortices as well as the prefrontal cortex was greater when attention was focused towards the somatosensory domain, essentially pointing to a prefrontal modulator of the alpha-somatosensory response. Notably, this effect was only observed for the alpha frequency band which is in line with other studies (i.e., Staines et al., 2002, Yamaguchi & Knight, 1990) whose findings also point to a prefrontal modulator of somatosensory processing. Lastly, somatosensory alpha coherence with the right cuneus was also markedly decreased when attention was focused on the somatosensory domain. This is not surprising considering past work (i.e., Bonnefond & Jensen (2012); Janssens et al. (2018); Klimesch et al. (2007); Wiesman et al. (2018); Wiesman & Wilson (2019)) which have provided evidence to support parieto-occipital alpha desynchronizations as an active disinhibition of visual processing circuits during certain visual tasks. With this knowledge in mind, it is intuitive that the relative reduction in somato-visual connectivity that was present in the attend somatosensory condition is indicative of a 'decoupling' of the somatosensory and visual processing circuits that transpires for the purpose

of facilitating more efficient performance on the somatosensory task at hand. With all that said, the results of this study are important as they further the current understanding for the functional role of somatosensory responses that are spectrally different, which is information that may act as a useful guide to interpret past research specific to aging and clinical populations (Wiesman & Wilson, 2020).

Another relevant study by Szczepanski et al. (2014) was interested in exploring how changes in phase-amplitude coupling could facilitate spatial attentional control in the fronto-parietal cortex. It is well known that both parietal and frontal brain areas—together referred to as the fronto-parietal attentional control network—play an important role in attentional allocation. What researchers wanted to determine was how parietal and frontal regions interact with each other to generate behaviour on a fine spatial (sub-centimeter) as well as temporal (sub-second) scale. To explore this, electrocorticography (ECoG) signals were recorded from subdural electrodes placed in patients going through intracranial monitoring for localization epileptic foci. All eight participants completed a spatial-cuing task, where visuospatial attention was directed to either the left or right visual field, and they were required to identify when a target was present. Researchers reported greater high gamma power (70-250 Hz) time-locked to trial onset that continued to be elevated across the attentional allocation period over visual, parietal, and frontal areas. Furthermore, these high gamma power elevations appeared to be altered by the phase of the ongoing delta/theta (2-5 Hz) oscillation with attentional allocation. Together, these findings provide support that coupling between high gamma amplitude and the phase of the delta/theta signal furthers processing in parietal, visual, and frontal areas with visuospatial attentional allocation (Szczepanski et al., 2014).

3.0 Rationale

Previous research has provided clear evidence to support the presence of crossmodal interactions that occur at the earliest stages of sensory cortical processing (Dionne et al., 2013; Kayser et al., 2007; Staines et al., 2014; Popovich & Staines, 2014). Additionally, many of these studies have provided new knowledge regarding: the temporal synchrony and spatial alignment of bisensory inputs (Murray et al., 2005); the presence of intermodal influences—found to occur as early as the P27 SEP component and be associated with both the relevancy of vibrotactile stimuli and spatial and temporal properties of the two modalities— (Meehan et al., 2009); and a better understanding regarding the relationship between the attention system and multisensory selection processes like sensory gating (Adams et al., 2019; Wiesman & Wilson, 2020). This new knowledge may be useful in contributing to future research in the following ways: 1) by providing additional explanations or a more comprehensive understanding of the mechanisms underlying early sensory-sensory interactions; 2) applying this new knowledge to clinical settings (i.e., rehabilitation centres for individuals who have had a stroke). That said, there are certainly current gaps in the literature that should be addressed. The first gap concerns the extent/unique contributions that the attentional system has on early sensory-sensory interactions (i.e., visual and tactile). For example, Meehan et al. (2009) was unable to isolate attentional effects and the intermodal effects related to the physical features of both the distractor and target modalities, raising questions about the underlying mechanisms at play. A potential explanation for this could be that there are low-level intermodal interactions contingent on the physical attributes of the bimodal stimulation, and thus, 'independent' from any attentional modulation by the dorsolateral prefrontal cortex. This, however, may be unlikely considering more recent findings (previously discussed) by Dionne et al. (2013) where it was found that modality-specific

components (P50, P100) were sensitive to both the temporal dynamics of crossmodal interactions (bottom-up sensory input), as well as their relevance to behaviour (top-down attention). Therefore, it is more possible that these low- level mechanisms communicate with attentional components to increase or decrease the salience of the distractor stimulus, ultimately modifying the processing of somatosensory information; however, further research is warranted to provide clarity.

A second gap in the literature concerns when the optimal timing for early crossmodal interactions (i.e., visual and tactile) to occur is. As will be discussed below, Popovich & Staines (2014) explored the unique contributions of the visual system in modulating early somatosensory ERPs (specifically P50), by manipulating the temporal onset of visual-tactile stimuli. While they did find that P50 was modulated based on both the timing and relevance of crossmodal interactions, researchers utilized a fixed latency period of 100ms between the onset of a visual and tactile stimulus. It would, therefore, be interesting to explore latencies ranging from 250-350ms and 200-400ms and observe how early somatosensory ERPs are modulated, since this has not yet been explored. The minimum amount required for crossmodal interactions to occur is at least 100ms, given that it takes approximately the same amount of time for a visual signal to reach the visual cortex (Popovich & Staines, 2014). Therefore, it is very likely that more time is needed for crossmodal interactions to occur and conducting a study that utilizes longer latencies may result in greater P50 and P100 amplitudes than that reported by Popovich & Staines (2014) if activation is still occurring. These findings would lead to a greater understanding of cortical processing and adaptation that can assist in furthering sensorimotor learning strategies and rehabilitation techniques for individuals who have had a stroke or sustained a traumatic brain

injury, by providing knowledge regarding what the optimal timing for crossmodal (visual-tactile) interactions to occur is.

That said, the goal of the proposed study in Fall 2020 was to examine both behavioural and neurophysiological data with specific focus on the modulation of early event-related potentials (primarily somatosensory P50), in response to manipulating the temporal onset and attentional relevance of visual-tactile stimuli. Given the current COVID-19 pandemic, I was unable to collect data of my own and therefore analyzed two datasets (both of which informed the proposed study) using a time-frequency analysis to be able to assess excitability changes of parietal cortex in a different way than originally planned while still addressing my general objectives and hypotheses. It is important to note that there is rationale for using this alternative approach given previous work by: 1) Wiesman & Wilson (2020), who found that attention modulates the gating of primary somatosensory oscillations (specifically the early theta (4-8 Hz), beta (20-26 Hz) and later alpha (8-14 Hz) responses)); 2) Barutchu et al. (2013), who found evidence for increased multisensory facilitation with stimulus relevance (more specifically, that optimal multisensory facilitation was linked to a latency shift of induced beta oscillations over parietal scalp regions at the right hemisphere); and lastly, 3) Lalo et al. (2006), who linked phasic increase in cortical beta activity to changes in sensory processing.

4.0 Objectives & Hypotheses

The general objective of the current work was to examine excitability changes of parietal cortex, as indexed by de(synchronizations) in mainly the beta, alpha, and theta frequencies, believed to occur in response to an experimental task where both the relevance and temporal onset of crossmodal (visual-tactile) stimuli were manipulated. The rationale for this approach is supported by past studies that have demonstrated links between beta, alpha and theta de(synchronizations) and a role in both sensorimotor integration and certain attentional processes (Barutchu et al., 2013; Lalo, Gilbertson, & Doyle, 2007; Siegel, Warden, & Miller). Essentially, de(synchronizations) of neuronal activity are connected to the coupling and uncoupling of functional networks in the brain (Bastiaansen, Mazaheri, Jensen, 2012). Therefore, it is thought that repetitive and synchronous neuronal firing promotes the activation of functional networks because it increases the chances that neurons entrain each other in synchronous firing and vice versa (Bastiaansen, Mazaheri, Jensen, 2012). The power of any frequency band may be used to observe synchronization changes in local neuronal ensembles (i.e., 'nodes' within the functional network working in synchrony with each other via long-range synchronizations) (Bastiaansen, Mazaheri, Jensen, 2012). Furthermore, coherence observed between electrode sites within a specific frequency band provides knowledge regarding synchronization changes between two or more local ensembles (i.e., amid different nodes) (Bastiaansen, Mazaheri, Jensen, 2012).

With this background information in mind, the general hypotheses were that beta band (13-30Hz) synchronization would be greatest when a visual stimulus preceded a tactile stimulus by 100ms (VTd) compared to when a tactile stimulus preceded a visual stimulus by 100ms (TVd), and that both theta and alpha synchronization would be influenced by the interaction of

31

attention and top-down/bottom-up influences, represented by the attentional demand and the temporal relationships of the sensory processing stimuli.

5.0 Methods

Note: As mentioned, given the current COVID-19 pandemic, I was unable to run an experiment of my own. Therefore, specifics on previous work by Popovich & Staines (2014) and Faerman & Staines (2019) is outlined below to provide context. Details on the time frequency analyses performed on these two datasets will follow.

5.1 Participants

Popovich & Staines (2014): Participants consisted of 20 healthy participants (mean age = 26, 10 males), of which 5 were excluded due to the presence of significant artifacts or poorly defined somatosensory ERPs of interest (specifically P50 and P100). Therefore, the final sample included a total of 15 participants (mean age = 27.5, 7 men). All experimental procedures were approved by the University of Waterloo Office of Research Ethics, and informed written consent was obtained from all subjects taking part in the experiment.

Faerman & Staines (2019): EEG was collected from 10 healthy participants (final sample= ages 18-22; 7 females, 3 males). All experimental procedures were approved by the University of Waterloo Research Ethics committee.

5.2 Experimental paradigm

For both experiments, participants were seated comfortably and asked to maintain visual fixation on the computer monitor in front of them. Additionally, they were asked to rest the volar surface of their left index finger on a vibrotactile device and grip a pressure-sensitive bulb placed

in their right hand (see Figure 1). Participants were asked to attend only to the crossmodal stimuli and determine the amplitude of both the visually presented horizontal bars as well as the vibrotactile stimuli. Their response consisted of a force graded motor response using a pressure sensitive bulb meant to represent the summation of both stimulus amplitudes. Participants had a window of 2.5 seconds to respond before the start of the next trial, for a total of 3.5 seconds per trial. For the Popovich & Staines (2014) study, each of the conditions were randomized and performed in six blocks of 120 trials (blocks were approximately five-minutes in length), while in the Faerman & Staines (2019) study, stimulus pairs were randomized and presented in twelve blocks.

Prior to EEG collection, participants underwent a five-minute training session, containing visual feedback to help familiarize themselves with the relationship between stimulus amplitude and the coinciding graded motor response to be applied using the pressure-sensitive bulb. More specifically, during the training session a horizontal target bar was displayed on the computer monitor placed in front of participants. Participants were then asked to respond using a pressure-sensitive bulb with sufficient force to raise another horizontal bar to the same level as the target bar. Vibrations from the vibrotactile device were also delivered to the volar surface of participants' left index fingers, and this vibration corresponded to how much force they exerted when squeezing the pressure-sensitive bulb (i.e., if a participant squeezed hard on the pressure-sensitive bulb, the amplitude of the vibration to his/her finger increased accordingly). In an effort to control for force related trial to trial differences, a single stimulus did not require a squeeze of more than 25% of an individual's maximum force, and for two stimuli a force of more than 50%.

The main difference between these two experiments were the conditions included. In the

Popovich & Staines (2014) study, there were a total of five conditions: 1) tactile-tactile (TT); 2)

visual-visual (VV); 3) visual-tactile simultaneous (SIM); 4) tactile-visual delay (TVd), where a

tactile stimulus preceded the onset of a visual stimulus by 100ms (TVd); and 5) visual-tactile

delay, where a visual stimulus preceded the onset of tactile stimulus by 100ms (VTd). The TVd

condition acted as a control as P50 would have been elicited before the onset of visual

information; thus, if any modulatory effects were observed, it could not be attributed to

crossmodal interactions. The VTd condition, on the other hand, was included to determine the

role of the visual system in modulating early somatosensory ERPs (specifically P50). This was

accomplished by simply manipulating the temporal onset of visual information relevant for

upcoming movement. The Faerman & Staines (2019) study included a total of 5 conditions: a

tactile-tactile pair; a tactile and visual pair with a 100-200 millisecond delay; and three remaining

conditions where visual information preceded tactile with latencies of onset ranging from 0-

100ms, 100-200ms, and 200-300ms.

