Attention and Age-Related Components of Visual-Tactile Modulation of Somatosensory Cortex and Motor Implications

By

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Author's Declaration

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

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Abstract

Successful interaction with the external world requires continual sensory detection, sensorimotor translations and goal-directed motor execution. Attention to task-relevant stimulation can facilitate sensory detection and improve behavioural performance. Crossmodal visual and somatosensory interaction within early sensory regions appears to further enhance processing, but required stimulus congruency for optimal sensorimotor communication is relatively unknown. This thesis first investigates the impact of visual-tactile temporal presentation on somatosensory activation within healthy young adults. As expected, findings revealed simultaneous crossmodal stimulation to maximally augment tactile event-related potentials (ERPs). These results were subsequently applied to determine the influence of attentional or low-level priming effects on motor performance within young and older adults. The bulk of this thesis assesses whether crossmodal interaction is similarly influential across age. Task-relevant visual-tactile stimulation was predicted to facilitate sensory regions and improve motor behaviour for both young and older subjects. Visual distraction was expected to limit tactile processing and impair performance only within older subjects. Tactile (P50, P100, N140, P230) and visual (N1) ERPs were recorded from 32 channels while healthy young and older subjects preformed a sensory integration task. Three conditions varying in modality of stimulation (tactile/visual) and task relevancy (relevant/irrelevant) required subjects to attend to stimuli and make an appropriately graded motor response. Blocked training prior to collection ensured stimulus-response associations and task demands were learned. Individual ERPs were time-locked to the onset of the first or second stimulus and quantified at CP3, CP4, FCZ, O1 and O2. Despite evidence of age-dependent effects in tactile processing, grand average waveforms suggest older adults maintain the ability to selectively attend to task-relevant information. Improved motor accuracy was not associated with crossmodal facilitation in either age group, however results indicate that performance of older adults declines with visual distraction. Differential N1 modulation across age suggests younger adults disengage from visual distraction after initial saliency (earlier latency with second distractor), while older adults may use a conscious strategy to shift attention away from distraction (latency unchanged but reduced amplitude with second distractor). Overall, these results follow previous studies and suggest older adults compensate for a general increase in processing background information by altering performance strategy. This vulnerability to distraction appears to negatively impact motor performance even within healthy aged adults.

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List of Abbreviations

EEG	Electroencephalography
ERP	Event-related potential
fMRI	Functional magnetic resonance imaging
ISI	Interstimulus interval
ITI	Intertrial interval
PFC	Prefrontal cortex
RT	Reaction time
SART	Sustained attention to response task
se	Standard error
SI	Primary somatosensory cortex
SII	Secondary somatosensory cortex
TT	Tactile stimulus, 50 ms delay, tactile stimulus
TTvv	Tactile-tactile stimulation with visual-visual distraction
VTdelay	Visual stimulus, 750 ms delay, tactile stimulus
VTimm	Visual stimulus, 50 ms delay, tactile stimulus
VTsim (VT)	Simultaneous visual-tactile stimulation
WCST	Wisconsin card sorting task

Introduction

The encompassing objective of this thesis is to provide insight into how crossmodal interactions between visual and tactile stimulation affect sensory processing within the somatosensory cortex. Of great interest is the potential behavioural advantage of cortical modulation following crossmodal presentation. Extending knowledge of sensory adaptation, interaction and processing will be key to recognizing the impact of cortical and functional consequences following sensory deficit. In particular, persons suffering a stroke often endure lasting somatosensory deficiencies frequently coupled with motor impairment. Recent studies within the stroke population have revealed that dual sensory and motor impairments present patients with a worse prognosis than motor impairment alone (Tyson et al, 2008). Further, patients maintaining normal sensation typically undergo a more prompt and robust recovery than those with impaired sensation (Tyson et al, 2008). Consequently, as stroke is the leading cause of neurological disability in North America (Heart & Stroke Foundation, 2008), it is vital that rehabilitation therapies involve optimal physiological and behavioural techniques. It may, for example, be possible to take advantage of sensorimotor interactions to an extent where appropriate sensory input could aid motor output. If sensory regions can be maximally facilitated by combined sensory stimulation, motor areas may be consequentially enhanced to allow more efficient induction of training-related plasticity in sensorimotor networks, leading to improved functional performance.

The somatosensory cortex is influenced by a combination of stimulus- and cognitively-driven networks. Reflexive ‘bottom-up’ attention to stimulus saliency paired with voluntary, focused ‘top-down’ attention enables prompt processing of attended and relevant incoming stimuli. Although less is known about crossmodal interactions within sensory-specific regions, relevant dual visual and tactile simulation appear to at least impact perceptual sensory processing (Eimer & vanVelzen, 2005). Additional evidence exists for a visual priming effect where sensory regions are facilitated concurrently or immediately following visual stimulation (Fiorio & Haggard, 2005). However, much work is needed to bridge the gap of sensorimotor interactions, especially following multimodal stimulation. Concurrent visual and tactile stimuli are perhaps the most intuitive starting ground, as both dominate in guiding motor behaviour. Research thus far indicates a multifaceted complex of sensory and higher cognitive regions as fundamental to the continual modulation of the somatosensory cortex. The healthy function of these cortical representations must first be understood before translations can be extended to neurorehabilitative techniques.

This thesis considers both electrophysiological and behavioural measures, allowing correlation between cortical sensory modulation and motor performance. These relationships could provide insight into the statistical and clinical significance related to sensory modulation following crossmodal stimulation. Healthy young and older adults will be considered both in isolation and across age, enabling stepwise comparisons between unimodal and crossmodal, relevant and irrelevant, and motor performance. Contrasting young and older adults will permit investigation of healthy age-related changes associated with sensory processing, revealing potential limitations in sensory gating and cortical processing speed. This thesis will help provide groundwork for future studies investigating the source of enhanced motor performance, be it facilitation of sensory sensitivity, or advanced feedforward communication to motor regions.

Chapter 1: Review of relevant literature

1.1 Physiology and electrophysiological measures

1.1.1 Electroencephalography

From the turn of the 20th century electroencephalography (EEG) has aided clinical diagnosis and research advancements as a non-invasive measure of cortical activity. By monitoring voltage differences between post-synaptic potentials from apical dendrites and a reference electrode centered over an area of non-activity, EEG reflects the summation of upper layer neuronal activity (Coles, Gratton & Fabiani, 1990). As EEG is a surface recording and the skull attenuates voltage fields, deep cortical structures cannot be sourced in isolation and any involvement is open to interpretation or external support. In contrast to functional magnetic resonance imaging (fMRI), EEG sacrifices spatial specificity for excellent temporal resolution: represented cognitive processing can be observed within milliseconds of neuronal activation. Within the research realm, EEG is a preferred method to infer timing and general localization of many motor and attentional processes. It presents the opportunity to track cortical decrements or plasticity associated with age and pathology, as well as providing a medium for biofeedback rehabilitation techniques.

Event-related potentials (ERPs) are an electrophysiological response to an internal or external stimulus. ERPs can be time-locked within EEG recordings to sensory, motor, or cognitive events and are selectively modulated by attention, stimulus relevancy, and task requirements. Most healthy young adults present with stable ERPs consistent in shape, amplitude and latency, and experimental paradigms eliciting waveform changes can be indicative of neural modulation. Most sensory ERPs are influenced by attention and are thought to reflect sensory information used in perceptual judgments (Hillyard, Vogel & Luck 1998). Early-latency ERPs are modality-specific and maximally elicited over primary sensory regions; activation is sensitive to exogenous (externally-driven) attention and variation in physical stimulus parameters (Eimer, 2001). Longer-latency ERPs present with broader distribution unrelated to modality and not directly influenced by stimulus parameters. Later potentials are indicative of endogenous (internally-driven) components linked to processing beyond initial detection, representative of stimulus identification and categorization, response selection and activation (Eimer, 2001).

1.1.2 Somatosensory organization

The somatosensory cortex lies within the post-central gyrus of the parietal lobe and is traditionally separated into primary (SI) and secondary (SII) regions. Further division of SI into Brodmann areas 3a, 3b, 1 and 2 (respectively running rostral to caudal) allows neuron-specific separation. Individual somatotopic sensory homunculi are represented within each Brodmann area of SI, with feet presented most medial and face most lateral. Peripheral sensory inputs are communicated to S1 by the dorsal-column medial-lemniscus pathway via thalamic sensory nuclei. Most thalamic input terminates in areas 3a and 3b, but there are some direct connections to areas 1 and 2. Cutaneous afferent information primarily travels to areas 3b and 1, while proprioceptive muscle and joint afferents are more directly transferred to areas 3a and 2. Sensory representations are mostly independent and specific within original cutaneous regions and gradually become integrated with additional information from areas 3a and 2. The functional organization of pathways leading to and within SI allows modality, spatial and temporal integrity of stimulation to be maintained from receptor to cortex.

Intracortical connections enable communication between neurons transmitting similar information. Once sensation has been processed within SI, cortico-cortical projections are sent to the posterior-parietal, temporal, and frontal lobes, as these areas receive no direct projections from thalamic sensory nuclei. SI also projects dense cortico-cortical connections to SII for somatosensory processing and association. SII is located immediately posterior to SI at the lateral-most border of the parietal lobe, just above the lateral sulcus. Somatotopic representations within SII are less precise than in SI, as SII is more important in governing higher-order processing of stimulus recognition and discrimination, tactile memory and learning, and somatosensory engagement of the motor system at the cortical level (Johansen-Berg & Lloyd, 2000).

1.2 Cortical modulation: bottom-up and top-down processing

Somatotopic representations of sensory and motor cortices reorganize in response to sustained changes in sensory input. Top-down control mediates this effect, as the amplitude of change is graded and dependent on the amount of conscious attention paid to incoming stimuli. If stimulation is ignored, excitatory effects from bottom-up influences (presence and salience of stimulus) are less effective than when paired with top-down demand (task-relevant attention). Hillyard and Anllo-Vento (1998) present a model of the role of attention during stimulation as a system of hierarchical filters modulating task-dependent processing, inclusive of both feedforward and feedback mechanisms. At the early feedforward level, selective attention may potentially rely on generalized suppression of background activity to enhance perceived sensation (e.g. reduced SI blood flow to homunculus regions separate from those anticipating touch) (Drevets, Burton & Videen, 1995). Early processing enhancement of primary sensory cortices may modulate the stimulus signal-to-noise ratio improving discernability and allowing more efficient and effective processing at higher levels (Corbetta et al, 1990). Changes in the synchrony of bottom-up cell firing can also change the synaptic efficacy of cortical stimulus representation (Johansen-Berg & Lloyd, 2000). Any feedforward convergence from sensory cortices to multimodal regions, regardless of causation, is predicted to be recycled as top-down feedback (Johansen-Berg & Lloyd, 2000).

A more anatomical model of attention (Corbetta & Shulman, 2002) delegates attention direction and reorientation to regions of the prefrontal cortex (PFC). When stimuli or behavioural requirements are ambiguous (e.g. novel events), the PFC is maximally engaged (Goldberg, Podell & Lovell, 1994). In a network with the thalamus, the prefrontal cortex is tasked with devoting cortical resources to relevant stimulation, inhibiting allocation to irrelevant stimuli, and modulating the mental effort dedicated to processing stimuli (Daffner et al, 2003). The parietal lobe contributes to top-down control of focal attention during target selection (Corbetta & Shulman, 2002). ‘Template matching’ between a given stimulus and learned stimulus-response associations appears to elicit maximal activity within posterior parietal regions (Chao, Nielsen-Bohlman & Knight, 1995). Frontal networks mediate sensory coordination during novel crossmodal associations to ensure the stimulus connection is learned (Calvert, 2001). Although some specific regional activation can be dependent on task requirements, attention to incoming stimuli demands primary sensory activation in conjunction with frontal and parietal networks.

1.3 Working memory and selective attention

Ongoing environmental interaction requires the merging of internally driven goal-directed decisions with simultaneous externally driven perceptual influences of stimulation. Executing suitable motor behaviour typically involves holding various sensations in working memory while selecting the most appropriate response to obtain a pre-set goal. As both share a regional interface of higher cognition areas, a systematic overlap runs between selective attention and working memory. The ability to accurately maintain information depends on the quality of stimulus representation at first perception, but the capacity of top-down networks to filter stimuli is resource limited. If networks are overwhelmed or impaired irrelevant and distracting stimuli can enter the processing stream, limiting the ability to preserve the desired stimulus. Integrity of any represented stimulus can be quickly subject to decline if top-down networks are inadequate (Gazzaley et al, 2005a). As stimuli vie for conscious awareness, representations are particularly susceptible to degradation in older adults or pathological populations.

Some research suggests individual working memory differences influence thalamic filtering and sensory enhancement (Rissman, Gazzaley & D'Esposito, 2009). The ability to augment or suppress modality-specific inputs is influenced by the capacity of sensory association regions to maintain stimulus representations. These networks may engage a common amodal processing component to share task load, especially in situations of high cognitive demand. For example, high levels of distraction in any modality can negatively impact modality-specific performance (Rissman, Gazzaley & D'Esposito, 2009). Active cognitive control may be essential to suppress irrelevant stimuli, and the ability to do so appears to vary between individuals. Even within healthy young adults, successful performance can differ with attention to distraction and task load (Rissman, Gazzaley & D'Esposito, 2009). Natural variations in neuronal recruitment and regional networks could be amplified by experience-dependent neuroplasticity, different for each individual. Cortical efficiency, activation thresholds, and regional integrity could all develop slightly distinct. Independent adaptations within the larger accepted networks of attention and selection are highly likely, and may partially account for population divergence in functional memory and distractibility.

1.4 Sensory priming and intermodal attention

Anticipatory attention prior to stimulation primes sensory regions to speed processing once the stimulus is experienced. Modality-specific expectations elicit a maximal priming effect within the primary sensory region, however subsequent processing of any modality is typically enhanced (Driver & Spence, 1998). The multimodal nature of this effect is supportive of crossmodal links in a separate-but-linked attentional system (Spence, 2002). Additional crossmodal effects can be observed prior to conscious attention and unrelated to residual preceding experience (Eimer, 2001), lending further validation to possible anatomical links advancing bottom-up processing in conjunction with later top-down control. Amedi and colleagues (2005) suggest sensory-specific representations within unimodal cortices are linked either directly or via crossmodal binding sites. Following this idea, the location of crossmodal convergence would be dependent on modality dominance and regional capacity, as well as task demands and behavioural goals. Specific to visual-tactile integration, the insula and claustrum may mediate communication between unimodal sensory regions to merge information as crossmodal (Amedi et al, 2005). Sensory association neural networks may be linked to object-specific representations within each modality in additional temporal, parietal and frontal regions (Amedi et al, 2005).

Intermodal attention (attending to one modality in the presence of others) enhances neural processing independent of the effects of spatial and selective attention (Karns & Knight, 2009). However, for most levels of intermodal interaction, a degree of congruent spatial attention is required to elicit early sensory modulation. The principle of spatial coincidence dictates that although receptive fields across modalities overlap, only stimuli falling within the overlap facilitate a response; stimulation outside of common fields depresses response processing (Kayser & Logothetis, 2007). Some very early (within 50 ms post-stimulus) modulations of SI are reported to persist regardless of spatial incongruence (Macaluso, 2006), but concisely the most robust modulations of stimulus processing follow temporal and spatial coincidence. Furthermore, sufficiently separated (i.e. no possibility of crossmodal stimulation occurring from the same source) temporal presentation of crossmodal stimuli are processed independently, comparable to unimodal stimulation in isolation (Kayser & Logothetis, 2007). The principle of inverse effectiveness also dominates within crossmodal stimulation. The level of peripheral modulatory influence depends on the effectiveness of the primary stimulus: stimuli weak in isolation but enhanced by other sensations display qualitatively different SI modulation than highly salient inputs. Single sensory stimulation sufficient to drive neuronal activation is less influenced by concurrent modalities and perhaps warrants less high-level interaction (Kayser & Logothetis, 2007).

Combining information across senses increases working knowledge about the surrounding environment, strengthening internal stimulus representations and making behavioural responses more certain. Supplementary or redundant modalities can improve stimulus recognition speed and movement accuracy (Kayser & Logothetis, 2007), but attentional coordination across modalities is dependent on the type of attention required and senses concerned.

1.5 Task switching and stimulus selection

Stimulus selection and attention set shifting are essential components to healthy function within daily activities. Attentional shifts enable concentration to reorient, switching focus and initiating new stimulus processing. Much research investigates these cognitive control functions, and regions of the prefrontal cortex have been implicated for both stimulus selection (frontal-thalamic sensory filter) and attention set switches. In absence of direct input-level mutual inhibition, top-down PFC signals are able to mediate both components (Gehring & Knight, 2002). The PFC is portrayed as a parallel-distributed processing model, allowing different effects for within (e.g. colour to colour) and between (e.g. colour to shape) dimension switching. Task switching across any dimension is performed equally within healthy young adults, but limitations can be observed within an older population. Age-matched controls (mean age 70 years) to a heterogeneous PFC lesion group presented with similar trends in task switching performance: between-dimension switching was performed slower and modality incompatible trials (incongruent distractor and target items; e.g. different letters, different colours versus compatible same letters, different colours) were performed with less accuracy than compatible trials (Gehring & Knight, 2002). PFC patients performed significantly slower and less accurately than age-matched controls, however a similar pattern of performance decline in comparison to younger adults strongly suggests the integrity of the prefrontal cortex is compromised within healthy aging, resulting in at least mild behavioural effects.

1.6 Visual-tactile interaction

Physical interaction with the external world allows multisensory experiences through visual, tactile, and proprioceptive inputs. As vision is a dominant sense in most individuals, external events are typically localized with a heavy reliance on vision rather than touch. Although vision and gaze are commonly paired in real-world situations, each appears to independently modulate the somatosensory cortex: direct visual input of a stimulated body part can facilitate SI, while gaze to the spatial location of stimulation in absence of vision (e.g. stimulated finger is covered by a box) modulates later higher-order somatosensation (Forster & Eimer, 2005). As such, crossmodal modulation associated specifically with visual-tactile interaction is primarily viewed as affecting early perceptual processing (Eimer & vanVelzen, 2005). Prolonged crossmodal effects may be more concerned with task-relevant modalities (Eimer, vanVelzen & Driver, 2002) or memory components (Ohara, Lenz & Zhou, 2006). Generally as processing proceeds within the visual or somatosensory hierarchy, activated crossmodal regions transition from contralateral to stimulation to bilateral (Macaluso & Driver, 2001). Regions in temporal, parietal, frontal and insular cortices are also involved in crossmodal binding of visual-tactile information, however not all areas are equally responsive to unimodal stimulation or specific combinations (Amedi et al, 2005).

The visual priming effect on somatosensory regions allows anticipatory preparation of SI neurons to maintain improved tactile acuity beyond visual presentation (Fiorio & Haggard, 2005). The visual dorsal stream of the posterior parietal cortex is regarded as a heteromodal region, housing neurons for both vision and touch and contributing to multisensory perceptions of peripersonal space. Descending signals from the parietal cortex prepare sensory regions to facilitate somatosensory information processing, allowing top-down modulation of a traditional ‘unimodal’ area. Specific to the tactile modality, simultaneous stimulation can be ‘decoupled’ (congruent stimuli cease to modulate SI) from relevant visual input if the tactile stimuli are consistently task-irrelevant (Eimer, vanVelzen & Driver, 2002). Subsequent processing within SII appears relatively unaffected by prior crossmodal associations, and is equally enhanced with learned (e.g. touch and vision of arm) or novel (e.g. touch and vision of object) visual stimuli (Press et al, 2008). Stimulus processing based on task or behavioural goals are influenced by the efficiency of these early SI and SII processes (Press et al, 2008).

1.7 Age-related sensory loss

1.7.1 Neurodegradation and compensation hypotheses

Cognitive impairment and cortical degeneration inevitably follow the aging process. Three standing hypotheses are debated as the source of the scaled decline: processing speed hypothesis wherein slowed neural connectivities manifest as impaired cognition (Salthouse, 1996); executive deficit frontal aging hypothesis, attributing early loss of executive functions to reduced frontal lobe integrity (West, 1996); and inhibitory deficit hypothesis where the ability to suppress interference is limited and irrelevant information confounds processing of relevant stimuli (Hasher & Zacks, 1988). Most likely these hypotheses are not mutually exclusive and any observable decline is biased by the combined capacity of neural correlates. It has long been established that normal aging alters the prefrontal cortex: healthy adults are less able to ignore irrelevant distractors than their younger counterparts (Rabbitt, 1965). Compromised cortical structure has traditionally been held accountable for the diminished ability, as evidence of age-related decline in neuron count (Creasey & Rapoport, 1985), dendrites (Jacobs & Scheibel, 1993) and synapses (Huttenlocher, 1979) has all been reported. Recently, a slightly shifted perspective illustrating the primary role of physiological neurotransmitter changes in cognitive decline has been presented (Gazzaley & D’Esposito, 2007). This emerging view suggests that decrements in neural signaling are perhaps more indicative of age-related cognitive decline than structural alterations.