It is important to stress how, in both experiments, the attentional demand/requirement

was held constant throughout as participants were instructed to attend and respond only to

crossmodal conditions. Controlling attention in this manner is crucial in order to be able to

extract the interaction of bottom-up influences (i.e., in this case, visual priming) on crossmodal

interactions.
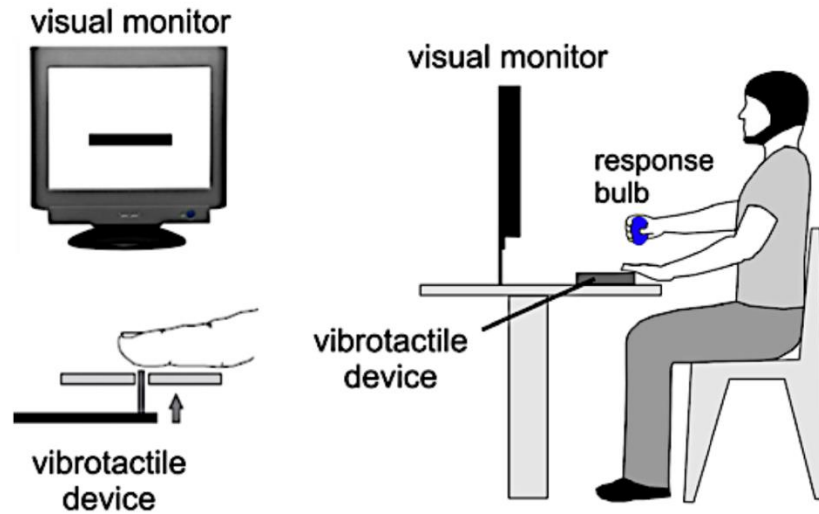
Figure 1. Experimental setup represented. Courtesy of Popovich & Staines (2014).

5.3 Stimuli

For both experiments, visual stimuli comprised of a horizontal bar (6 cm wide) displayed centrally on a computer monitor placed in front of each participant at 50cm. This bar varied in height for the purpose of representing different visual amplitudes. Vibrotactile stimulation was delivered via a customized vibrotactile device to the volar surface of the left index finger of each participant. Vibrotactile stimulation itself was controlled/managed in the following manner: first, by converting digitally generated waveforms to an analog signal (DAQCard 6024E: National Instruments, Austin, TX); and second, by increasing the intensity of the analog signal (Bryston 2BLP, Peterborough, Ontario, Canada) via a customized program written in LabView (version 8.5; National Instruments). With that said, any alterations in the amplitude of the driving voltage to the vibrotactile device would result in corresponding changes in the type of vibration delivered to the participants' fingers. The amplitude of each discrete vibration remained consistent within a single trial, with random variations introduced between trials. Notably, the average stimulus

amplitude over all trials involving a tactile stimulus remained consistent across all experimental conditions. The frequency of the vibration was fixed at 25 Hz, and 70db of whitenoise (Stim2; Neuroscan, Compudics USA, Charlotte, NC) was played during the training period as well as the experimental blocks for the purpose of tuning out any hardware vibration sounds that may have resulted in auditory perception of the vibrotactile stimulus by participants.

5.4 Data Acquisition

EEG was collected from 32 electrode sites (32-channel Quik-Cap, Neuroscan, Compudics, NC, USA) during all experimental blocks. Main electrodes of interest (based on the international 10-20 system for electrode placement) included: Fcz, Cz, C3, C4, Cp3, P3, Cp4, and P4 (all for somatosensory ERP detection). Electrodes were referenced to linked mastoids (impedance <5 kOhms), and EEG recordings were filtered (DC-200 Hz) and digitized at sample rate of 500Hz (Neuroscan 4.5, Compumedics, USA) prior to being saved for analysis. Stimulus onset as well as participant responses were collected using the LabVIEW program and identifying event codes were then generated and inserted into the EEG data stream. Individual EEG traces were also scanned for the presence of artifacts, such as eye movements and blinks or muscle contractions (i.e., clenching of the jaw muscles). Epochs affected by any of these artifacts were removed prior to averaging. Furthermore, event-related potentials were averaged to each stimulus onset relative to a pre-stimulus baseline of 100ms. Somatosensory ERPs were measured from individual participant averages from each task condition. Additionally, mean ERP amplitudes as well as latencies were determined for each participant within a time frame based on the post-stimulus latencies of early somatosensory ERP components: P50 (40-70ms), P100 (90-125ms). The amplitude of each potential was also measured from pre-selected electrode sites, where scalp regions displayed the highest voltage within the corresponding latency window

(being C4, CP4, P4 for the P50 component—all being areas approximately over right sensory-motor cortex and contralateral to the vibrotactile stimulus—and P3, PZ, and P4 for the P100 component). All amplitudes were measured as a raw voltage corresponding to the pre-stimulus baseline.

## 5.5 Data Analysis: Time Frequency Analysis (Event-related Spectral Perturbation)

Data was analyzed using EEGLab (Swartz Center for Computational Neurosciences, CA, USA) software. All continuous data files were epoched from -100 to 450ms for each stimulus type. Epochs were screened for artifacts and noise most likely originating from outside generators (non-biological or biological in nature), and then averaged for each stimulus type (Popovich & Staines data: TT, VV, SIM, TVd, VTd; Faerman & Staines data: TT, TVd, VTd 0-100ms, VTd 100-200ms, VTd 200-300ms).

Initially, to plot the time-frequency transform, the channel number for each electrode site of interest (i.e., CP4, C4 & P4—all electrode sites roughly overlying right sensory-motor cortex, as well as contralateral to the vibrotactile stimulus—and FZ) was specified manually. Additional settings specified in EEGLAB as part of this process included the: sub-epoch time (-100, 1000); frequency limits (0, 50); and wavelet cycle (the fast Fourier transform). To avoid changing the parameters manually each time, the '*newtimef*' function in MATLAB (The MathWorks Incorporation, MA, USA. Version 9.8 (R2020a)) was used for the remainder of the time-frequency analysis, to generate the time-frequency transforms and return the event-related spectral perturbation (ERSP) values. Rows corresponding to the frequency range of interest and columns corresponding to the time range of interest were extracted. A mean ERSP of the extracted data was then created.

Notably, the ERSP measures average dynamic alterations in amplitude of the broad band

EEG frequency spectrum as a function of time in reference to an experimental event (Makeig,

1993). In other words, the ERSP measures the average temporal profile of relative changes in the

spontaneous EEG amplitude spectrum elicited by a set of experimental events similar in nature

(Makeig, 1993). These spectral changes tend to involve more than one frequency band. The

general process to compute an ERSP involves calculating baseline spectra from the EEG prior to

each event (Makeig, 1993). The epochs are then separated into short, overlapping data windows

of which a moving average of the amplitude spectra is generated (Makeig, 1993). Following this,

the spectral transforms of individual response epochs are normalized by dividing by their

corresponding mean baseline spectra (Makeig, 1993). The normalized response transforms for

several trials are averaged, which results in an average ERSP plot (see Figure 2).

Latencies for ERSP power analyses were taken from visual inspection of the plots and

averaged across the five different stimulus types for each dataset. Latencies used for the Faerman

& Staines (2019) data were as follows: 0-50ms for the beta 1 and beta 4 frequency bands; 150-

250ms for the alpha 1 frequency band; 150-200ms for the theta band; and 250-350ms for the

alpha 2 frequency band. These same latencies were used for the Popovich & Staines (2014) data,

with an additional latency time range of 50-100ms for the beta 1, beta 4, and theta frequency

bands (see Table 1 below).
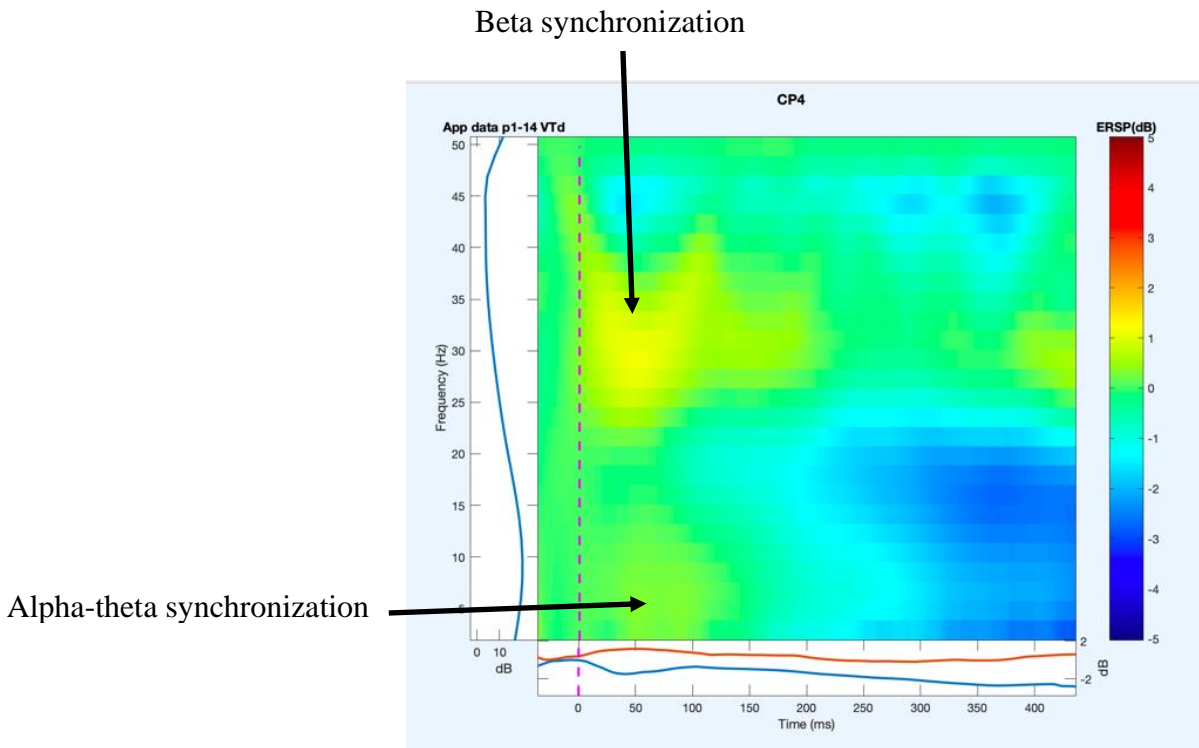
Figure 2 – ERSP Analysis: Time Points for latency extraction for each condition visually taken from ERSP plots. ERSPs were taken from -100ms pre-stimulus to 450ms post stimulus. Plots were visually inspected for any spectral changes occurring, as well as averaged for the purpose of determining temporal intervals.

Theta (4-6 Hz)	150-200ms (&0-50ms only for the Popovich & Staines (2014) data))
Alpha 1 (8-12 Hz)	150-200ms
Alpha 2 = 8-12 Hz	250-350ms
Beta 1 (18-25 Hz)	0-50ms (& 50-100ms only for the Popovich & Staines (2014) data))
Beta 4 (25-35 Hz)	0-50ms (& 50-100ms only for the Popovich & Staines (2014) data))

Table 1: *Mean ERSPs for extraction.*
Time-locked to tactile (T-T, V-T) & T-VT)

5.6 Statistical Analysis:

Popovich & Staines (2014) data

To address the study objectives previously outlined, a one-way repeated analysis of variance (ANOVA) was conducted, with stimulus as a factor and five different levels (SIM, VTD, TVD, TT, VV). A contrast was performed to test the hypothesis that beta synchronization would be greatest for the crossmodal visual-tactile task with a 100ms temporal delay between stimulus onsets (VTd), relative to the tactile-visual delay (TVd) condition. Tukey's post-hoc test was carried out on any main effects to determine which levels of the ANOVA were significantly different.

Faerman & Staines (2019) data:

A one-way repeated measures ANOVA with stimulus as a factor and five different levels (TT, VTd 0-100ms, VTd 100-200ms, VTd 200-300ms, TVd 100-200ms) was conducted. This was performed to *explore* whether theta and alpha synchronization would be influenced by the interaction of attention and top-down/bottom-up influences, represented by the attentional demand and the temporal relationships of the sensory processing stimuli. Tukey's post-hoc test was carried out on any main effects to determine which levels of the ANOVA were significantly different.

6.0 Results

Popovich & Staines (2014) data:

In the Popovich & Staines (2014) study, modulatory effects on P50 differed based on the temporal delay of crossmodal stimuli. More specifically, P50 amplitude was most enhanced for the VTd condition when compared to all other experimental conditions, with the smallest amplitude reported for the irrelevant unimodal tactile condition (TT) (Popovich & Staines, 2014). Furthermore, the P100 ERP component was also enhanced in response to relevant, simultaneous crossmodal interactions (SIM condition), with no effect observed in the TVd or irrelevant unimodal conditions (Popovich & Staines, 2014). This pattern suggests that P100 increases only when visual-tactile events involve selective attention and take place in temporal synchrony. Notably, behavioural results of this study showed response differences in the amount of force participants exerted on the pressure-sensitive bulb. Specifically, participants over-squeezed the pressure sensitive bulb when summating TVd stimuli in comparison to VTd stimuli (Popovich & Staines, 2014). This pattern may be due to different cognitive strategies being applied to process the different stimuli. Figure 3 below depicts a grand averaged trace, which quite clearly shows that in the VTd condition there is an increased amplitude of the P50 component (depicted in blue) relative to all other conditions. The topographic maps shown on the bottom half of the same figure complements the P50 results by showing that vibrotactile stimulation elicited neural activation in somatosensory regions contralateral to stimulation, while the VV condition showed minimal activation overall. Furthermore, graph 4A) depicts mean P50 amplitudes measured at sites CP4, C4, and P4, while graph 4B) depicts the mean P100 amplitude at P3, Pz, and P4, respectively. The blue bars represent the VTd condition; red bars represent the

TVd condition; grey bars represent the SIM condition, and black represent the TT condition.