Cortical effort to maintain functional integrity involves adaptive neuroplasticity to counter age-related neurodegenerative and neurochemical changes. Task-dependent patterns of cortical activity emerge in older adults different than those observed in young adults: stronger activation or additional regional activation is observed to mask inefficiencies and improve task performance. These age-related effects are reported during both movement (Heuninckx et al, 2005) and cognitive tasks (Nielsen-Bohlman & Knight, 1999). Two countering hypotheses explain this altered cortical activation: the compensation hypothesis assumes increased cortical activation and additional recruitment offsets neural and behavioural deficits (Madden et al, 1999). The dedifferentiation hypothesis observes extra activation as general and nonfunctional, resulting from lost neural specialization and neurotransmission deficits (Li & Lindenberger, 1999). Recent work by Heuninckx, Wenderoth and Swinnen (2008) investigated these hypotheses by correlating motor performance ability and cortical activation in older adults. A significant relationship between increased activation and high performance, amplified during demanding tasks, suggests non-functional general dedifferentiation does not dictate activation patterns. Observations of compensatory recruitment exposed an extensive network of motor, higher sensorimotor, and frontal regions, all indicating better performance in older adults is reliant on cognitive reserve. Nonetheless, to match performance across age and individual, it remains probable that local and distributed cortical networks function as a combination of neural dysfunction (dedifferentiation) and compensation.

1.7.2 Working memory and distractibility in older adults

Working memory for many older adults presents as a more cluttered and functionally smaller system than in young adults (Hasher & Zacks, 1988), abetting distractibility and forgetfulness. Within most memory tests, aged adults present with more errors and longer delays in recollection; additional intervening distractor items and lengthened intervals before a required response promote even more impairment (Chao & Knight, 1997). With age, levels of the attention system become compromised, amplifying vulnerability to distraction and prompting inefficient processing of relevant information. However, as control over irrelevant suppression differs from relevant facilitation, each mechanism is differentially affected. The capacity of older adults to attend and enhance cortical activity to relevant stimulation is generally preserved while suppression of irrelevant stimuli becomes inadequate (Gazzaley et al, 2005b). A delayed compensatory system suppressing task-irrelevant stimuli does persist, but the millisecond delay causes a ‘load shift’ of cognitive processing. Distractor stimuli are allowed minute access into working memory and overload the processing capacity; stimulus representations quickly degrade and desired stimuli are processed less efficiently. Behavioural implications of a limited sensory-filter are not universal and some aged adults continue to function seamlessly, however a slighted working memory typically translates to slow reaction time, reduced accuracy, and inappropriate recognition of irrelevant cues (Gazzaley et al, 2008).

Chapter 2: General objectives and hypotheses

The main objectives of this thesis target better understanding of crossmodal sensory processing within the somatosensory cortex. Mechanisms underlying the sensorimotor interaction of visual and tactile stimulation are investigated and inferred through modulation of tactile ERPs and motor behaviour responses. Comparisons within task-relevancy conditions and between methods of stimulation (i.e. tactile or visual-tactile) will consider the importance of bottom-up modality and top-down attentional components. Ideally, insight will be gained into the possible use of low-level priming or conscious attention to train motor behaviour. Understanding age-related cortical decline and its impact on healthy sensorimotor processing could potentially extend the use of these training methods to populations that may benefit from functional intervention.

1) To determine how crossmodal interactions between visual and tactile stimulation modulate somatosensory activity.

Hypothesis: When relevancy and spatial congruency are maintained, presentation of temporally aligned visual and tactile stimuli will enhance somatosensory activation in comparison to unimodal or temporally distinct visual-tactile stimulation.

2) To determine how age-related components will affect simultaneous tactile-relevant visual-irrelevant sensory processing within the somatosensory cortex.

Hypothesis: When tactile-relevant and visual-irrelevant stimuli are presented simultaneously, attention to vision will impede tactile processing within older adults. This impairment will present as reduced somatosensory activation, below facilitation observed in relevant visual-tactile tasks, and may correlate with slowed cognitive processing of relevant tactile stimuli. Younger adults will be able to ignore visual distraction and process tactile-relevant stimuli as if they were presented in isolation.

3) To determine the behavioural implications of somatosensory modulation following visual-tactile stimulation.

Hypothesis: Enhanced somatosensory activation elicited by relevancy or temporal congruency will translate to improved motor response accuracy. Depressed somatosensory activation, if observed following visual distraction during tactile-relevant stimulation, will degrade performance below relevant visual-tactile presentation.

Chapter 3: *Temporal integrity of visual-tactile modulation of somatosensory cortex in young adults*

3.1 Rationale

Crossmodal attention can facilitate somatosensory activity, but the importance of temporal congruency within crossmodal stimulation and its impact on cortical modulation are not well known. The purpose of this pilot work is to consider temporal specificity of visual-tactile stimulation, and subsequent limits of visual priming or facilitation of tactile processing regions. This experiment holds stimulus attributes fixed, with the sole manipulation of interstimulus interval (ISI) delay periods. Results will dictate the protocol used within the following study comparing healthy young and older adults.

Somatosensory modulation is inferred through tactile ERP components P50, P100 and N140. Generated in SI, P50 is the earliest consistent tactile peak and can be elicited by vibrotactile stimulation. Its distribution is contralateral to somatosensory stimulation and it is modulated by changes in tactile detection and stimulus saliency (Allison et al, 1991). P100 is a bilaterally produced potential primarily sourced by SII (Allison, McCarthy & Wood, 1992). Some reports suggest a P100 network involving the medial prefrontal cortex (Ku et al, 2007) or parietal lobe (Tomberg et al, 2005) because of its possible sensitivity to overt attention and crossmodal stimulation. The N140 also responds to attention and crossmodal manipulation (Ku et al, 2007), but it appears sourced by multiple generators and has a widespread distribution across the cortex. It is generally thought to reflect later somatosensory activity in a network with frontal regions (Ku et al, 2007). Some evidence suggests transient rather than sustained attention most modulates P100 and N140 (Eimer & Forster, 2003), which could imply that brief simultaneous stimulation will be more modulatory than temporally distinct stimuli requiring prolonged concentration. Crossmodal stimulation eliciting maximal ERP amplitudes, and thus facilitation of somatosensory and associated networks, will be replicated within task-relevancy experiments. Optimal temporal congruency should enable a more efficient and sensitive investigation of age-related and relevancy effects.

3.2 Specific objectives and hypotheses

1) To determine the optimal visual-tactile temporal congruency required to maximally facilitate somatosensory cortex.

Hypothesis: Presentation of temporally aligned visual and tactile stimuli will enhance somatosensory activation in comparison to unimodal or temporally distinct visual-tactile stimulation. Somatosensory facilitation will be reflected as increased tactile ERP amplitude. As stimuli become temporally separate, visual facilitation of early tactile processing (P50, P100) modulation will rapidly degrade. Temporal effects of visual-tactile processing on later tactile components (N140) will be graded, being most influential (evoking the highest amplitudes) at simultaneous presentation, and least in conditions with long ISI.

2) To determine behavioural implications of somatosensory modulation following temporally manipulated visual-tactile stimulation.

Hypothesis: Simultaneous crossmodal stimulation will most facilitate somatosensory regions, enabling more efficient sensorimotor translations and improving motor accuracy. Behaviour will degrade as visual-tactile stimuli become temporally distinct, mirroring gradations of somatosensory modulation.

3.3 Methods

3.3.1 Subjects

Behavioural and EEG data were collected from 8 neurologically healthy volunteers (mean age 25 yrs; range 20-33 yrs; 2 male). All subjects had normal or corrected-to-normal vision. All subjects provided informed written consent. Experimental procedures were approved by the Office of Research Ethics at the University of Waterloo.

3.3.2 Experimental design

Immediately prior to testing subjects completed a brief training protocol to limit the confounding effect of learning within the experiment. The 5-minute training session allowed subjects to learn amplitude associations between the visual and tactile stimuli, and the corresponding motor force required to match the stimulus amplitude. A horizontal target bar was visually presented on a central screen at a random height; subjects moved a second bar to match the target by squeezing a pressure-sensitive bulb with the right hand. Concurrent vibrotactile stimulation (25 Hz) was applied to the left index finger at an amplitude equal to the force applied to the bulb (i.e. the harder the subject squeezed, the higher the amplitude of the vibration). This protocol enabled real-time visual and tactile feedback for individuals to become familiar with the associated stimulus-response relationships, but did not allow direct practice on experimental conditions.

The experimental paradigm presented subjects with two stimuli: two tactile (unimodal) or visual and tactile (crossmodal). Four conditions manipulated temporal congruency: visual-tactile simultaneous (VTsim), vision first followed ‘immediately’ by tactile (ISI 50 ms; VTimm), vision followed by tactile after a delay (ISI 750 ms; VTdelay), and tactile-tactile (ISI 50 ms; TT). All stimuli were presented for 500 ms. The visual stimulus was a central horizontal bar of varying heights, and the tactile stimulus was a discrete vibration (25 Hz) of varying voltage applied to the left index finger. Subjects were told to fixate centrally while judging individual stimulus amplitudes (i.e. higher visual bar placement and harder vibration representative of increased amplitude). Four amplitude levels were randomly presented within each modality. A visual response cue (500 ms) was presented 1 s after the second stimulus, indicating the motor response should be initiated. The task required subjects to squeeze a pressure-sensitive bulb at a force equivalent to the summation of both stimulus amplitudes. The required response force never exceeded 50 percent of an individual’s maximum. Subjects received no feedback throughout the experiment, but were instructed to be as accurate and consistent within and between conditions as possible. Seventy-five sets of stimuli were presented within each condition; each condition lasted 5 minutes and was repeated twice in a random order. Breaks were permitted as necessary. White noise (70 dB; Compumedics Neuroscan Stim^2, USA) played concurrently during all conditions to mask the auditory noise of the vibrotactile apparatus.

3.3.3 Data acquisition

Subjects were seated at a desk in a sound-attenuating booth with the vibrotactile apparatus, response bulb, and computer monitor positioned in front of them (refer to Figure 1). EEG was recorded continuously throughout testing although not analyzed for the training task. EEG was collected from 32 electrode sites using a Quick-Cap (Neuroscan, Compumedics, USA) and adhering to the international 10-20 system for electrode placement. All recording sites had a maximum impedance of 5 kΩ and were referenced to linked mastoids. Online EEG was amplified and digitized at a sampling rate of 500 Hz (SynAmps^2, Neuroscan 4.3, Compumedics, USA). Behavioural data of reaction time and force applied to the bulb were collected within the stimulus presentation program created on LabVIEW (version 8.5, National Instruments, USA).