Two key takeaways from these graphs are as follows: 1) that the modulation of P50 amplitude depends on the temporal onset of crossmodal stimuli, and this appears to be greatest when visual events occur prior to tactile events; 2) that the amplitude of the P100 was larger in the SIM condition relative to TVd and TT conditions. Both findings provide support for the attentional system influencing crossmodal interactions at early stages of cortical processing, in modality-specific sensory ERP components.
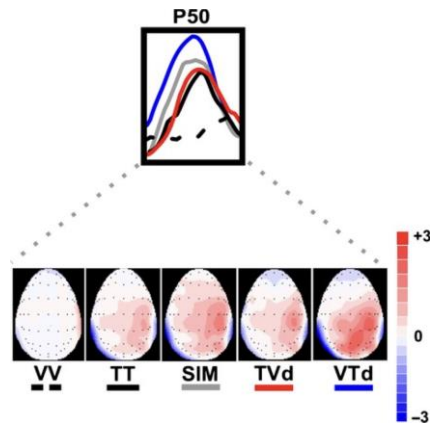
Figure 3. *Scalp topography maps of the P50 component. Blue, red, and gray traces depict the VTd, TVd, and SIM conditions, with the dashed trace representing the VV condition and black solid line, the TT condition. Group averaged data of peak areas for cortical activity within a time frame of 40-70ms around the P50 ERP peak.*
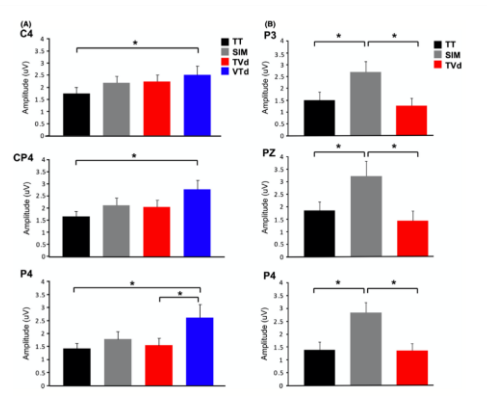
Figure 4. *Group ERP means for sites C4, CP4, & P4 & P3,PZ, P4: A) Depicts group means for the P50 ERP component and B) for the P100 ERP component. Blue bars represent the VTd condition, red bars, the TVd condition, gray bars, the SIM condition, and black bars, the TT condition. * Indicates the significance value P< 0.05, and error bars show SEM.*

Courtesy of Popovich & Staines, 2014

Faerman & Staines (2019) data:

It was mentioned earlier that a main limitation of the Popovich & Staines (2014) study has to do with the 100ms temporal delay used in the TVd and VTd conditions. Essentially, this

temporal delay interfered with the timing of some early somatosensory responses (i.e., the P100 component, particularly in the VTd condition), as well as all ERPs with a late onset (i.e., N140), leaving researchers unable to comment on crossmodal effects for these components. Additionally, the minimum amount required for crossmodal interactions to occur is at least 100ms, given that it takes approximately the same amount of time for a visual signal to reach the visual cortex (Popovich & Staines, 2014). Therefore, it is very likely that more time is needed for crossmodal interactions to occur. For this reason, a second dataset, which included three conditions where visual information preceded tactile stimuli with longer latencies of onset ranging from 0-100ms, 100-200ms, and 200-300ms, was also analyzed using a time-frequency analysis. In the Faerman & Staines (2019) study, P50 amplitude for the VTd 200-300ms condition had a larger amplitude relative to the other conditions (TT; VTd 0-100ms; VTd 100-200ms; VTd 200-300ms; VTd 100-200ms). A one-tailed t-test was performed to test the researcher's hypothesis that either of the VTd conditions with onset latencies beyond 100ms would result in a statistically significant increase in P50 amplitude compared to the TVd 100-200ms condition. Both the one-tailed t-test and one-way ANOVA confirmed that the difference between the amplitude of the P50 in the VTd 200-300ms condition and the TVd 100-200ms condition were statistically significant. This suggests that there are certainly temporal interactions occurring in early cortical processing, and more specifically, that the onset of a visual and tactile stimulus results in a greater P50 amplitude generated in S1.

6.1 ERSP Analysis Results

Popovich & Staines (2014) data:

For beta 4 at electrode sites CP4 and P4, no main effect of stimulus was found ($F_{(4, 13)} = 0.86$, $p=0.49$)) and ($F_{(4,13)} = 0.77$, $p=0.5486$)), respectively. For beta 1_lt (note: 'lt' denotes the 0-50ms time range) at C4 the same patterns were found, with no main effect for stimulus type ($F_{(4,13)} = 1.12$, $p=0.36$)). Interestingly, a strong effect of stimulus was found for theta (150-200ms) at FZ (see Figure 5) ($F_{(4,13)} = 4.09$, $p=0.005$)). Tukey's post-hoc test revealed a significant difference between the SIM and TVd stimulus types (see Figure 5). Theta synchronizations have often been interpreted as being a symbol of a top-down source of modulation (Szczepanski et al. (2014); Wiesman & Wilson (2020)). Therefore, it could be the crossmodal nature of the task used that is driving, at least in part, the theta synchronizations observed in the current work. The significance of this result in connection with past work will be discussed in greater detail in the 'Discussion' portion below.
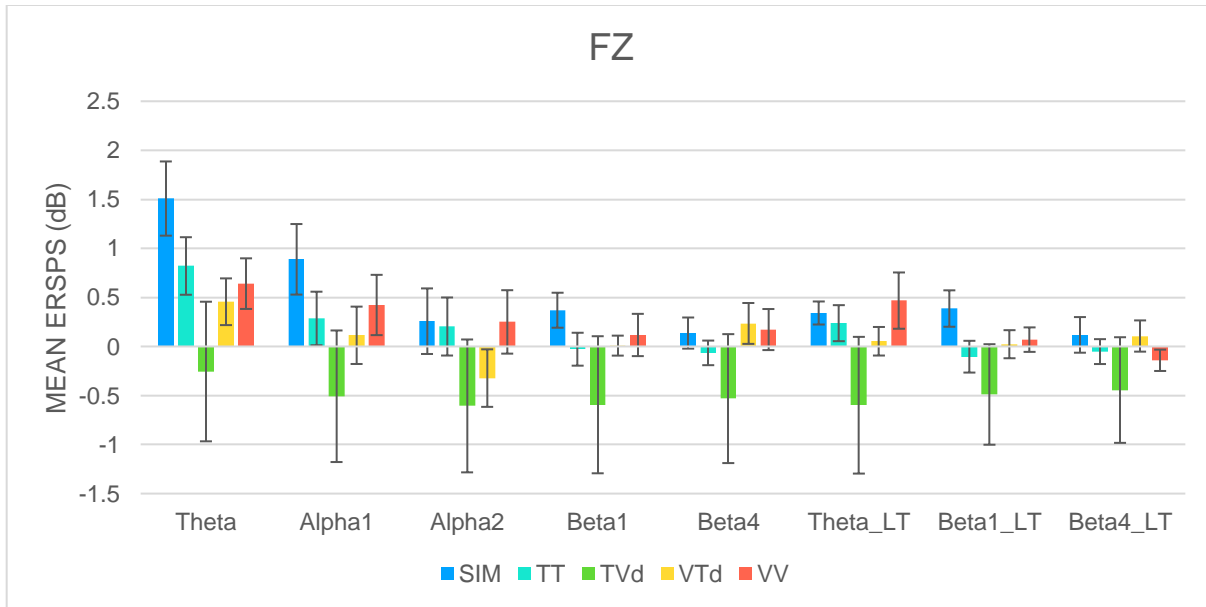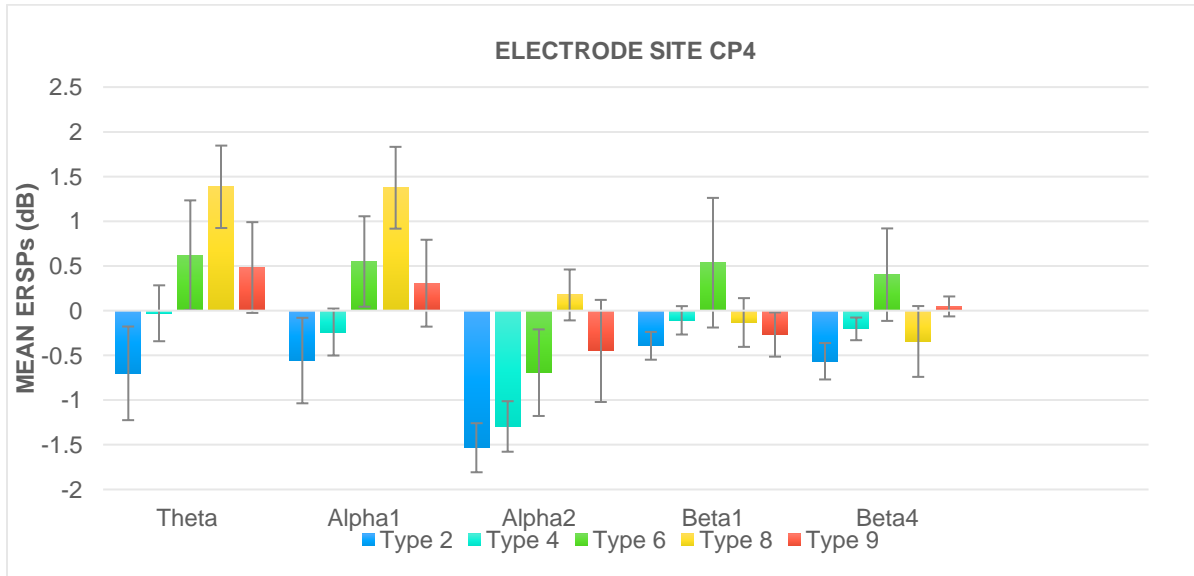
Figure 5: Mean ERSP amplitudes for all 5 conditions. Blue bars represent the simultaneous condition; teal bars represent the tactile-tactile condition; greens bars represent the tactile-visual condition with 100ms onset delay; yellow bars represent the visual-tactile condition with 100ms onset delay; and red bars represent the visual- visual condition.

Faerman & Staines (2019) data:

There was a main effect of stimulus found for alpha 1 at CP4 ($F_{(4,9)} = 2.99$, p=0.03)). Tukey's post-hoc test revealed a significant difference between the VTd 200-300ms condition (type2) and TVd 100-200ms condition (type8) (see Figure 6). A main effect of stimulus was also observed for alpha 2 at CP4 ($F_{(4,9)} = 4.33$, p=0.006)). Tukey's post-hoc test revealed a significant difference between VTd 100-200ms (type4) and TVd 100-200ms (type8) (see Figure 6). No main effect of stimulus was found for alpha 1, alpha 2, or theta at FCZ (p>0.05). A main effect of stimulus was observed for alpha1 at CP3 ($F_{(4,9)} = 3.15$, p=0.03)), with Tukey's post-hoc test revealing a significant difference between VTd 200-300ms (type2) and TVd 100-200ms

(type8) (see Figure 7). Lastly, a strong trend towards significance was found for theta at CP3 (F

$(4,9) = 2.58$, p=0.053)), with Tukey's post-hoc test revealing a significant difference between

VTd 200-300ms (type2) and TVd 100-200ms (type8) (see Figure 7).

Figure 6. Mean ERSP amplitudes for all 5 conditions. Blue bars represent the VTd 200-300ms condition (type

2); teal bars represent the VTd 100-200ms condition (type 4); green bars represent the VTd 0-100ms condition

(type 6); yellow bars represent the TVd 100-200ms condition (type 8); and red bars represent the tactile- tactile
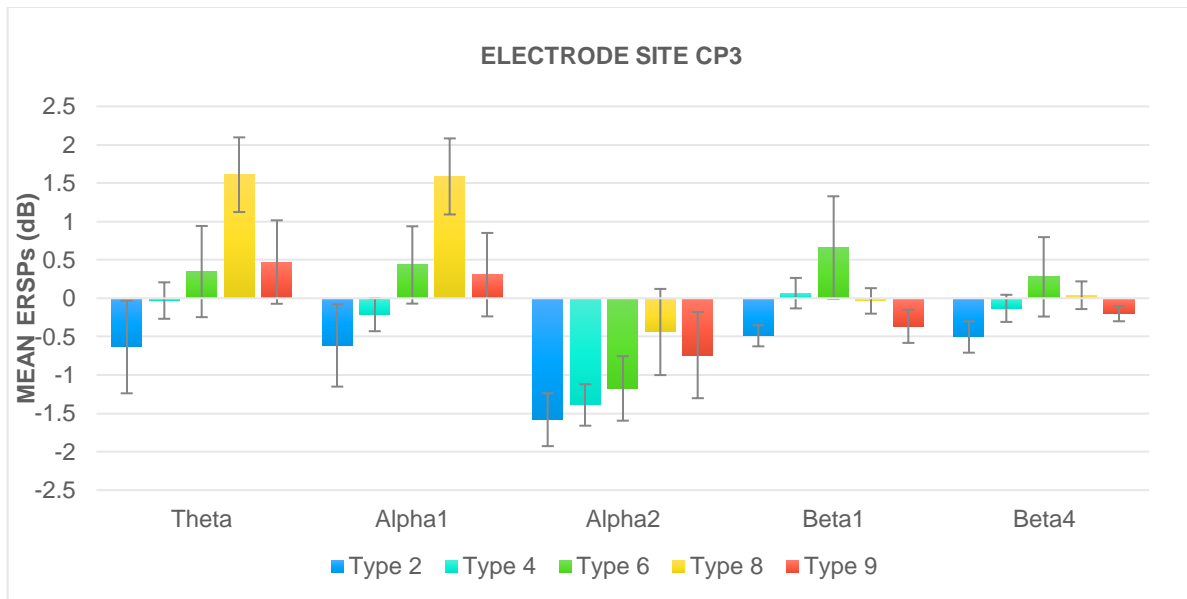
condition (type 9).

Figure 7: Mean ERSP amplitudes for all 5 conditions. Blue bars represent the VTd 200-300ms condition (type 2); teal bars represent the VTd 100-200ms condition (type 4); green bars represent the VTd 0-100ms condition (type 6); yellow bars represent the TVd 100-200ms condition (type 8); and red bars represent the tactile- tactile condition (type 9).

The alpha-theta trends previously outlined are also represented in the time frequency plots displayed below, where a strong alpha-theta synchronization is seen within the time range of 150-200ms is seen for both the VTd 0-100ms and TVd 100-200ms conditions (see Figures 8a and 8b).

A)

B)

VTd 0-100ms/Type 6 (p1-p10)　　　　　　TVd 100-200ms/Type 8 (p1-p10)
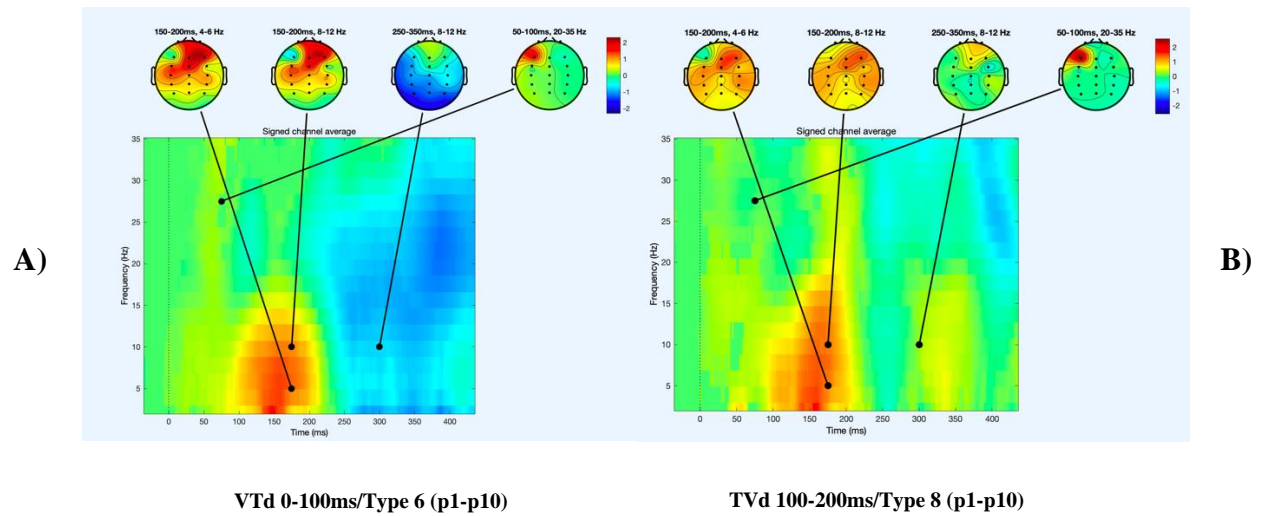
Figure 8: A topographic display of ERSPs for the VTd 0-100ms and TVd 100-200ms for all 10 participants in Faerman & Staines (2019) experiment

7.0 Discussion

Several past studies have provided strong evidence to suggest that oscillatory signals subserve essential functions in the human brain, and act to control the timing of neuronal firing. More specifically, oscillations assist spike-timing dependent plasticity and can temporally synchronize the transportation of information over various brain regions (Engel & Fries, 2010). That said, what remains unclear is whether these frequencies, such as theta and beta (being most relevant to the current work) support specific cognitive or sensorimotor functions (Engel & Fries, 2010). Essentially, the theta frequency has been mainly associated with working memory and fear conditioning, while the beta frequency has been traditionally linked to sensorimotor functions. Some studies have suggested, however, that it is difficult to assign a specific cognitive function *directly* to oscillatory activity within a particular frequency band, and that it may be unlikely that a single frequency band is *crucial* for subserving a specific cognitive function (Engel & Fries, 2010). That said, other studies have provided sufficient evidence to support oscillations at different frequencies being indicative of global state changes that occur within the brain (i.e., fast oscillations reflect increased arousal) (Engel & Fries, 2010).

Beta Band Activity and Attentional Processes

Recent work by Siegel, Warden & Miller (2009) examined how oscillations may interact across different frequencies, and specifically, how nesting of beta and theta oscillations could be a tool for sequential encoding of items processed in working memory and long-term memory recollection. In their study in awake monkeys, researchers found that slow oscillations occurring during sleep assists in memory consolidation processes via synchronizing thalamo-cortical

spindles and hippocampal sharp wave-ripples (Siegel, Warden & Miller, 2009). This, in turn, furthers the transfer of re-activated information between the neocortex as well as the hippocampus (Siegel, Warden, & Miller, 2009). Furthermore, despite beta-band oscillations being mostly linked to motor control, recent studies have shown that interactions in the beta band are prevalent when tasks require top-down processes. One such study in awake monkeys was able to demonstrate how endogenously driven choices during a search task resulted in higher beta band activity relative to stimulus instruction decisions (Pesaran, Nelson, & Andersen, 2008). Several other studies have also linked beta band activity to attentional top-down processing. For example, two studies by Buschman & Miller (2007; 2009) trained monkeys to identify a target in the presence of several distractors in either a pop-out or a serial search system. In their analysis of coherence between frontal and parietal signals, researchers found that interactions happened mainly in the beta band during search (or in other words, in the experimental condition, where strong endogenous top-down processing was required) (Buschman & Miller, 2007). The opposite was found for the gamma-band, which was more prominent in the pop-out condition, where performance was contingent on the saliency of the target stimulus (Buschman & Miller, 2007). This particular study demonstrates that endogenously driven top-down attention is linked to large-scale communication specific to low frequency bands, while for higher frequencies bands, coupling takes place when bottom-up signals must be relayed. This makes sense given other studies that have shown a link between beta-band activity and target stimulus processing when target saliency is purposely kept low (i.e., the attentional blink paradigm) (Kranczioch et al., 2007).

Notably, there are studies on attention whose findings do not support the beta band activity changes described above. One study by Fries et al. (2001) and Gregoriou et al. (2001)

reported increased gamma-band activity and coherence within neural assemblies responsible for

processing the stimulus being attended to, with the data suggesting that both beta band activity

and coherence was greater for the non-attended to stimulus. These apparent discrepancies could

potentially have to do with beta band activity being related to the contents of the top-down

signal, and not merely to their involvement in top-down processing. In other words, it is possible

that gamma band activity increases/becomes more prevalent when stimulus changes are

expected, while the opposite holds true for beta-band activity where the 'status quo' is weighted

more heavily than new distractive signals (Engel & Fries, 2010). This rationale is supported by

studies focusing on alterations of oscillatory activity in movement disorders like Parkinson's

disease (PD), where aberrant enhancement of beta-band activity occurs due to aberrant

persistence of the status quo, and consequently, a decline of adaptive cognitive and behavioural

control (Cassidy et al., 2002; Sharott et al., 2005).

Beta Band Activity and Sensorimotor Integration

There is some evidence that suggests a role for certain frequency bands in sensorimotor

integration. Work by Lalo, Gilbertson, & Doyle (2007) focused on determining whether cortical

beta activity is correlated with an up-regulation of sensory inputs pertinent to the organization of

the motor response elicited, as well as whether beta band activities in sensory cortices and the

primary motor cortex are autonomous or coherent. If found to be coherent, this would suggest

that beta-band activity could have a role in sensorimotor integration. Researchers reported an

increase of the $N20_b$ and $P30_b$ components of the centro-parietal SEP when evoked by median

nerve stimuli triggered off increases of beta-frequency activity in fronto-central EEG (Lalo,

Gilbertson, & Doyle, 2006). In other words, early processing of afferent information shifted during the period of transient beta-frequency synchrony, where the motor cortex was partly involved (Lalo, Gilbertson, & Doyle, 2006). Furthermore, heightened cortico-muscular coupling was found to coincide with elevations of beta activity occurring around the fronto-central region (Lalo, Gilbertson, & Doyle, 2006). That said, the extent to which beta-bursts impacted the processing of peripheral afferent information was unclear in this study; however, given that the N20 and P30 originate in the posterior bank of the central fissure, it is quite possible that the phasic increases in synchrony in the beta-frequency band observed had contributions from sensory as well as motor cortices (Lalo, Gilbertson, & Doyle, 2006). This assumption is supported by high-resolution EcoG recordings that the researchers did on two patients, where discriminating between primary sensory and motor cortices, specifically with respect to the presence and functional relevance of beta-synchrony, was challenging given that the activity in these areas were robustly coherent in the beta-frequency band. Essentially, oscillations in the motor cortex for the beta-frequency band are coupled to parallel oscillatory activity in the sensory cortex, which could directly impact the intrinsic processing of afferent inputs in S1 (Lalo, Gilbertson, & Doyle, 2006). Together, these findings demonstrate that the effects of beta-activity in the sensorimotor cortex can modulate sensory processing and are not merely motor. Furthermore, the coherence reported between beta-activities anterior and posterior to the central sulcus highly suggests that the prime role of sensorimotor beta-activities is sensorimotor integration (Lalo, Gilbertson, & Doyle, 2006).

It is well documented that multisensory facilitation is enhanced with stimulus relevance. A study by Barutchu et al. (2013) that compliments the study discussed above examined the interplay between multisensory processes and top-down/bottom-up influences by observing

neural responses which occurred in response to newly paired audiovisual stimuli diverged from their intended relevance. Researchers reported the greatest facilitation of motor actions for newly associated audiovisual stimuli when both elements of the audiovisual stimuli were targets. More specifically, relevant auditory stimuli heightened the amplitudes of event-related potentials (P1) at the occipital pole 100ms post-stimulus onset (Barutchu et al., 2013). This early amplitude modulation could be due to the attentional influences at play, with the relevance of auditory signals modifying the responsiveness and tuning of cells in V1 (Barutchu et al., 2013). Past studies have linked top-down influences and multisensory integration with attention, reporting modulation of neural activity in both visual and parietal sites that occurs in response to anticipating stimuli before onset (Corbetta et al., 2000; Kastner et al., 1999). Additionally, optimal multisensory facilitation was linked to a latency shift of induced oscillations in the beta frequency in right hemisphere parietal scalp sites (Barutchu et al., 2013). Lastly, neural activity corresponding to multisensory behavioural facilitation occurred 166ms post-stimulus at both occipital as well as left central sites, indicating that early and late neural processes both have a role in then facilitative effects of multisensory integration on motor responses (Barutchu et al., 2013).

Given what was discussed in the studies above, where beta band activity has been associated with sensorimotor integration and certain attentional processes, there is rationale to suggest a link between certain neural synchronizations (such as beta band synchronizations) and P50 changes reported in past work (i.e., Popovich & Staines, 2014). Essentially, the P50 ERP component is thought to reflect a preattentional inhibitory filter mechanism, which is important for sensory gating of irrelevant stimuli (Freedman et al., 1991; White & Yee, 2006). Furthermore, as discussed by Schubert et al. (2008), P50 modulation relies on the attentional

demands of a task such that a more difficult task would yield a greater facilitation of P50 amplitude. Therefore, the rationale for the current thesis work was that beta synchronizations observed around the 50ms time frame could be related to the P50 ERP component and what it is thought to represent. However, our findings did not support as no statistically significant effects were found for the beta band. This, perhaps, is not surprising given that the beta frequency is traditionally linked to motor control. Essentially, the motor task required from participants in both analyzed experiments (Popovich & Staines (2014) and Faerman & Staines (2019)) throughout all conditions was the *same*, as participants were required to make a graded motor response using a pressure sensitive bulb meant to represent the summation of visual and tactile stimuli. Therefore, if the beta band is more strongly associated with motor control, despite links to certain attentional processes, for example, it makes sense that no difference was observed in the current work as there was no variation in the required motor task.

Despite the lack of findings for the beta frequency, statistically significant effects were observed for the alpha and theta frequency bands at select electrode sites. The significance of these findings will be discussed in the paragraphs below.