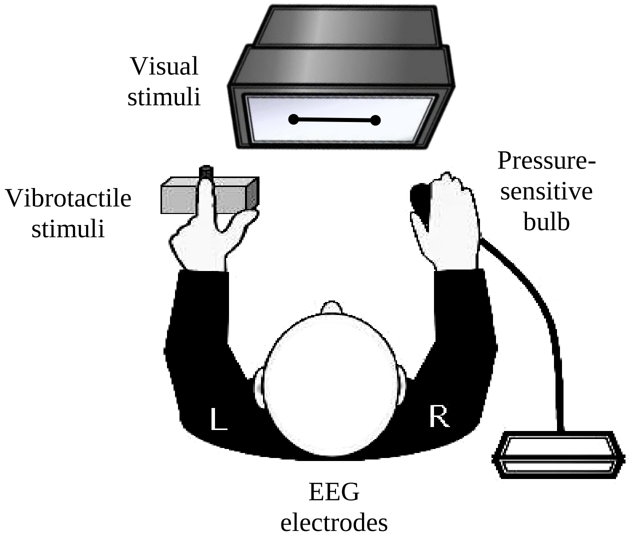

Figure 1: Experimental set-up within sound-attenuating booth. Tactile stimulation delivered to the left index finger; central computer screen delivered visual stimulation; motor responses made with the right hand.

3.3.4 Data analyses

Behavioural data:

Behavioural data gathered from bulb squeeze responses during the testing conditions was analyzed relative to each subject. Motor responses were calculated as an absolute percent of the ideal expected force (i.e. applied force as percent of the summation of forces associated with given stimulus amplitudes). A one-way ANOVA was performed to observe any behavioural modulation between conditions. Training data was not analyzed.

Electrophysiological data:

ERPs of interest were time-locked to the onset of the first tactile stimulus between 200 ms pre-stimulus and 600 ms post-stimulus. Individual traces were bandpass filtered at 0.1 to 30 Hz. Peak to peak instead of absolute amplitude measures were calculated because of high variability within the pre-stimulus baseline. Visual inspection permitted omission of epochs contaminated with blinks, saccades or muscular contraction; remaining ERPs were averaged within condition for each subject.

Amplitude and latency measures were quantified at P50, P100 and N140. All potentials were measured from electrode site CP4, representing the right SI contralateral to tactile stimulation. P100 and N140 were additionally measured at CP3, representing SI ipsilateral to stimulation. Although all 32 channels were considered, CP3 and CP4 were chosen for primary analyses because ERP components were maximal in at least one of the sites. Amplitudes were measured as raw voltage peak-to-peak differences (P50: baseline to P50; P100: N70 to P100; N140: P100 to N140). Note that while N70 was recorded, it was used only to calculate P100 amplitude and not independently analyzed. Following the P50, N70 is thought to be generated from SI activation. One-way ANOVAs were applied to amplitude data to investigate the effect of condition on ERP amplitude. Specific hypotheses were tested with a-priori contrasts (modality: tactile-tactile versus combined visual-tactile conditions; temporal: VTsim versus VTimm, and VTsim versus VTdelay conditions). Post-hoc Tukey tests were performed to detect any other task-related differences.

3.4 Results

3.4.1 Behavioural data

One subject was excluded from behavioural analyses because the corresponding electrophysiological data was not useable (n = 7). Results suggest training was not sufficient for subjects to learn stimulus-response associations, as responses generally did not meet task requirements. Behavioural data (Figure 2) comparing response accuracy between testing conditions was not significant.

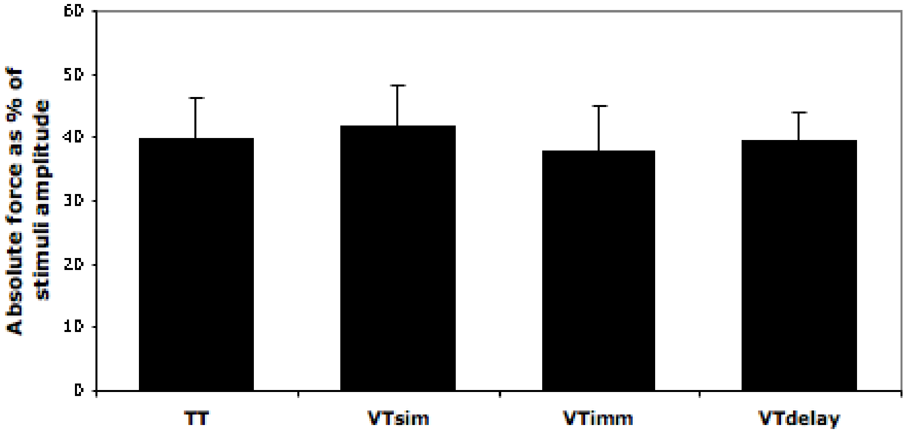

Figure 2: Performance in experimental tasks with standard error bars; response accuracy calculated as an absolute percent of the summed force of stimulus amplitudes. Conditions abbreviated as TT – tactile unimodal, 50 ms ISI; VTsim – simultaneous visual-tactile; VTimm – visual first, tactile second, 50 ms ISI; VTdelay – visual first, tactile second, 750 ms ISI.

3.4.2 Electrophysiological data

Seven of the 8 subjects presented with similar waveform morphologies across conditions, each eliciting somatosensory potentials P50 (group average latency 63 ms; se +/-1.09), P100 (113 ms; se +/-1.69), and N140 (169 ms; se +/-3.30). Distribution across all 32 EEG channels qualitatively portrayed potentials maximal around somatosensory regions with spread to frontal and proximal parietal areas. One subject was excluded from ERP analysis because of technological difficulties during online EEG recording. Figure 3 depicts grand average waveforms recorded at CP3 (A) and CP4 (B).

P50 amplitude (Figure 3 C) was not significantly modulated between experimental conditions; contrasts were also not significant. Trends of P100 amplitude (Figure 3 D) modulation were consistent at both CP3 and CP4, but the main effect of condition was only significant at CP3 ($F_{3, 18} = 3.50$; $p = 0.04$). The modality contrast testing the effect of vision showed crossmodal conditions to have significantly greater P100 amplitude than tactile unimodal at CP3 ($F_{1, 18} = 6.63$; $p = 0.02$). Temporal contrasts found VTsim not different from VTimm or VTdelay. Tukey's test including all four conditions showed P100 amplitude greatest during VTsim and lowest in TT. N140 amplitude (Figure 3 E) was significantly affected by condition at CP3 ($F_{3, 18} = 6.17$; $p = 0.005$) and CP4 ($F_{3, 18} = 6.09$; $p = 0.005$). The modality contrast was also significant at CP3 ($F_{1, 18} = 8.23$; $p = 0.01$) and CP4 ($F_{1, 18} = 4.34$; $p = 0.05$), revealing higher amplitudes during crossmodal than unimodal conditions. The temporal contrast between VTsim and VTdelay was significant at CP3 ($F_{1, 6} = 8.36$; $p = 0.03$) and CP4 ($F_{1, 6} = 6.91$; $p = 0.04$), revealing more facilitation during simultaneous than distinctly separate (ISI 750 ms) crossmodal stimulation. Tukey's test found N140 amplitude higher during VTsim than in TT and VTdelay conditions at both CP3 and CP4.

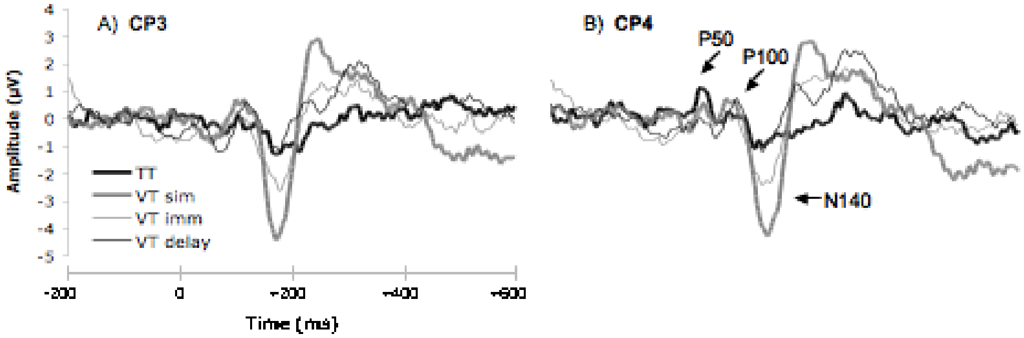

Figure 3: Grand average waveforms from somatosensory regions ipsilateral (A) CP3 and contralateral (B) CP4 to stimulation. First stimulus onset occurred at time 0.

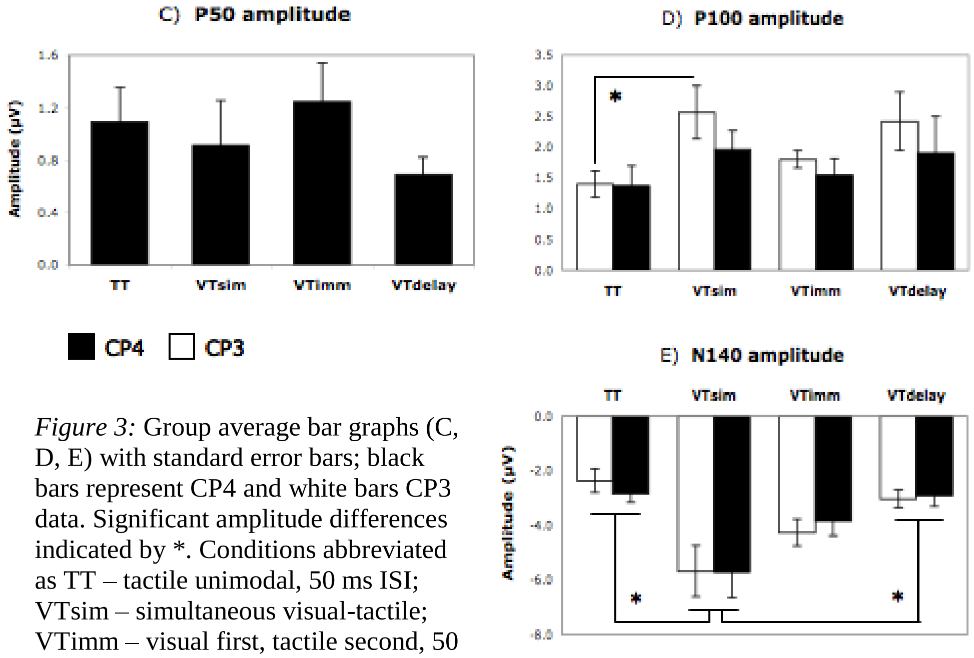

Figure 3: Group average bar graphs (C, D, E) with standard error bars; black bars represent CP4 and white bars CP3 data. Significant amplitude differences indicated by *. Conditions abbreviated as TT – tactile unimodal, 50 ms ISI; VTsim – simultaneous visual-tactile; VTimm – visual first, tactile second, 50 ms ISI; VTdelay – visual first, tactile second, 750 ms ISI.