Theta and Alpha Oscillatory Activity and Attention

To reiterate, upon analysis of the Popovich & Staines (2014) data, a strong effect of stimulus was reported for the theta frequency band (150-200ms) at electrode site FZ, with Tukey's post-hoc test revealing a significant difference between the SIM and TVd stimulus types. Theta synchronizations have often been interpreted as being a symbol of a top-down source of modulation (Szczepanski et al., 2014; Wiesman & Wilson, 2020). Therefore, it could be the crossmodal nature of the task employed in both analyzed experiments that is driving, at

least in part, the theta synchronizations observed in the current work. Essentially, in the SIM condition in the Popovich & Staines (2014) data (which is most demanding as the stimuli from two distinct modalities are connected in time and must be integrated), the theta synchronization was greatest. Furthermore, the way in which attention is shifted is dictated on the order of the stimuli that occur, thus in the VTd condition, the participant must attend to the visual stimulus then shift to the tactile stimulus when it comes on with a delay present. The ERSPs are time-locked to the tactile stimulus, meaning that there is a crossmodal interaction; however, in the TVd condition the participant must attend to the tactile stimulus then shift to the visual stimulus, but the ERSPs are time-locked to the tactile stimulus. This shift in attention is likely not captured in the time frame (150-200ms) where the ERSP was measured in the current work, and therefore, the observed theta synchronizations reported for the Popovich & Staines (2014) data could have more to do with a prefrontal engagement.

The theta frequency band has been linked to memory encoding and retrieval processes, novelty detection, working memory retention, as well as tasks requiring top-down control (Cavanagh et al., 2012; Jacobs et al., 2006; Rustishauser et al., 2010). Specifically, past EEG studies have proposed that theta oscillatory activity could be essential in the integration of information from both attentional as well as motivational pathways that come together in the medial prefrontal cortex. Mas-Herrero & Marco-Pallarés (2016) ran a study on seventeen healthy individuals who performed a reversal learning task in two separate sessions, both of which EEG as well as fMRI were recorded. Researchers reported increases of mid-frontal theta power activity, 200-400ms after feedback onset that were responsive to shifts of unsigned prediction error in addition to the valence of the outcome—two aspects of feedback evaluation that are thought to indicate attentional functions of the medial prefrontal cortex (Mas-Herrero & Marco-

Pallarés, 2016). Another very recent study by Wiesman & Wilson (2020) found that attention in the direction of somatosensation considerably modified the gating of all three population-level neural oscillatory (early theta, later alpha, and beta) responses to the paired-pulse stimuli in their experiment (Wiesman & Wilson, 2020). Furthermore, the observed gating effect varied according to the spectro-temporal profile of the response. More precisely, sensory gating of the early theta response was greater when attention was focused towards the somatosensory domain. Alternatively, gating of beta and alpha responses were lower in the same attentional state (Wiesman & Wilson, 2020). This finding provides support for the conceptualization of the early theta component as a representation of low-level stimulus recognition, as well as feature encoding as supported by several other past studies including those by Andersen & Lundqvist (2019), Hlushchuk & Hari (2006), and Wiesman et al. (2016).

The findings from the Wiesman & Wilson (2020) study discussed above also compliments the findings reported for the alpha 1 and theta frequency bands in the Faerman & Staines (2019) data. To reiterate, a main effect of stimulus was found for alpha 1 at CP4, with Tukey's post-hoc test revealing a significant difference between the VTd 200-300ms condition (type2) and TVd 100-200ms condition (type8). Furthermore, a strong trend towards significance was found for theta at CP3. Tukey's post-hoc test revealed a significant difference between VTd 200-300ms (type2) and TVd 100-200ms (type8). Lastly, a main effect of stimulus was also observed for alpha 2 at CP4, with Tukey's post-hoc test revealing a significant difference between VTd 100-200ms (type4) and TVd 100-200ms (type8). The greater synchronizations, mainly for the alpha frequency band, suggests that presentation of *relevant* visual information for upcoming movement modulates somatosensory processing. Alpha band oscillations in primary somatosensory cortices have been associated with both attentional as well as anticipatory

57

processes (Bardouille et al., 2010; Haegens et al., 2012; van Ede et al., 2014). To reiterate, Wiesman & Wilson (2020) reported prefrontal alpha band coherence with the primary somatosensory cortex, which was enhanced with attention that was directed towards the somatosensory domain, providing evidence in support of a frontal modulatory effect on the alpha response in primary somatosensory regions. Other studies have also linked frontal and parietal alpha oscillations with attentional modulation of cross-modal matching. For example, in a study by Misselhorn, Friese, & Engel (2019), participants were presented with the same trimodal stimuli in two separate attentional conditions (visual-tactile or audio-visual components), and participants were required to assess amplitude changes in cross-modal congruence while EEG was recorded. Researchers reported alpha band effects in bilateral frontal and right parietal cortex and suggested that frontal alpha oscillations are likely indicative of top-down control regulating perceptual gains and that alterations of parietal alpha oscillations are reflective of intersensory re-orienting (Misselhorn, Fries, & Engel, 2019).

8.0 Limitations

The main limitation of the current work has to do with linking changes in specific frequency bands over certain time periods (50-100ms and 150-200ms) to P50 changes reported in previous work (i.e., Popovich & Staines, 2014). Essentially, some studies have suggested that it is difficult to assign specific cognitive functions directly to oscillatory activity within a particular frequency band, and that it may be unlikely that a single frequency band is crucial for subserving a specific cognitive function (Engel & Fries, 2010). That said, as mentioned earlier, several other studies have provided sufficient evidence to support oscillations at different frequencies being indicative of global state changes that occur within the brain (i.e., nesting of slow and fast oscillations have been shown to facilitate crossmodal interactions for sensory channels processing information disparate time scales (Schroeder et al., 2008)). The second limitation concerns not being able to run another experiment with more participants and employing a slightly different setup (i.e., implementing conditions with later latencies of onset between visual and tactile stimuli, such as 250-350ms and 300-400ms, to better explore what the optimal timing for crossmodal interactions between these two modalities to occur is).

Nonetheless, the findings/trends discussed in the current work outline a framework for future research directions. Though mainly exploratory in nature, the synchronizations in the alpha and theta frequency bands reported in the current work, compliments findings reported in past studies who have reported crossmodal attentional effects occurring at early stages in modality-specific sensory ERP components (i.e., P50 & P100) (Dionne et al., 2013; Eimer & Driver, 2000; Taylor-Clarke et al., 2002). Furthermore, the current work offers an additional way

(using neural oscillatory activity/trends) in which to explore how the brain merges sensory

information from distinct modalities to accomplish goal-oriented behaviors.

9.0 Conclusion & Future Directions

Although no specific conclusion can be drawn, two main trends were observed in the current work that perhaps compliments past studies focusing on early crossmodal interactions and attention. The first was the strong effect of stimulus for theta (150-200ms) at FZ, and the significant Tukey's post-hoc test that revealed a difference between the SIM and TVd stimulus types in the Popovich & Staines (2014) data. The second was the main effect of stimulus for alpha 1 and alpha 2 at CP4, and a trend towards significance for theta at CP3 in the Faerman & Staines (2019) data. These patterns are relatively similar to what was observed in the Popovich & Staines (2014) study, where P50 amplitude was significantly greater in the VTd compared to the TVd condition at electrode site P4 (F (1,14= 4.87, p = 0.033)), with a strong trend towards significance for the same effect at CP4 (F (1,14) =3.37, p = 0.07)). These patterns are also similar to what was reported in the Faerman & Staines (2019) study, where P50 amplitude was greatest in the VTd 200-300ms condition relative to the remaining conditions (TT, TVd 100-200ms, VTd 0-100ms, VTd 100-200ms). Essentially, it may be possible that the crossmodal nature of the task used in both experiments is driving, at least in part, the theta and alpha synchronizations discussed, perhaps in a similar manner to the modulations of specific ERP components (such as the P50 and P100) reported in past studies. That said, future research should continue to explore when the optimal timing for early crossmodal interactions (i.e., visual and tactile) to occur is using specific ERP components, as neural markers since this continues to remain unclear. Although Popovich & Staines (2014) did find that P50 was modulated based on both the timing and relevance of crossmodal interactions, researchers utilized a fixed latency period of 100ms between the onset of a visual and tactile stimulus. The minimum amount required for crossmodal interactions to occur is at least 100ms, given that it takes approximately

the same amount of time for a visual signal to reach the visual cortex. It would, therefore, be interesting to explore latencies later than this, and observe how early somatosensory ERPs like P50 are modulated. Findings could be used to further the current understanding of cortical processing and adaptation and, therefore, advance sensorimotor learning strategies and rehabilitation techniques (i.e., stroke patients; individuals with a traumatic brain injury).

Furthermore, future research should continue to explore the extent/unique contributions that the attention system has on early sensory-sensory interactions (i.e., visual and tactile). Perhaps running a study using the same experimental paradigm as what was outlined in the 'Methods' section of the current work for the Popovich & Staines (2014) and Faerman & Staines (2019) experiments, but manipulating the instructions participants received (i.e., six blocks where they were instructed to attend and respond to crossmodal visual-tactile stimuli, followed by another six blocks where they were instructed to attend and respond only to visual stimuli), would provide a better means to explore attentional contributions in crossmodal facilitation.

10.0 References

Adams, M., Andrew, D., & Staines, W.R. (2019). The contribution of the prefrontal cortex to

    relevancy-based gating of visual and tactile stimuli. *Experimental Brain Research,*

    237(10), 2747-2759. doi: 10.1007/*s*00221-019-05633-9

Akatsuka, K., Wasaka, T., Nakata, H., Inui, K., Hoshiyama, M., & Kakigi, R. (2005). Mismatch

    responses related to temporal discrimination of somatosensory stimulation. *Clinical*

    Neurophysiology: Official journal of the International Federation of Clinical

    Neurophysiology, *116*(8), 1930–1937. https://doi.org/10.1016/j.clinph.2005.04.021

Alais, D., & Burr, D. (2004). The ventriloquist effect results from near-optimal bimodal

    integration. *Current biology: CB*, *14*(3), 257–262.

    https://doi.org/10.1016/j.cub.2004.01.029

Alitto, H. J., & Usrey, W. M. (2003). Corticothalamic feedback and sensory processing. *Current*

    opinion in neurobiology, *13*(4), 440–445.

    https://doi-org.proxy.lib.uwaterloo.ca/10.1016/s0959-4388(03)00096-5

Andrew, D., Ibey, R., & Staines, R. (2020). Transient inhibition of the cerebellum impairs

    change-detection processes: Cerebellar contributions to sensorimotor integration.

    Behavioural Brain Research,378. https://doi.org/10.1016/j.bbr.2019.112273

Andersen, L., & Lundqvist, D. (2019). Somatosensory responses to nothing: An MEG study of

    expectations during omission of tactile stimulations. *Neuroimage, 184*(1), 78-89.

    https://doi.org/10.1016/j.neuroimage.2018.09.014

Astikainen, P., Ruusuvirta, T., Wikgren, J., & Korhonen, T. (2004). The human brain processes

    visual changes that are not cued by attended auditory stimulation. *Neuroscience letters*,

    368(2), 231–234. https://doi.org/10.1016/j.neulet.2004.07.025

Ayzenshtat, I., Jackson, J., & Yuste, R. (2016). Orientation Tuning Depends on Spatial

    Frequency in Mouse Visual Cortex. *eNeuro*, *3*(5), ENEURO.0217-16.2016.

    https://doi.org/10.1523/ENEURO.0217-16.2016

Badde, S., Navarro, K., & Landy, M. (2020). Modality-specific attention attenuates visual-tactile

    integration and recalibration effects by reducing prior expectations of a common source

    for vision and touch. *Cognition, 197,* 104170. doi: 10.1016/j.cognition.2019.104170

Baldeweg T. (2006). Repetition effects to sounds: evidence for predictive coding in the auditory

    system. *Trends in cognitive sciences*, *10*(3), 93–94.

    https://doi.org/10.1016/j.tics.2006.01.010

Barutchu, A., Freestone, D. R., Innes-Brown, H., Crewther, D. P., & Crewther, S. G. (2013).

    Evidence for enhanced multisensory facilitation with stimulus relevance: an

    electrophysiological investigation. *PloS one*, *8*(1), e52978.

    https://doi.org/10.1371/journal.pone.0052978

Bardouille, T., Picton, T. W., & Ross, B. (2010). Attention modulates beta oscillations during

    prolonged tactile stimulation. *The European Journal of Neuroscience*, *31*(4), 761–769.

    https://doi.org/10.1111/j.1460-9568.2010.07094.x

Bastiaansen, M., Mazaheri, A., & Jensen, O. (2012). Beyond ERPs: Oscillatory neuronal

    dynamics. In S. J. Luck & E. S. Kappenman (Eds.), *The Oxford Handbook of Event-

    related Potential Components* (pp. 31–49). Oxford University Press.

Beres, A. (2017). Time is of the essence: a review of electroencephalography (EEG) and event-

    related brain potentials (ERPs) in language research. *Applied Psychophysiology and

    Biofeedback, 42*(4), 247-255. doi: 10.1007/s10484-017-9371-3

Berger, D., & Bülthoff, H. (2009). The role of attention on the integration of visual and inertial

    cues. *Experimental Brain Research, 198*(2-3), 287-300.

    https://dx.doi.org/10.1016%2Fj.cognition.2019.104170

Bickford M. E. (2016). Thalamic Circuit Diversity: Modulation of the Driver/Modulator Framework. *Frontiers in neural circuits*, *9*, 86. https://doi.org/10.3389/fncir.2015.00086

Bledowski, C., Prvulovic, D., Hoechstetter, K., Scherg, M., Wibral, M., Goebel, R., & Linden,D. (2004). Localizing P300 generators in visual target and distractor processing: a combined event-related potential and functional magnetic resonance imaging study. *The Journal of Neuroscience, 24*(42), 9353-9360. doi:10.1523/JNEUROSCI.1897-04.2004

Bolton, D. A., & Staines, W. R. (2011). Transient inhibition of the dorsolateral prefrontal cortex disrupts attention-based modulation of tactile stimuli at early stages of somatosensory processing. *Neuropsychologia*, *49*(7), 1928–1937. https://doi.org/10.1016/j.neuropsychologia.2011.03.020

Bonnefond & Jensen. (2012). Alpha oscillations serve to protect working memory maintenance against anticipated distracters. *Current Biology, 22*(20), 1969-1974. https://doi.org/10.1016/j.cub.2012.08.029

Brang, D., Towle, V. L., Suzuki, S., Hillyard, S. A., Di Tusa, S., Dai, Z., Tao, J., Wu, S., & Grabowecky, M. (2015). Peripheral sounds rapidly activate visual cortex: evidence from electrocorticography. *Journal of Neurophysiology*, *114*(5), 3023–3028. https://doi.org/10.1152/jn.00728.2015

Buschman, T. J., & Miller, E. K. (2009). Serial, covert shifts of attention during visual search are

    reflected by the frontal eye fields and correlated with population

    oscillations. *Neuron*, *63*(3), 386–396. https://doi.org/10.1016/j.neuron.2009.06.020

Buschman, T. J., & Miller, E. K. (2007). Top-down versus bottom-up control of attention in the

    prefrontal and posterior parietal cortices. *Science (New York, N.Y.)*, *315*(5820), 1860–

    1862. https://doi.org/10.1126/science.1138071

Calvert, G. A. (2001). Crossmodal processing in the human brain: insights from functional

    neuroimaging studies. *Cerebral Cortex (New York, N.Y.: 1991)*, *11*(12), 1110–1123.

    https://doi.org/10.1093/cercor/11.12.1110

Cassidy, M., Mazzone, P., Oliviero, A., Insola, A., Tonali, P., Di Lazzaro, V., & Brown, P.

    (2002). Movement-related changes in synchronization in the human basal

    ganglia. *Brain: a Journal of Neurology*, *125*(Pt 6), 1235–1246.

    https://doi.org/10.1093/brain/awf135

Cavanagh, J. F., & Frank, M. J. (2014). Frontal theta as a mechanism for cognitive

    control. *Trends in Cognitive Sciences*, *18*(8), 414–421.

    https://doi.org/10.1016/j.tics.2014.04.012

Chung, S., Hoy, K., & Fitzgerald, P. (2014). Theta-burst stimulation: a new form of TMS

    treatment for depression? *Depression & Anxiety, 32*(3), 182-192.

https://doi-org.proxy.lib.uwaterloo.ca/10.1002/da.22335

Clementz, B. A., Geyer, M. A., & Braff, D. L. (1998). Poor P50 suppression among

schizophrenia patients and their first-degree biological relatives. *The American Journal*

of Psychiatry, *155*(12), 1691–1694. https://doi.org/10.1176/ajp.155.12.1691

Corbetta, M., & Shulman, G. (2002). Control of goal-directed and stimulus-driven attention in

the brain. *Nature Reviews Neuroscience, 3.* 201-215.

https://doi-org.proxy.lib.uwaterloo.ca/10.1038/nrn755

Corbetta, S., Mantovani, G., Lania, A., Borgato, S., Vicentini, L., Beretta, E., Faglia, G., Di

Blasio, A. M., & Spada, A. (2000). Calcium-sensing receptor expression and signalling

in human parathyroid adenomas and primary hyperplasia. *Clinical Endocrinology*, *52*(3),

339–348. https://doi.org/10.1046/j.1365-2265.2000.00933.x

Corbetta, M., Akbudak, E., Conturo, T. E., Snyder, A. Z., Ollinger, J. M., Drury, H. A.,

Linenweber, M. R., Petersen, S. E., Raichle, M. E., Van Essen, D. C., & Shulman, G. L.

(1998). A common network of functional areas for attention and eye

movements. *Neuron*, *21*(4), 761–773. https://doi.org/10.1016/s0896-6273(00)80593-0

Crabtree, J., Collingridge, G., & Isaac, J. (1998). A new intrathalamic pathway linking modality-related nuclei in the dorsal thalamus. *Nature Neuroscience, 1*(5), 389-394. doi:10.1038/1603

Crabtree, J., & Isaac, J. (2002). New intrathalamic pathways allowing modality-related and cross-modality switching in the dorsal thalamus. *The Journal of Neuroscience, 22*(19), 8754-8761. doi: 10.1523/JNEUROSCI.22-19-08754.2002

Croft, R. J., Lee, A., Bertolot, J., & Gruzelier, J. H. (2001). Associations of P50 suppression and desensitization with perceptual and cognitive features of "unreality" in schizotypy. *Biological Psychiatry*, *50*(6), 441–446. https://doi.org/10.1016/s0006-3223(01)01082-4

de la Mothe, L., Blumell, S., Kajikawa, Y., & Hackett, T. (2006). Thalamic connections of auditory cortex in marmoset monkeys: core and medial belt regions. *The Journal of Comparative Neurology, 496*(1), 72-96. https://doi.org/10.1002/cne.20924

Desmedt, J. E., Huy, N. T., & Bourguet, M. (1983). The cognitive P40, N60 and P100 components of somatosensory evoked potentials and the earliest electrical signs of sensory processing in man. *Electroencephalography and Clinical Neurophysiology*, *56*(4), 272–282. https://doi.org/10.1016/0013-4694(83)90252-3

Desmedt, J. E., & Robertson, D. (1977). Differential enhancement of early and late components

of the cerebral somatosensory evoked potentials during forced-paced cognitive tasks in

man. *The Journal of Physiology*, *271*(3), 761–782.

https://doi.org/10.1113 jphysiol.1977.sp012025

Desmedt, J. E., & Tomberg, C. (1989). Mapping early somatosensory evoked potentials in

selective attention: critical evaluation of control conditions used for titrating by

difference the cognitive P30, P40, P100 and N140. *Electroencephalography and Clinical

Neurophysiology*, *74*(5), 321–346. https://doi.org/10.1016/0168-5597(89)90001-4

Dionne, J. K., Legon, W., & Staines, W. R. (2013). Crossmodal influences on early

somatosensory processing: interaction of vision, touch, and task-relevance. *Experimental

Brain Research*, *226*(4), 503–512. https://doi.org/10.1007/s00221-013-3462-z

Dionne, J., Meehan, S., Legon, W., & Staines, R. (2010). Crossmodal influences in

somatosensory cortex: interaction of vision and touch. *Human Brain Mapping, 31*(1)*,

14-25. https://doi.org/10.1002/hbm.20841

Eimer, M., & Driver, J. (2000). An event-related brain potential study of cross-modal links in

spatial attention between vision and touch. *Psychophysiology*, *37*(5), 697–705.

Eimer, M. (2001). Crossmodal links in spatial attention between vision, audition, and touch:

evidence from event-related brain potentials. *Neuropsychologia*, *39*(12), 1292–1303.

https://doi.org/10.1016/s0028-3932(01)00118-x

Eimer, M., & Forster, B. (2003). Modulations of early somatosensory ERP components by

transient and sustained spatial attention. *Experimental Brain Research*, *151*(1), 24–31.

https://doi.org/10.1007/s00221-003-1437-1

Engel, A. K., & Fries, P. (2010). Beta-band oscillations--signalling the status quo?. *Current*

Opinion in Neurobiology, *20*(2), 156–165. https://doi.org/10.1016/j.conb.2010.02.015

Faerman, M., & Staines, R. (2019). Evidence for Temporal Interactions at Early Stages of

Cortical Processing. *Biology 499 Seniors Honours Project*

Freedman, R., Waldo, M., Bickford-Wimer, P., & Nagamoto, H. (1991). Elementary neuronal

dysfunctions in schizophrenia. *Schizophrenia Research*, *4*(2), 233–243.

https://doi.org/10.1016/0920-9964(91)90035-p

Frens, M., & Van Opstal, A. (1995). A quantitative study of auditory-evoked saccadic eye

movements in two dimensions. *Experimental Brain Research, 107*(1), 103-117.

doi: 10.1007/bf00228022

Fries, P., Reynolds, J. H., Rorie, A. E., & Desimone, R. (2001). Modulation of oscillatory

    neuronal synchronization by selective visual attention. *Science (New York,*

    N.Y.), *291*(5508), 1560–1563. https://doi.org/10.1126/science.1055465

Friston K. (2003). Learning and inference in the brain. *Neural networks: The Official Journal of*

    the International Neural Network Society, *16*(9), 1325–1352.

    https://doi.org/10.1016/j.neunet.2003.06.005

Friston K. (2005). A theory of cortical responses. *Philosophical Transactions of the Royal*

    Society of London. Series B, Biological Sciences, *360*(1456), 815–836.

    https://doi.org/10.1098/rstb.2005.1622

Garrido, M., Kilner, J., Stephan, K., & Friston, K. (2009). The mismatch negativity: A review of

    underlying mechanisms. *Clinical Neurophysiology, 120*(3), 453-463.

    doi: 10.1016/j.clinph.2008.11.029

Ghisolfi, E. S., Heldt, E., Zanardo, A. P., Strimitzer, I. M., Jr, Prokopiuk, A. S., Becker, J.,

    Cordioli, A. V., Manfro, G. G., & Lara, D. R. (2006). P50 sensory gating in panic

    disorder. *Journal of Psychiatric Research*, *40*(6), 535–540.

    https://doi.org/10.1016/j.jpsychires.2006.02.006

Grosbras, M. H., & Paus, T. (2002). Transcranial magnetic stimulation of the human frontal eye
field: effects on visual perception and attention. *Journal of Cognitive
Neuroscience*, *14*(7), 1109–1120. https://doi.org/10.1162/089892902320474553

Goff, G. D., Matsumiya, Y., Allison, T., & Goff, W. R. (1977). The scalp topography of human
somatosensory and auditory evoked potentials. *Electroencephalography and Clinical
Neurophysiology*, *42*(1), 57–76. https://doi.org/10.1016/0013-4694(77)90151-1

Guterman, Y., Josiassen, R. C., & Bashore, T. R., Jr (1992). Attentional influence on the P50
component of the auditory event-related brain potential. *International Journal of
Psychophysiology: Official Journal of the International Organization of
Psychophysiology*, *12*(2), 197–209. https://doi.org/10.1016/0167-8760(92)90011-y

Guterman, Y., & Josiassen, R. C. (1994). Sensory gating deviance in schizophrenia in the
context of task related effects. *International Journal of Psychophysiology: Official
Journal of the International Organization of Psychophysiology*, *18*(1), 1–12.
https://doi.org/10.1016/0167-8760(84)90010-2

Hämäläinen, H., Kekoni, J., Sams, M., Reinikainen, K., & Näätänen, R. (1990). Human
somatosensory evoked potentials to mechanical pulses and vibration: contributions of SI
and SII somatosensory cortices to P50 and P100 components. *Electroencephalography
and Clinical Neurophysiology*, *75*(2), 13–21. https://doi.org/10.1016/0013-
4694(90)90148-d

Haegens, S., Händel, B. F., & Jensen, O. (2011). Top-down controlled alpha band activity in

    somatosensory areas determines behavioral performance in a discrimination task. *The*

    Journal of Neuroscience: the official journal of the Society for Neuroscience, *31*(14),

    5197–5204.

Hari, R., Reinikainen, K., Kaukoranta, E., Hämäläinen, M., Ilmoniemi, R., Penttinen, A.,

    Salminen, J., & Teszner, D. (1984). Somatosensory evoked cerebral magnetic fields from

    SI and SII in man. *Electroencephalography and Clinical Neurophysiology*, *57*(3), 254–

    263. https://doi.org/10.1016/0013-4694(84)90126-3

Hershenson, M. (1962). Reaction time as a measure of intersensory facilitation. *Journal of*

    Experimental Psychology, 63(3), 289-293. https://doi.org/10.1037/h0039516

Hlushchuk, Y., & Hari, R. (2006). Transient suppression of ipsilateral primary somatosensory

    cortex during tactile finger stimulation. *The Journal of Neuroscience: The Official*

    Journal of the Society for Neuroscience, *26*(21), 5819–5824.

    https://doi.org/10.1523/JNEUROSCI.5536-05.2006

Jacobs, J., Hwang, G., Curran, T., & Kahana, M. J. (2006). EEG oscillations and recognition

    memory: theta correlates of memory retrieval and decision making. *NeuroImage*, *32*(2),

    978–987. https://doi.org/10.1016/j.neuroimage.2006.02.018

Janssens, C., De Loof, E., Boehler, N., Pourtois, G., & Verguts, T. (2018). Occipital alpha power

    reveals fast attentional inhibition of incongruent distractors. *Psychophysiology, 55(*3).

    https://doi.org/10.1111/psyp.13011

Jäncke, L., Mirzazade, S., & Shah, N. J. (1999). Attention modulates activity in the primary and

    the secondary auditory cortex: a functional magnetic resonance imaging study in human

    subjects. *Neuroscience Letters*, *266*(2), 125–128.

    https://doi.org/10.1016/s0304-3940(99)00288-8

Jessen, F., Kucharski, C., Fries, T., Papassotiropoulos, A., Hoenig, K., Maier, W., & Heun, R.