3.5 Discussion

The lack of significant P50 modulation contradicts our original hypothesis that crossmodal stimulation facilitates early SI sensory processing. It appears as though the initial stages of somatosensory processing are primarily activated by incoming tactile information with little impact from vision, regardless of temporal congruency. Within the constructs of this experiment, evidence of visual priming of somatosensory regions occurs slightly later within the tactile ERP. In retrospect, considering the earliest visual ERP components typically present 80 to 100 ms post-stimulus (N80 and P100), it is not surprising that the addition of vision fails to modulate SI potential P50. However, fMRI (Dionne et al, 2010) and ERP (Dionne et al, in preparation) studies using a similar task paradigm and motor response requirements do report crossmodal modulation of tactile P50. As all conditions were presented in blocks, such early facilitation may be related to the expectation (rather than direct anatomical connections) of receiving visual information in addition to the vibratory stimulus. There is some suggestion (Adam, Hommel & Umilta, 2003) that a central cognitive set involving motor planning can enhance early sensory modulation associated with stimulus anticipation. Hence, the current absence of crossmodal P50 facilitation paired with poor group performance may be indicative of inadequate task comprehension. Although parameters slightly differ between the current and reported studies, it is unclear why anticipatory modulation of SI was not replicated.

Alternatively, significant modulation of P100 and N140 potentials suggest somatosensory regions of SII and associated frontal networks are sensitive to relevant vision when in conjunction with tactile stimulation. P100 is significantly facilitated above unimodal activation when simultaneous crossmodal stimulation is provided, however this facilitation is not different from 50 ms or 750 ms ISI conditions. In support of Ku and colleagues (2007) SII does appear sensitive to crossmodal manipulation, but the effect of temporal congruency is not yet clear. Amplitude measures of N140 follow our hypothesis that temporal crossmodal effects are graded within later potentials. N140 is clearly enhanced with simultaneous visual-tactile stimulation, while stimulus separation of 750 ms degrades activation to amplitude levels of unimodal stimulation. Although only a non-significant trend, the shorter 50 ms ISI condition produces N140 amplitudes smaller than in simultaneous stimulation, but greater than unimodal and long delay conditions. Prior work in our lab (Dionne et al, in preparation) has demonstrated that an ISI of 300 ms is sufficient to limit visual-tactile crossmodal effects on N140. Perhaps as Eimer and Forster (2003) suggest, N140 is responsive to the type and duration of attention. The current paradigm required blocked sustained attention (i.e. spatial attention was not cued for each trial), however when stimuli were presented in close temporal congruency, it is likely that subjects rapidly switched between each stimulus. Simultaneous presentation demanded only 500 ms of concentration and proved most excitatory, perhaps similar to the facilitatory effects of transient attention (Eimer & Forster, 2003). Crossmodal stimulation with temporal delay required longer attention duration, which may be less demanding or modulatory of somatosensory and frontal neural correlates. Frontal generators of N140 may be sensitive to temporal congruency if activation must increase to maintain stimulus representation while shifting between visual and tactile stimuli, a task only required during simultaneous stimulation.

Behavioural measures show no functional importance of modality or temporal presentation. Although a more sensitive measure of motor behaviour may have better represented performance modulation, perhaps conditions were not diverse enough to differentially impact performance of healthy young adults. Facilitation of somatosensory and frontal regions associated with crossmodal stimulation was evidently not to the extent required to improve functional sensorimotor efficiency.

In light of experimental limitations discovered throughout this pilot, slight changes were made for the execution of the following study. Of major concern was the inability of subjects to successfully complete the behavioural task. The response requirement to summate two stimuli is novel and challenging, and necessitates high levels of attention and vigilance. As testing conditions were long (40 minute duration) and without feedback it is possible subjects became bored and uninterested in successful task completion. It is difficult to mediate this, but data suggest performance was relatively consistent across testing and that fatigue was not limiting. It appears likely that subjects were not appropriately trained and thus did not fully comprehend the basis of a suitable response. To investigate the potential confounding influence of poor training, multiple additional behavioural pilot studies considered different aspects of task learning. Block-training subjects for 3 minutes (exact methodology as discussed above) with subsequent practice trials and feedback most improved performance on testing conditions. This method of repeating training-practice blocks significantly improved comprehension and performance of the task (paired t-test accuracy comparisons between block 1 & 2 (p = 0.03), and block 1 & 3 (p = 0.004); n = 4). This new regime accompanied by normalized behavioural measures allowed for more sensitive data collection across conditions within the subsequent study.

Stimulus presentation was slightly modified to maintain task consistency and limit potential variability. The simultaneous crossmodal condition presented stimulation for 500 ms; this was increased to 1000 ms in an attempt to equate attention requirements across conditions. Minor changes to testing conditions included longer intertrial intervals (ITI). N140 appears to have a role in re-orientating attention (Herrmann & Knight, 2001), and it is possible that preceding stimulation could be modulatory if delay periods are not long enough for proper dissociation and new attentional allocation. It is not expected that reported N140 effects within the pilot work were falsely modulated in this manner, as time between the second stimulus and new trial ranged between 2250 ms (long delay condition) and 3500 ms (simultaneous condition). However, as the pilot study presented 75 stimuli within each 5-minute condition, each trial was only 4 s with 750 ms, 1450 ms, or 2000 ms allotted to respond before the next trial began. The following study presented only 60 trials within each condition, allowing 5 s per trial and ITI/response window of 2450 ms or 2500 ms. Finally, based on the findings that simultaneous visual-tactile stimulation significantly modulated the somatosensory cortex more than the long delay condition, and that the immediate condition was not different from any other conditions, optimal crossmodal temporal congruency was deemed to be simultaneous presentation. Only tactile unimodal and visual-tactile simultaneous conditions were carried into the age-related study.

Chapter 4: *Attention and age-related components of visual-tactile modulation of somatosensory networks*

4.1 Rationale

Crossmodal studies within the healthy young population have revealed various levels of sensory modulation following attentional and perceptual manipulation. However, very limited investigation has considered the impact of healthy age-related cortical changes on crossmodal sensory processing. Most attention-related studies focusing on older adults present subjects with variations of relevant and distracting unimodal stimuli. Functional measures within these experiments centre upon cognition and working memory, and rarely consider translation into motor behaviour. Regardless of task demands or required output, widespread findings report general increased cortical responses with preferential activation of the frontal lobe and associated attentional networks with age. Additional work (Peiffer et al, 2009) has reported task-specific crossmodal inhibition (i.e. reduced neural activity in unexpected and interfering modalities) to follow different cortical patterns across healthy age groups. Peiffer and colleagues suggest shifted regional activation represent different task strategies utilized by older subjects. Older adults may choose to focus attention on specific situational traits instead of global stimulus processing, especially during overwhelming multimodal events. This functional cortical variation cannot be entirely explained by age-related structural and neurochemical changes, and likely involves degradation of sensory organs as well as re-balancing of bottom-up and top-down control. Although even ‘successfully’ aged adults present with decrements in frontal-sensory networks, they may not translate to behavioural impairments beyond increased perceptual thresholds. Such decrements are, however, evident within amplitude and latency shifts in unimodal ERP recordings of attention (Gehring & Knight, 2002) and task relevancy (Gazzaley et al, 2005b).

The ability to switch between attentional sets and successfully initiate new stimulus processing is dependent, in part, on the prefrontal cortex. In conjunction with thalamic regions, the PFC maintains a sensory filter, enhancing processing of task-relevant and suppressing task-irrelevant stimulus processing. The PFC is also important in mediating the amount of conscious attention and mental effort delegated to tasks and stimulation (Daffner et al, 2003). With age, through a combination of factors, the integrity of the prefrontal cortex begins to degrade. The ability of older adults to ignore and suppress cortical activity to distracting stimulation becomes limited (Gazzaley et al, 2005b). A compensatory system is able to restrict processing of irrelevant stimuli, but the delayed onset of this network causes a ‘load shift’ of cognitive processing. Cortical representations of distractor stimuli are formed and overwhelm the ability to successfully retain working memory of the desired stimuli. This delay can be observed within unimodal ERP recordings time-locked to task-irrelevant stimuli, and is thought to indicate inefficient sensory processing (Gazzaley et al, 2005b). An appropriate cognitive battery can assess behavioural consequences of PFC function and track age-related decline. Correlating these results to physiological measures provides insight into the importance of structural and chemical integrity to executive function. Many studies have related anatomy and performance decrements, and as such selected cognitive tests can be used to infer PFC decline (e.g. West, 2004 - Stroop; Barcelo & Knight, 2002 - WCST). This study will evaluate PFC integrity within older adults through Stroop, Wisconsin card sorting task (WCST) and sustained attention to response task (SART). The Stroop tasks measure the effect of interference between an appropriate response and a salient, automated response. Cognitive flexibility and efficient stimulus processing are inferred. WCST evaluates the ability to shift attentional demands based on changing rule sets; new sets must be engaged while old governing rules are disregarded. Working memory and response requirements must be continually recalled and updated. SART assesses sustained attention and inhibition of response; mindfulness and vigilance must be internally monitored to ensure task-appropriate responses. Each of these tests reliably report age-related differences within healthy control groups and are supported in their assessment of cognitive executive function.

Physiologically, fine motor control of force is also affected by natural age-related changes. Degeneration in muscle composition coupled with reduced motoneurons limits the ability to precisely control low amplitude force (Voelcker-Rehage, Stronge & Albert, 2006). The potential parallel decline of attentional resources could contribute to difficulties in tasks requiring controlled and maintained force production. Voelcker-Rehage and colleagues (2006) report age-related differences within healthy populations first become apparent in force control when subjects are challenged with secondary cognitive tasks. Although it is well known that dual-task performance becomes more challenging with age, most literature neglects motor behaviour subsequent to sensory processing. Attention to simultaneous crossmodal stimulation may prove too attentionally demanding for older subjects; even young adults may strategize by switching between both stimuli. Older subjects enacting the same technique may face more difficulty because of the associated PFC decline. However, if stimuli remain able to facilitate sensory processing in healthy older adults, a potential venue could open regarding rehabilitation of sensation and sensorimotor interaction commonly required in aged individuals after stroke or impairment.