    (2001). Sensory gating deficit expressed by a disturbed suppression of the P50 event-

    related potential in patients with Alzheimer's disease. *The American Journal of*

    Psychiatry, *158*(8), 1319–1321. doi: 10.1176/appi.ajp.158.8.1319

Johansen-Berg, H., Christensen, V., Woolrich, M., & Matthews, P. M. (2000). Attention to touch

    modulates activity in both primary and secondary somatosensory areas. *Neuroreport*,

    11(6), 1237–1241. https://doi.org/10.1097/00001756-200004270-00019

Josiassen, R. C., Shagass, C., Roemer, R. A., Slepner, S., & Czartorysky, B. (1990). Early

    cognitive components of somatosensory event-related potentials. *International Journal*

    of Psychophysiology : Official Journal of the International Organization of

    Psychophysiology, *9*(2), 139–149. https://doi.org/10.1016/0167-8760(90)90068-o

Kastner, S., Pinsk, M. A., De Weerd, P., Desimone, R., & Ungerleider, L. G. (1999). Increased

   activity in human visual cortex during directed attention in the absence of visual

   stimulation. *Neuron*, *22*(4), 751–761. https://doi.org/10.1016/s0896-6273(00)80734-5

Kayser, C., & Logothetis, N. (2007). Do early sensory cortices integrate cross-modal

   information. *Brain Structure & Function, 212*(12), 121-132.

   doi: 10.1007/s00429-007-0154-0

Kayser, C., Petkov, C., Augath, M., & Logothetis, N. (2007). Functional imaging reveals visual

   modulation of specific fields in auditory cortex. *The Journal of Neuroscience, 27*(8),

   1824-1835. doi: 10.1523/JNEUROSCI.4737-06.2007

Klimesch, W., Sauseng, P., Hanslmayr, S. (2007). EEG alpha oscillations: The inhibition-timing

   hypothesis. *Brain Research Reviews, 53*(1), 63-88.

   https://doi.org/10.1016/j.brainresrev.2006.06.003

Knight, R.T. (1994). Attention Regulation and Human Prefrontal Cortex. In Thierry A.M.,

   Glowinski J., Goldman-Rakic P.S., Christen Y. (Eds.), *Motor and Cognitive Functions of

   the Prefrontal Cortex. Research and Perspectives in Neurosciences* (pp. 160-173).

   Springer, Berlin, Heidelberg

Knight, R. T. (1984). Decreased response to novel stimuli after prefrontal lesions in

    man. *Electroencephalography and Clinical Neurophysiology*, *59*(1), 9–20.

    https://doi.org/10.1016/0168-5597(84)90016-9

Knight, R. T., Hillyard, S. A., Woods, D. L., & Neville, H. J. (1981). The effects of frontal

    cortex lesions on event-related potentials during auditory selective attention.

    Electroencephalography and Clinical Neurophysiology, *52*(6), 571–582.

    https://doi.org/10.1016/0013-4694(81)91431-0

Knight, R. T., Scabini, D., & Woods, D. L. (1989). Prefrontal cortex gating of auditory

    transmission in humans. *Brain Research*, *504*(2), 338–342.

    https://doi.org/10.1016/0006-8993(89)91381-4

Knight, R. T., Staines, W. R., Swick, D., & Chao, L. L. (1999). Prefrontal cortex regulates

    inhibition and excitation in distributed neural networks. *Acta Psychologica*, *101*(2-3),

    159–178. https://doi.org/10.1016/s0001-6918(99)00004-9

Kranczioch, C., Debener, S., Maye, A., & Engel, A. K. (2007). Temporal dynamics of access to

    consciousness in the attentional blink. *NeuroImage*, *37*(3), 947–955.

    https://doi.org/10.1016/j.neuroimage.2007.05.044

Kumar, S., Rao, S. L., Nair, R. G., Pillai, S., Chandramouli, B. A., & Subbakrishna, D. K.

    (2005). Sensory gating impairment in development of post-concussive symptoms in mild

    head injury. *Psychiatry and Clinical Neurosciences*, *59*(4), 466–472.

    https://doi.org/10.1111/j.1440-1819.2005.01400.x

Light, G., & Braff, D. (2003). Sensory gating deficits in schizophrenia: can we parse the effects

    of medication, nicotine use, and changes in clinical status? *Clinical Neuroscience.*

    Research, 3(1-2), 47-54. https://doi.org/10.1016/S1566-2772(03)00018-5

Lalo, E., Gilbertson, T., Doyle, L., Di Lazzaro, V., Cioni, B., & Brown, P. (2007). Phasic

    increases in cortical beta activity are associated with alterations in sensory processing in

    the human. *Experimental brain research*, *177*(1), 137–145.

    https://doi.org/10.1007/s00221-006-0655-8

Lundy-Ekman, L. (2018). *Neuroscience: Fundamentals for Rehabilitation Fifth Edition.* Elsevier

    Incorporation

Luck, S. (2005). *An Introduction to the Event-Related Potential Technique, First Edition.*

    A Bradford Book

Macaluso, E. (2006). Multisensory processing in sensory-specific cortical areas. *The Neuroscientist: A Review Journal bringing Neurobiology, Neurology and Psychiatry*, *12*(4), 327–338. https://doi.org/10.1177/1073858406287908

Macaluso, E., Frith, C. D., & Driver, J. (2000). Modulation of human visual cortex by crossmodal spatial attention. *Science (New York, N.Y.)*, *289*(5482), 1206–1208. https://doi.org/10.1126/science.289.5482.1206

Macaluso, E., Frith, C. D., & Driver, J. (2002). Crossmodal spatial influences of touch on extrastriate visual areas take current gaze direction into account. *Neuron*, *34*(4), 647–658. https://doi.org/10.1016/s0896-6273(02)00678-5

Makeig S. (1993). Auditory event-related dynamics of the EEG spectrum and effects of exposure to tones. *Electroencephalography and Clinical Neurophysiology*, *86*(4), 283–293. https://doi.org/10.1016/0013-4694(93)90110-h

Mazaheri, A., van Schouwenburg, M. R., Dimitrijevic, A., Denys, D., Cools, R., & Jensen, O. (2014). Region-specific modulations in oscillatory alpha activity serve to facilitate processing in the visual and auditory modalities. *NeuroImage*, *87*, 356–362. https://doi.org/10.1016/j.neuroimage.2013.10.052

McCallum, W., & Walter, G. (1968). The effects of attention and distraction on the contingent negative variation in normal and neurotic subjects. *Electroencephalography and Clinical Neurophysiology, 25*(4), 319-329. https://doi.org/10.1016/0013-4694(68)90172-7

McClure, J. P., Jr, & Polack, P. O. (2019). Pure tones modulate the representation of orientation and direction in the primary visual cortex. *Journal of Neurophysiology*, *121*(6), 2202–2214. https://doi.org/10.1152/jn.00069.2019

McGurk, H., & MacDonald, J. (1976). Hearing lips and seeing voices. *Nature*, *264*(5588), 746–748. https://doi.org/10.1038/264746a0

McIlroy, W. E., Bishop, D. C., Staines, W. R., Nelson, A. J., Maki, B. E., & Brooke, J. D. (2003). Modulation of afferent inflow during the control of balancing tasks using the lower limbs. *Brain Research*, *961*(1), 73–80. https://doi.org/10.1016/s0006-8993(02)03845-3

Meehan, S., Legon, W., & Staines, R. (2009). Spatiotemporal properties modulate intermodal influences on early somatosensory processing during sensory-guided movement. *Clinical Neurophysiology, 120*(7), 1371-1380. https://doi.org/10.1016/j.clinph.2009.05.005

Meehan, S., & Staines, R. (2007). The effect of task-relevance on primary somatosensory cortex during continuous sensory-guided movement in the presence of bimodal competition. *Brain Research, 1138*, 148-158. https://doi-org.proxy.lib.uwaterloo.ca/10.1016/j.brainres.2006.12.067

Mima, T., Nagamine, T., Nakamura, K., & Shibasaki, H. (1998). Attention modulates both primary and second somatosensory cortical activities in humans: a magnetoencephalographic study. *Journal of Neurophysiology*, *80*(4), 2215–2221. https://doi.org/10.1152/jn.1998.80.4.2215

Misselhorn, J., Friese, U., & Engel, A. K. (2019). Frontal and parietal alpha oscillations reflect attentional modulation of cross-modal matching. *Scientific Reports*, *9*(1), 5030. https://doi.org/10.1038/s41598-019-41636-w

Misselhorn, J., Daume, J., Engel, A. K., & Friese, U. (2016). A matter of attention: Crossmodal congruence enhances and impairs performance in a novel trimodal matching paradigm. *Neuropsychologia*, *88*, 113–122. https://doi.org/10.1016/j.neuropsychologia.2015.07.022

Moore, T., & Armstrong, K. M. (2003). Selective gating of visual signals by microstimulation of frontal cortex. *Nature*, *421*(6921), 370–373. https://doi.org/10.1038/nature01341

Mozolic, J. L., Hugenschmidt, C. E., Peiffer, A. M., & Laurienti, P. J. (2008). Modality-specific

    selective attention attenuates multisensory integration. *Experimental Brain*

    Research, *184*(1), 39–52. https://doi.org/10.1007/s00221-007-1080-3

Mumford D. (1992). On the computational architecture of the neocortex. II. The role of cortico-

    cortical loops. *Biological Cybernetics*, *66*(3), 241–251.

    https://doi.org/10.1007/BF00198477

Murray, M., Molholm, S., Michel, C., Heslenfeld, D., Ritter, W., Javitt, D., Schroeder, C., &

    Foxe, J. (2005). Grabbing your ear: rapid auditory-somatosensory multisensory

    interactions in low-level sensory cortices are not constrained by stimulus alignment.

    Cerebral Cortex, 15(7), 963-974. doi:10.1093/cercor/bhh197

Näätänen, R., & Alho, K. (1995). Mismatch negativity--a unique measure of sensory processing

    in audition. *The International Journal of Neuroscience*, *80*(1-4), 317–337.

    https://doi.org/ 10.3109/00207459508986107

Näätänen, R., Gaillard, A. W., & Mäntysalo, S. (1978). Early selective-attention effect on

    evoked potential reinterpreted. *Acta Psychologica*, *42*(4), 313–329.

    https://doi.org/10.1016/0001-6918(78)90006-9

Näätänen, R., Tervaniemi, M., Sussman, E., Paavilainen, P., & Winkler, I. (2001). "Primitive

intelligence" in the auditory cortex. *Trends in Neurosciences*, *24*(5), 283–288.

https://doi.org/10.1016/s0166-2236(00)01790-2

Nunez, P., & Srinivasan, R. (2006). *Electric Fields of the Brain: The Neurophysics of EEG,*

Second Edition. Oxford University Press

Olincy, A., Ross, R. G., Harris, J. G., Young, D. A., McAndrews, M. A., Cawthra, E., McRae, K.

A., Sullivan, B., Adler, L. E., & Freedman, R. (2000). The P50 auditory event-evoked

potential in adult attention-deficit disorder: comparison with schizophrenia. *Biological*

Psychiatry, *47*(11), 969–977. https://doi.org/10.1016/s0006-3223(00)00239-0

Pandya, D., Rosene, D., & Doolittle, A. (1994). Corticothalamic connections of auditory-related

areas of the temporal lobe in the rhesus monkey. *The Journal of Comparative Neurology,*

345(3), 447-471. doi:10.1002/cne.903450311

Patterson, J. V., Hetrick, W. P., Boutros, N. N., Jin, Y., Sandman, C., Stern, H., Potkin, S., &

Bunney, W. E., Jr (2008). P50 sensory gating ratios in schizophrenics and controls: a

review and data analysis. *Psychiatry Research*, *158*(2), 226–247.

https://doi.org/10.1016/j.psychres.2007.02.009

Patrick, C. J., Bernat, E. M., Malone, S. M., Iacono, W. G., Krueger, R. F., & McGue, M.

    (2006). P300 amplitude as an indicator of externalizing in adolescent males.

    Psychophysiology, *43*(1), 84–92. https://doi.org/10.1111/j.1469-8986.2006.00376.x

Pazo-Alvarez, P., Cadaveira, F., & Amenedo, E. (2003). MMN in the visual modality: a review.