This study expands crossmodal literature with contrasts of sensory integration within and between age groups. Visual and vibratory stimulation are delivered to subjects with the requirement to integrate stimuli into one sensory-guided motor response. P50, P100, N140 and P230 components of tactile stimulus-locked ERPs and visual ERP N1 are explored to gain a better understanding of somatosensory modulation following manipulations of modality and relevancy. As tactile attention is held constant across conditions, the impact visual relevancy may differentially affect each component based on stimulus saliency or focused concentration, depending on anatomical connections and neural correlates. This study approaches 3 main objectives through two experiments, 1) to determine how crossmodal interactions between visual and tactile stimulation modulate activity in the somatosensory cortex; 2) to determine how age-related components will affect simultaneous tactile-relevant visual-irrelevant sensory processing within the somatosensory cortex; and 3) to determine the behavioural implications of somatosensory modulation following visual-tactile stimulation. Firstly, following the pilot study and prior literature, it is predicted that task-relevant simultaneous visual-tactile stimulation will enhance somatosensory activation (increase tactile ERP amplitudes) in comparison to tactile unimodal stimulation. Secondly, considering age-related components, it is hypothesized that attention to task-irrelevant vision will impede tactile processing within older adults. This gating impairment will present as reduced somatosensory activation, below facilitation observed in relevant visual-tactile tasks. Younger adults are expected to successfully ignore visual distractions, presenting tactile ERPs similar to the tactile unimodal condition. It is further hypothesized that impaired sensory gating within older adults will correspond with slowed cognitive processing. Gazzaley and colleagues (2008) found older adults displayed a delayed ability to suppress irrelevant distraction, and although this study presented only variations in visual stimuli, we extend the findings to crossmodal stimulation. It is predicted that inappropriate attention to vision will delay the onset of peak amplitude tactile ERPs, beyond onset latencies during relevant tactile-tactile or visual-tactile tasks. Conversely, the experimental conditions are not expected to challenge attentional capacities of young adults to a point warranting observable ERP decrements. Within younger adults, peak amplitude latencies are predicted to remain consistent across conditions. Moreover, amplitude or latency modulation observed in older adults may correlate to performance on cognitive tasks measuring attention and response inhibition. Post-hoc division of subjects (Gazzaley et al, 2008) based on working memory performance found older adults who were functionally affected by distraction (reduced working memory) to present with the most prominent ERP deficiencies (delayed latency and reduced amplitude). Following, it is hypothesized in this study that poor PFC function on a small cognitive battery will parallel minimal somatosensory modulation. Low test scores are predicted to correlate with nominal difference scores between relevant visual-tactile and tactile-relevant visual-irrelevant conditions, suggesting that vision is processed to the same extent in both conditions and indicative of poor stimuli suppression. Lastly, considering behavioural measures, it is hypothesized that enhanced somatosensory activation elicited by relevant visual-tactile stimulation will translate to improved motor response accuracy across age. Poor sensory gating within older adults during tactile-relevant visual-irrelevant stimulation is predicted to degrade performance below relevant visual-tactile accuracy. Visual distraction is anticipated to not be sufficiently taxing on processing capacities of younger adults, and thus visual-irrelevant information is predicted to not negatively impact young adult performance.

4.2 Methods

Experimental procedures were similar those described within Chapter 3, only exceptions and modifications are discussed below.

4.2.1 Subjects

Behavioural and EEG data were collected from 11 young volunteers (mean age 26.4 yrs; range 21-34 yrs; 2 males) and 13 older adults (mean age 70.5 yrs; range 63-85 yrs; 7 female). Young adults were recruited from the University of Waterloo undergraduate and graduate student population. Older adults volunteered through the Waterloo Research in Aging Pool orchestrated by the University of Waterloo. All subjects had normal or corrected-to-normal vision, were in general good physical and mental health, and had never experienced a stroke. Each subject completed the Revised Waterloo Handedness Questionnaire (Bryden, 1977) (1 left-hand dominant young adult, 2 older adults) and a brief neurological history questionnaire. All subjects provided informed written consent and received $10/hr in appreciation for study participation. Experimental procedures were approved by the Office of Research Ethics at the University of Waterloo.

4.2.2 Experimental design

Prior to training and testing the response device was calibrated for older subjects by having each individual maximally squeeze the pressure-sensitive bulb. This ensured required responses were relative to individual ability. Younger subjects did not complete this calibration because of a ceiling effect on the amount of force that could be applied to the bulb. Subjects received 3 consecutive training and practice blocks to ensure force-amplitude associations and motor task requirements were learned and understood. After each 3-minute training session (40 trials) subjects practiced single modality trials (15 visual, 15 tactile; 6 blocks in total delivered in 3 sets). Practice trials followed the experimental protocol with the exception that only one stimulus was presented; subjects waited for the cue before squeezing the bulb at a force that matched the stimulus amplitude. After each block subjects were given visual and verbal feedback of performance accuracy. No practice was permitted on crossmodal or summation trials. Limited practice and the lack of feedback within testing conditions were chosen to limit the potential of automatic responses. As set amplitude levels were used for tactile and visual stimuli within testing, the absence of feedback was anticipated to avoid subjects responding with predetermined response forces and encourage accuracy and consistency across conditions. Minimal practice trials allowed the experimental concept to be learned while maintaining task difficulty. The order of visual and tactile block trials were randomized between subjects.

Subjects completed two conditions where both stimuli were relevant to the required response: visual-tactile simultaneous (VT) and sequential tactile-tactile (TT; ISI 50 ms). A third condition manipulated task-relevancy: tactile-tactile stimuli (ISI 50 ms) were presented at the same time as visual-visual stimuli (TTvv). Subjects were instructed to fixate centrally to experience the visual stimuli, but to covertly attend only to vibrotactile stimulation. Once cued subjects responded with a summation force of the two tactile amplitudes, ignoring all visual information. In an attempt to maintain attentional demands across conditions, VT stimuli were presented for a total of 1000 ms. All other stimuli were maintained at 500 ms, such that total time for stimulus delivery was always constant. To allow more time to refocus attention between trials only 60 sets of stimuli were presented throughout each 5-minute condition, allowing individual trials to be 5 s in duration. Each experimental condition was repeated twice in randomized order.

4.2.2.1 Experiment 2: methods specific to older adults

Session 1: Cognitive testing

Older adults initially completed a small battery of cognitive tests evaluating frontal lobe function and vibrotactile sensitivity. The sustained attention to response task, Wisconsin card sorting task and Stroop tasks are assumed indicators of PFC function, and target an individual's ability to attend, update, shift and inhibit responses. Working memory 3-back, and biothesiometer sensitivity tests were also conducted. All subjects completed tests as they are described in the order presented below. Test results were predicted to provide insight into age-related cortical effects on attentional modulation and to ensure that vibrotactile stimulation was appropriately experienced. Test stimuli (SART, 3-back) were generated using Gentask Editor (Compumedics, NeuroScan Stim^2, USA); WCST and Stroop were administered through pre-set programs within the same software. An affiliated response pad was used to collect motor behaviour requirements, stored for analysis within Compumedics (with the exception of the biothesiometer test). Session 2 electrophysiological testing took place within one week of session 1, as availability permitted.

Biothesiometer:

Evaluation of index finger sensitivity to vibrotactile stimulation, with and without distraction, was evaluated with a biothesiometer (Vibratron II; Physitemp Instruments Inc., USA). Seated with eyes closed, subjects placed their right index finger on a peg at a comfortable height and distance in front of them. Initially stationary, the vibrotactile stimulation was slowly increased until subjects verbally indicated they perceived sensation. Threshold detection was completed 3 to 5 times each in absence of, and with distraction. Additional continuous vibration was administered during distraction trials to the left index finger by the experimental vibrotactile apparatus (50 percent of lowest testing amplitude). Threshold values were recorded in amplitude excursion distance and converted into microns; significant outliers were disregarded and remaining values were averaged for vibration sensitivity measures.

SART:

SART is a measure of vigilance and attention and affected by fatigue and motivation, consequently it was the first computer-based test administered. A standard SART paradigm was used with a single digit visually presented for 250 ms followed by a 900 ms mask. Subjects were required to attend to each digit, responding with a button press for every number except for 3. Numeric digits 1 through 9 appeared in various font sizes as white upon a black backdrop. One block of 225 randomized trials, including 25 nogo (number 3) trials, was completed with subject instruction to respond as accurately as possible. Performance accuracy as percent correct nogo responses was the measure of interest.

Stroop:

The Stroop effect is a measure of selective attention, cognitive flexibility and processing speed. A computerized version of Stroop requiring manual responses was administered in 3 blocks. Within each block single trials presented one word (red, blue, green, yellow) on a black backdrop. In two blocks, words were written in either congruent (name matched ink) or incongruent (name did not match ink) colour font; in the third block all words were presented in white ink (neutral condition). Subjects were instructed to respond to each word by pressing a coloured button that matched either word name (word and neutral conditions) or colour ink (colour condition). Each block was completed once and consisted of 50 trials; each word was presented for 200 ms followed by a 1500 ms response window/ITI. Prior to testing subjects completed 20 practice trials to familiarize themselves with task requirements and the response pad.

Reaction time of the correct incongruent trials, presented as a percent of total trial reaction time, for both word and colour conditions was the behavioural measure of interest.

WCST:

WCST assesses the ability to shift attentional focus and is sensitive to frontal lobe dysfunction. A computerized version of this test displayed four constant key cards, to which the subject matched a randomly selected card based upon colour, symbol, or number. Subjects placed each card by pressing one of four response buttons paired to the individual key cards. After placement visual feedback informed the subject if the card was correctly or incorrectly assigned. After 10 correct matches the subject was unknowingly advanced to the next category. Colour, symbol and number categories were each completed once in randomized order, in two consecutive rounds. Card placement was self-paced, but the test discontinued at 8 minutes. Perseveration and total errors were behavioural measures of interest. Perseveration errors were defined as the repetition of an incorrect matching attempt, excluding response choices that may have matched multiple categories by chance.