    Biological Psychology, *63*(3), 199–236. https://doi.org/10.1016/s0301-0511(03)00049-8

Pesaran, B., Nelson, M. J., & Andersen, R. A. (2008). Free choice activates a decision circuit

    between frontal and parietal cortex. *Nature*, *453*(7193), 406–409.

    https://doi.org/10.1038/nature06849

Peterson, N. N., Schroeder, C. E., & Arezzo, J. C. (1995). Neural generators of early cortical

    somatosensory evoked potentials in the awake monkey. *Electroencephalography and*

    Clinical Neurophysiology, *96*(3), 248–260. https://doi.org/10.1016/0168-5597(95)00006-e

Picton T. W. (1992). The P300 wave of the human event-related potential. *Journal of Clinical*

    Neurophysiology: Official Publication of the American Electroencephalographic Society,

    9(4), 456–479. https://doi.org/10.1097/00004691-199210000-00002

Popovich, C., & Staines, W.R. (2014). The attentional-relevance and temporal dynamics of

    visual-tactile crossmodal interactions differentially influence early stages of

    somatosensory processing. *Brain and Behavior, 4*(2), 247-260.

    https://doi.org/10.1002/brb3.210

Ruff, C. C., Blankenburg, F., Bjoertomt, O., Bestmann, S., Freeman, E., Haynes, J. D., Rees, G.,

    Josephs, O., Deichmann, R., & Driver, J. (2006). Concurrent TMS-fMRI and

    psychophysics reveals frontal influences on human retinotopic visual cortex. *Current*

    biology: CB, *16*(15), 1479–1488. https://doi.org/10.1016/j.cub.2006.06.057

Rutishauser, U., Ross, I. B., Mamelak, A. N., & Schuman, E. M. (2010). Human memory

    strength is predicted by theta-frequency phase-locking of single

    neurons. *Nature*, *464*(7290), 903–907. https://doi.org/10.1038/nature08860

Saalmann, Y., Pinsk, M., Wang, L., Li, X., & Kastner, S. (2012). The pulvinar regulations

    information transmission between cortical areas based on attention demands. *Science,*

    337(6095), 753-756. https://doi.org/10.1126/science.1223082

Sams, M., Paavilainen, P., Alho, K., & Näätänen, R. (1985). Auditory frequency discrimination

    and event-related potentials. *Electroencephalography and Clinical Neurophysiology*,

    62(6), 437–448. https://doi.org/10.1016/0168-5597(85)90054-1

Sanna, A., Fattore, L., Badas, P., Corona, G., Cocco, V., & Diana, M. (2019). Intermittent theta

burst stimulation of the prefrontal cortex in cocaine use disorder: a pilot study.

Frontiers in Neuroscience, *13*, 765. https://doi.org/10.3389/fnins.2019.00765

Schubert, R., Ritter, P., Wüstenberg, T., Preuschhof, C., Curio, G., Sommer, W., & Villringer, A.

(2008). Spatial attention related SEP amplitude modulations covary with BOLD signal in

S1--a simultaneous EEG--fMRI study. *Cerebral Cortex (New York, N.Y.: 1991)*, *18*(11),

2686–2700.

Schubert, R., Blankenburg, F., Lemm, S., Villringer, A., & Curio, G. (2006). Now you feel it—

now you don't: ERP correlates of somatosensory awareness. *Psychophysiology*, *43*(1),

31–40. https://doi.org/10.1111/j.1469-8986.2006.00379.x

Schroeder, C. E., Lakatos, P., Kajikawa, Y., Partan, S., & Puce, A. (2008). Neuronal oscillations

and visual amplification of speech. *Trends in Cognitive Sciences*, *12*(3), 106–113.

https://doi.org/10.1016/j.tics.2008.01.002

Szczepanski, S. M., Crone, N. E., Kuperman, R. A., Auguste, K. I., Parvizi, J., & Knight, R. T.

(2014). Dynamic changes in phase-amplitude coupling facilitate spatial attention control

in fronto-parietal cortex. *PLoS Biology*, *12*(8), e1001936.

https://doi.org/10.1371/journal.pbio.1001936

Sharott, A., Magill, P. J., Harnack, D., Kupsch, A., Meissner, W., & Brown, P. (2005).

    Dopamine depletion increases the power and coherence of beta-oscillations in the

    cerebral cortex and subthalamic nucleus of the awake rat. *The European Journal of*

    Neuroscience, *21*(5), 1413–1422.

Sherman S. M. (2016). Thalamus plays a central role in ongoing cortical functioning. *Nature*

    Neuroscience, *19*(4), 533–541. https://doi.org/10.1038/nn.4269

Shomstein, S., & Yantis, S. (2004). Control of attention shifts between vision and audition in

    human cortex. *Journal of Neuroscience,24*(47), 10702-10706.

    doi: https://doi.org/10.1523/JNEUROSCI.2939-04.2004

Siegel, M., Warden, M. R., & Miller, E. K. (2009). Phase-dependent neuronal coding of objects

    in short-term memory. *Proceedings of the National Academy of Sciences of the United*

    States of America, *106*(50), 21341–21346. https://doi.org/10.1073/pnas.0908193106

Smiley, J. F., Hackett, T. A., Ulbert, I., Karmas, G., Lakatos, P., Javitt, D. C., & Schroeder, C. E.

    (2007). Multisensory convergence in auditory cortex, I. Cortical connections of the

    caudal superior temporal plane in macaque monkeys. *The Journal of Comparative*

    Neurology, *502*(6), 894–923. https://doi.org/10.1002/cne.21325

Staines, W. R., Graham, S. J., Black, S. E., & McIlroy, W. E. (2002). Task-relevant modulation

    of contralateral and ipsilateral primary somatosensory cortex and the role of a prefrontal-

    cortical sensory gating system. *NeuroImage*, *15*(1), 190–199.

    https://doi.org/10.1006/nimg.2001.0953

Staines, R., Popovich, C., Legon, J., & Adams, M. (2014). Early modality-specific

    somatosensory cortical regions are modulated by attended visual stimuli: interaction of

    vision, touch, and behavioural intent. *Frontiers in Psychology, 5*(351).

    doi:10.3389/fpsyg.2014.00351

Starke, J., Ball, F., Heinze, H., & Noesselt, T. (2017). The spatio-temporal profile of

    multisensory integration. *European Journal of Neuroscience, 51*(5), 1210-1223.

    https://doi.org/10.1111/ejn.13753

Stein, B., & Wallace, M. (1996). Comparisons of cross-modality integration in midbrain and

    cortex. *Progress in Brain Research, 112*, 289-299. doi: 10.1016/s0079-6123(08)63336-1

Sutton, S., Braren, M., Zubin, J., & John, E. R. (1965). Evoked-potential correlates of stimulus

    uncertainty. *Science (New York, N.Y.)*, *150*(3700), 1187–1188.

    https://doi.org/10.1126/science.150.3700.1187

Sur, S., & Sinha, V. K. (2009). Event-related potential: An overview. *Industrial Psychiatry Journal*, *18*(1), 70–73. https://doi.org/10.4103/0972-6748.57865

Talsma, D., Senkowski, D., Soto-Faraco, S., & Woldorff, M. (2010). The multifaceted interplay between attention and multisensory integration. *Trends in Cognitive Sciences, 14*(9), 400-410. doi: 10.1016/j.tics.2010.06.008.

Taylor-Clarke, M., Kennett, S., & Haggard, P. (2002). Vision modulates somatosensory cortical processing. *Current Biology: CB*, *12*(3), 233–236. https://doi.org/10.1016/s0960-9822(01)00681-9

Taylor-Clarke, M., Kennett, S., & Haggard, P. (2004). Persistence of visual-tactile enhancement in humans. *Neuroscience Letters*, *354*(1), 22–25. https://doi.org/10.1016/j.neulet.2003.09.068

Thomas, C., vom Berg, I., Rupp, A., Seidl, U., Schröder, J., Roesch-Ely, D., Kreisel, S. H., Mundt, C., & Weisbrod, M. (2010). P50 gating deficit in Alzheimer dementia correlates to frontal neuropsychological function. *Neurobiology of Aging*, *31*(3), 416–424. https://doi.org/10.1016/j.neurobiolaging.2008.05.002

Vanderah, T., Gould, D. (2015). *Nolte's The Human Brain, 7th Edition.* Elsevier.

van Ede, F., Niklaus, M., & Nobre, A. C. (2017). Temporal Expectations Guide Dynamic

    Prioritization in Visual Working Memory through Attenuated α Oscillations. *The*

    Journal of Neuroscience: the Official Journal of the Society for Neuroscience, *37*(2),

    437–445. https://doi.org/10.1523/JNEUROSCI.2272-16.2016

Villafuerte, G., Miguel-Puga, A., & Arias-Carrión, O. (2019). Continuous theta burst

    stimulation over the right orbitofrontal cortex impairs conscious olfactory perception.

    Frontiers in Neuroscience, *13*, 555. https://doi.org/10.3389/fnins.2019.00555

Walter, W. G., Cooper, R., Aldridge, V. J., McCallum, W. C., & Winter, W. G. (1964).

    Contingent negative variation: An electrical sign of sensorimotor association and

    expectancy in the human brain. *Nature*, *203*, 380–384. https://doi.org/10.1038/203380a0

Wasaka, T., Nakata, H., Kida, T., & Kakigi, R. (2005). Gating of SEPs by contraction of the

    contralateral homologous muscle during the preparatory period of self-initiated plantar

    flexion. *Brain research. Cognitive Brain Research*, *23*(2-3), 354–360.

    https://doi.org/10.1016/j.cogbrainres.2004.11.002

Warren, D. H., Welch, R. B., & McCarthy, T. J. (1981). The role of visual-auditory

    "compellingness" in the ventriloquism effect: implications for transitivity among the

    spatial senses. *Perception & Psychophysics*, *30*(6), 557–564.

    https://doi.org/10.3758/bf03202010

White, P. M., & Yee, C. M. (2006). P50 sensitivity to physical and psychological state influences. *Psychophysiology*, *43*(3), 320–328. https://doi.org/10.1111/j.1469-8986.2006.00408.x

Wiesman, A. I., Heinrichs-Graham, E., Coolidge, N. M., Gehringer, J. E., Kurz, M. J., & Wilson, T. W. (2017). Oscillatory dynamics and functional connectivity during gating of primary somatosensory responses. *The Journal of Physiology*, *595*(4), 1365–1375. https://doi.org/10.1113/JP273192

Wiesman, A., Groff, B., Wilson, T. (2018). Frontoparietal networks mediate the behavioral impact of alpha inhibition in visual cortex. *Cerebral Cortex,29*(8), 3503-3513. https://doi.org/10.1093/cercor/bhy220

Wiesman, A. I., & Wilson, T. W. (2019). Alpha Frequency Entrainment Reduces the Effect of Visual Distractors. *Journal of Cognitive Neuroscience*, *31*(9), 1392–1403. https://doi.org/10.1162/jocn_a_01422

Wiesman, A. I., & Wilson, T. W. (2020). Attention modulates the gating of primary somatosensory oscillations. *NeuroImage*, *211*, 116610. https://doi.org/10.1016/j.neuroimage.2020.116610

Woodman, G. (2010). A brief introduction to the use of event-related potentials (ERPs) in

    studies of perception and attention. *Attention, Perception, & Psychophysics, 72*(8).

    doi: 10.3758/APP.72.8.2031

Yadon, C., Bugg, J., Kisley, M., & Davalos, D. (2010). P50 sensory gating is related to

    performance on select tasks of cognitive inhibition. *Cognitive, Affective, & Behavioral*

    Neuroscience, 9(4), 448-458. doi: 10.3758/CABN.9.4.448

Yamaguchi, S., & Knight, R. T. (1990). Gating of somatosensory input by human prefrontal

    cortex. *Brain Research*, *521*(1-2), 281–288. https://doi.org/10.1016/0006-

    8993(90)91553-s

Yau, J. M., DeAngelis, G. C., & Angelaki, D. E. (2015). Dissecting neural circuits for

    multisensory integration and crossmodal processing. *Philosophical transactions of the*

    Royal Society of London. Series B, Biological sciences, *370*(1677), 20140203.

    https://doi.org/10.1098/rstb.2014.0203

Yingling, C. D., & Skinner, J. E. (1976). Selective regulation of thalamic sensory relay nuclei by

    nucleus reticularis thalami. *Electroencephalography and Clinical Neurophysiology*,

    41(5), 476–482. https://doi.org/10.1016/0013-4694(76)90059-6

Zatorre, R., Bellin, P., & Penhune, V. (2002). Structure and function of auditory cortex: music

    and speech. *Trends in Cognitive Sciences, 6*(1), 37-46.

    doi: 10.1016/s1364-6613(00)01816-7

Zhu, Z., Disbrow, E. A., Zumer, J. M., McGonigle, D. J., & Nagarajan, S. S. (2007).

    Spatiotemporal integration of tactile information in human somatosensory cortex. *BMC*

    Neuroscience, *8*, 21. https://doi.org/10.1186/1471-2202-8-21

Zikopoulos, B., & Barbas, H. (2006). Prefrontal projections to the thalamic reticular nucleus

    form a unique circuit for attentional mechanisms. *The Journal of Neuroscience, 12*(26),

    7348-7361. doi:10.1523/JNEUROSCI.5511-05.2006