3-Back

The working memory 3-back test was used to verify the potential confounding affect of poor stimulus retention during the experimental delay-to-cue (1 s). A standard n-back paradigm was used with a single lowercase English letter visually presented for 800 ms followed by a 1500 ms response window (2300 ms ITI). Subjects were required to attend and remember each letter, responding with a button press if every fourth letter matched (i.e. if, in a string of letters, the first and fourth matched, or second and fifth, etcetera). The top 20 most frequently used English letters were presented in isolation as a continuous sequence. One block of 60 letters, including 20 matching sets, was completed. Performance accuracy as total percent correct responses was the measure of interest.

4.2.3 Data acquisition

EEG was collected from 34 electrode sites using a 32 channel Quick-Cap (Neuroscan, Compumedics, USA) and 2 drop electrodes for horizontal ocular measurements. Additional ocular channels were included to monitor horizontal saccades and ensure that subjects overtly focused centrally during all conditions.

4.2.4 Data analyses

Behavioural data:

Behavioural data gathered from bulb squeeze responses during testing conditions were analyzed relative to each subject. Motor response accuracy was calculated within each condition as the average difference between response force and the summed force associated with the given stimuli. This difference score was normalized by expressing it as a percent of maximum force, individual to each older subject; a standard maximum force was used for younger subjects. To consider the impact of stimulation modality on accuracy, one-way ANOVAs within age were performed to observe behavioural modulation between conditions. Student’s t-tests were conducted on specific task comparisons within (VT versus TTvv) and across (TTvv) age groups.

Electrophysiological data:

ERPs of interest were time-locked to the onset of the tactile stimulus (first tactile stimulus in unimodal and visual-distractor conditions) between 200 ms pre-stimulus and 600 ms post-stimulus. Individual traces were bandpass filtered at 1 to 30 Hz and baseline corrected to activity within the pre-stimulus interval. ERPs were manually analyzed for raw voltage peak amplitude and latency measures at P50, P100, N140, and P230. Primary sites of analyses were chosen based on the topographical distribution of tactile ERPs. CP4 represents SI contralateral to, and thus initially processing, vibrotactile stimulation; all potentials were measured at this site, and here P50 and P100 were maximal. P100 as a bilateral potential was also maximal and measured at CP3 (representing SI ipsilateral to stimulation), N140 and P230 were also analyzed at this site. N140 and P230 were maximal at central and frontal sites, with the largest complex measured at FCZ. All individual potentials must have been clearly identifiable in at least 2 of the 3 conditions to be included within group analyses. If potentials were not evident within 1 condition, a value of 0 was assigned; if potentials were absent in 2 or 3 conditions, the subject's data was excluded from the specific potential and electrode site analysis. Post-hoc consideration of occipital activity during irrelevant visual stimulation required ERPs to be time-locked to the second stimulus within the TTvv condition. Based on grand average waveforms, N1 was most influenced by vision and maximal at O1 and O2 during the second stimulation of TTvv. Only N1 peak amplitude and latency were measured at this epoch. Unless specifically stated, TTvv comparisons refer to the first stimulus epoch.

One-way ANOVAs were applied to P50, P100, N140 and P230 peak amplitude and latency data to investigate the effect of condition on ERP amplitude. Specific hypotheses were tested with a-priori contrasts: crossmodal facilitation was considered between vision-present (VT and TTvv) and tactile-tactile conditions; task-relevancy was tested between visual-tactile simultaneous and visual-distractor conditions. Post-hoc Tukey tests were performed to detect any other task-related differences. Mixed two-way ANOVAs were completed on peak amplitude and latency of each potential to observe main and interaction effects of age and condition. Significant interactions were followed with Student's t-tests. To observe potential differential processing of visual distractors, N1 amplitude and latency were compared between first and second stimulus sets of TTvv within and across age with t-tests.

Population probabilities were examined with t-tests between young and older adult N140 and P230 peak amplitude and latency values at electrode sites CP3, CP4, and FCZ. T-tests were also conducted between groups on three difference scores (VT subtracted from TT; TTvv subtracted from TT; TTvv subtracted from VT). Calculation and comparisons of these difference scores allowed investigation of the extent of modulation following crossmodal and relevancy manipulation, rather than absolute ERP shifts permitted by the above ANOVAs. Topographical maps were constructed within Neuroscan software to illustrate mean qualitative data across all electrode sites for given time intervals within each age group.

4.2.4.1 Experiment 2: analyses specific to older adults

Session 1 cognitive test results were compared against published normative data to gain a general perspective of individual subject functional ability. Age-specific norms could not be found within computerized, manual response Stroop tests (verbal interference results for older adults, and computerized results for younger adults only), or for 3-back working memory test (2-back age-related data of total percent correct prior to first error included, Voelcker-Rehage, Stronge & Albert, 2006). Planned Pearson correlation coefficients between group test performance and session 2 behavioural difference scores were not completed because of high test performance and relatively low score variability.

4.3 Results

4.3.1 Experiment 1: young adults

EEG data recorded from two subjects was inadmissible due to excessive noise, or blinking and muscle artifacts, severely limiting the amount of useable data. Behavioural and electrophysiological data of the remaining 9 subjects are presented.

4.3.1.1 Behavioural data

Group data (Figure 4) of young adults suggests equal performance ability across all conditions. Because of a ceiling effect in potential bulb depression, individual subject response data were normalized against a standard maximum force. TT was completed with 6.00% average error; VT average error 6.33%; TTvv average error 6.28%.

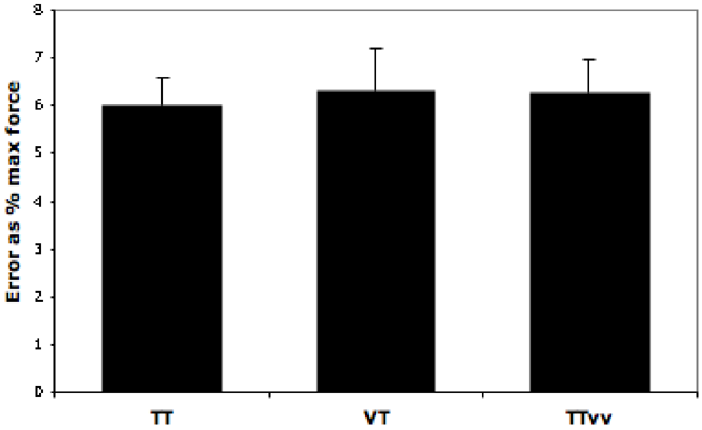

Figure 4: Young adult group response error as percent of standard maximum force. Standard error bars indicated. Conditions abbreviated as TT – tactile unimodal, 50 ms ISI; VT – simultaneous visual-tactile; TTvv – TT paired with concurrent visual-visual distraction.

4.3.4.2 Electrophysiological data

Peak amplitude:

Peak amplitude modulation was very consistent across each electrode site. Grand average waveforms are displayed in Figure 5 (A). Investigating condition with a one-way ANOVA at CP3 revealed a significant effect for N140 ($F_{2, 16} = 18.05$; $p < 0.0001$) and P230 ($F_{2, 16} = 5.43$; $p = 0.02$) amplitude, but not P100. Significant modality contrasts were also found at N140 ($F_{1, 16} = 36.10$; $p < 0.0001$) and P230 ($F_{1, 16} = 9.74$; $p = 0.007$). A post-hoc Tukey test on N140 peak amplitude found TT significantly less negative than VT and TTvv. VT and TTvv were not different from one another. Tukey's test on P230 revealed TT to be significantly less than VT, but not different from TTvv. In turn, VT was not significantly different from TTvv. Figure 5 group average bar graphs illustrate significant main and contrast effects at N140 (B) and P230 (C).

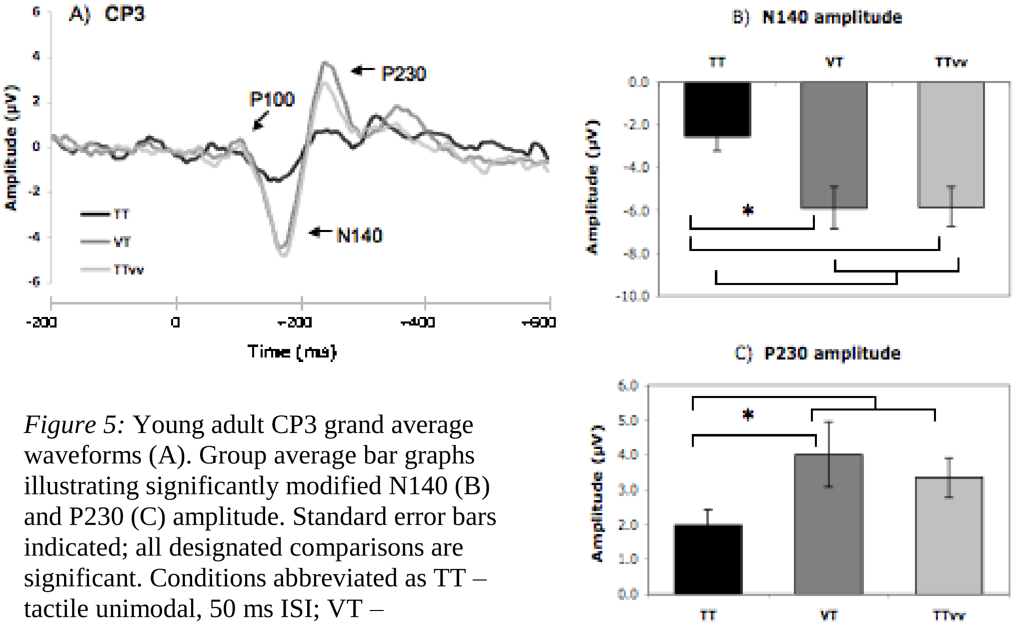

Figure 5: Young adult CP3 grand average waveforms (A). Group average bar graphs illustrating significantly modified N140 (B) and P230 (C) amplitude. Standard error bars indicated; all designated comparisons are significant. Conditions abbreviated as TT – tactile unimodal, 50 ms ISI; VT – simultaneous visual-tactile; TTvv – TT paired with concurrent visual-visual distraction.

Findings at CP4 reflect those at CP3. Grand average waveforms are displayed in Figure 6 (A). P50 and P100 were not modulated across condition at CP4, however both N140 and P230 showed a significant effect of condition ($F_{2, 16} = 17.38$, $p < 0.0001$; $F_{2, 16} = 4.56$, $p = 0.03$ respectively) and modality contrast ($F_{1, 16} = 34.74$, $p < 0.0001$; $F_{1, 16} = 7.27$, $p = 0.02$ respectively). Tukey's test on N140 found TT amplitude to be significantly less negative than VT and TTvv, but VT was not different from TTvv. At P230 Tukey's test showed TT amplitude significantly lower than VT, but not different from TTvv. Following CP3, VT and TTvv amplitudes were not different. Figure 6 group average bar graphs illustrate significant main and contrast effects at N140 (B) and P230 (C).

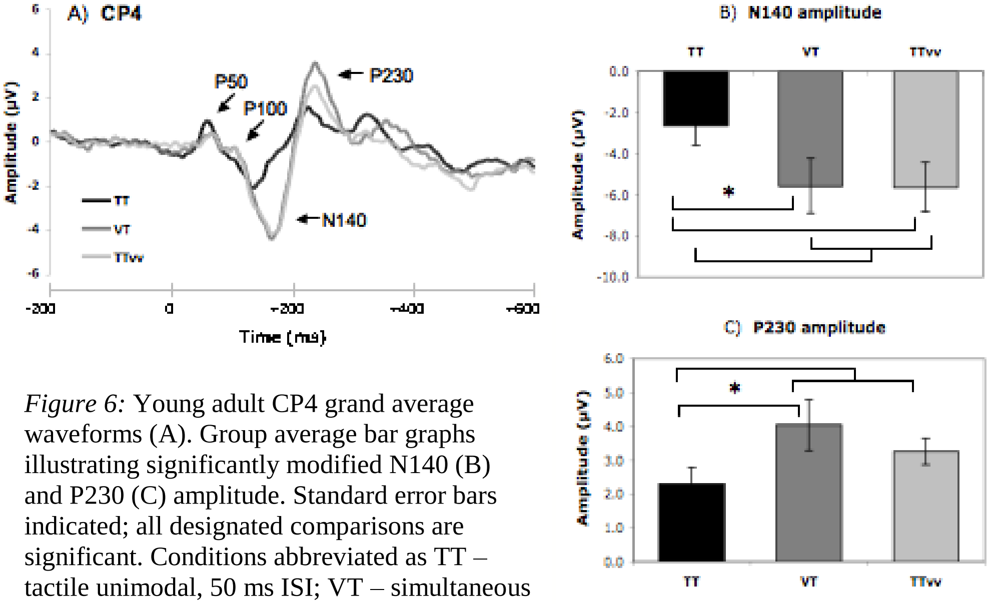

Figure 6: Young adult CP4 grand average waveforms (A). Group average bar graphs illustrating significantly modified N140 (B) and P230 (C) amplitude. Standard error bars indicated; all designated comparisons are significant. Conditions abbreviated as TT – tactile unimodal, 50 ms ISI; VT – simultaneous visual-tactile; TTvv – TT paired with concurrent visual-visual distraction.

One subject was not included within FCZ P230 analyses (n = 8, peak and latency) because the potential failed to clearly present within all three conditions. This subject was included for N140 analyses, as the negativity was visibly evident. Grand average waveforms (n = 9) are displayed in Figure 7 (A). A significant effect of condition and significant modality contrasts were found for both N140 ($F_{2, 16} = 11.98$, p = 0.0007; $F_{1, 16} = 23.88$, p = 0.0002 respectively) and P230 ($F_{2, 14} = 4.96$, p = 0.02; $F_{1, 14} = 6.96$, p = 0.02 respectively). As within CP3 and CP4, Tukey's test on N140 revealed TT amplitude to be significantly less negative than VT and TTvv, while the latter two were not different from one another. At P230 TT amplitude was significantly lower than VT, but not different from TTvv. Again, VT was not different from TTvv. Figure 7 group average bar graphs illustrate significant main and contrast effects at N140 (B) and P230 (C).

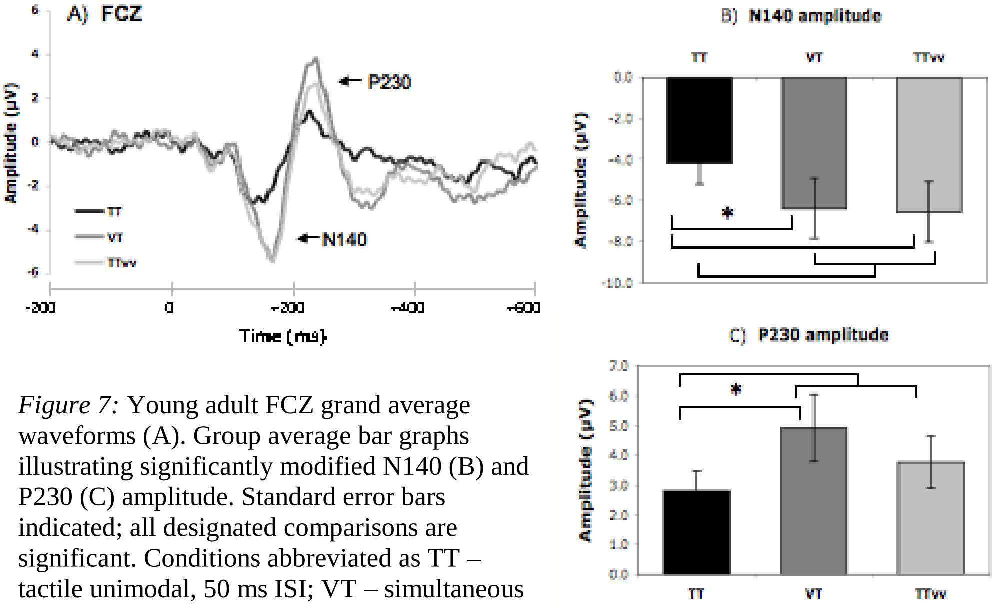

Figure 7: Young adult FCZ grand average waveforms (A). Group average bar graphs illustrating significantly modified N140 (B) and P230 (C) amplitude. Standard error bars indicated; all designated comparisons are significant. Conditions abbreviated as TT – tactile unimodal, 50 ms ISI; VT – simultaneous visual-tactile; TTvv – TT paired with concurrent visual-visual distraction.

Latency:

Condition was determined to have an effect on peak amplitude latency at CP4 (Figure 8 C). N140 was significantly modulated by condition ($F_{2, 16} = 21.67$; $p < 0.0001$) and modality (contrast $F_{1, 16} = 42.18$; $p < 0.0001$). Tukey's test on group latencies showed TT peak amplitude to occur significantly earlier than VT and the first stimulus of TTvv.

A t-test of N1 latency between the first and second TTvv stimuli sets showed significance at O2 (p = 0.04): N1 reached peak amplitude earlier following the second stimuli than the first. Figure 8 depicts O2 grand average waveforms for first and second stimuli sets within TTvv (A) and associated latency group average bar graph (B).

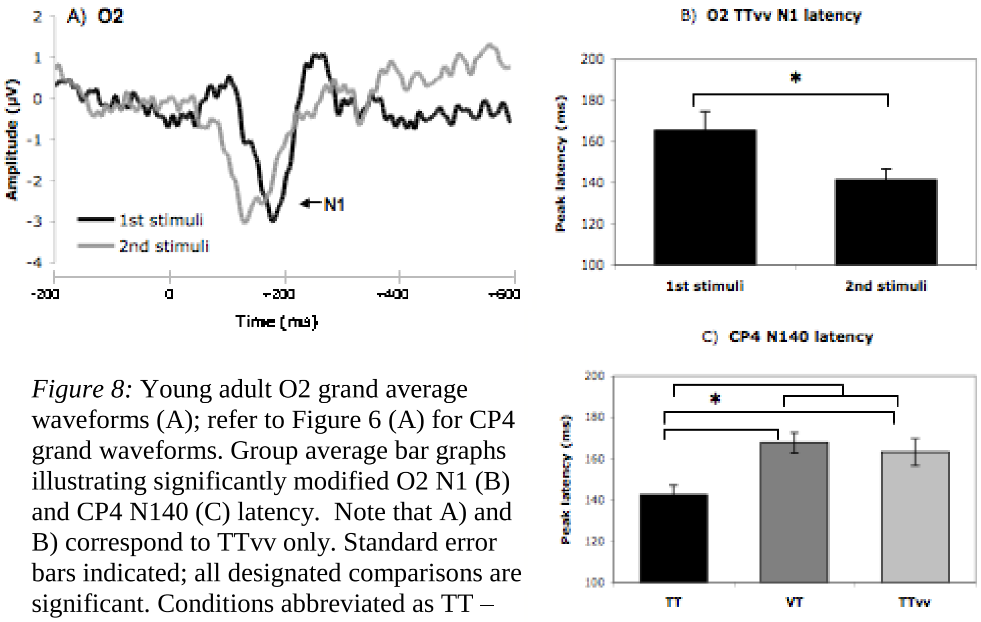

Figure 8: Young adult O2 grand average waveforms (A); refer to Figure 6 (A) for CP4 grand waveforms. Group average bar graphs illustrating significantly modified O2 N1 (B) and CP4 N140 (C) latency. Note that A) and B) correspond to TTvv only. Standard error bars indicated; all designated comparisons are significant. Conditions abbreviated as TT – tactile unimodal, 50 ms ISI; VT – simultaneous visual-tactile; TTvv – TT paired with concurrent visual-visual distraction.

4.3.2 Experiment 2: older adults

Thirteen subjects completed session 2, but four did not yield suitable EEG recordings. Three subjects had excessive noise in the EEG from blinking or muscle artifacts, severely limiting the amount of useable data. EEG from one subject was entirely absent of any tactile ERP components across all conditions. Only cognitive and behavioural data sets with corresponding EEG data are presented within behavioural results: 9 cognitive and 7 behavioural data sets. Two additional subjects presented with usable EEG data, but one failed to respond appropriately during the experimental tasks (squeezed the bulb immediately following stimulation instead of waiting for cue), and technological difficulties prevented the use of the remaining set.

4.3.2.1 Behavioural data

Session 1: Cognitive data

Table 1 reports a complete list of subject information and individual cognitive test results. All but one subject fell below normative data on at least one test, however no significant performance trends were found. Low variability between subjects permitted limited benefit to PFC-ERP correlations therefore these are not presented.

sex (hand)	**age**	**biothesio-meter**	**bio. w/ distraction**	**SART**	**Stroop word**	**Stroop colour**	**WCST**	**3-back**
normative data		51-66 yrs: 1.05[1] >65 yrs: 1.22[1]		64 yrs: 68[2]	65-75 yrs: 54[3] (verbal interference score)		66 yrs: 0.6[4]	70 yrs 2-back: 58[5]
M (r)	83	1.3*	1.4*	73.1	37.2	38.7	1(9)	72
M (r)	78	0.8	0.9	26.9*	-	-	0(16)	77
F (r)	64	0.7	0.8	80.8	33.0	42.7	3(30)*	73
M (r)	68	1.0	1.0	61.5*	33.8	0 correct	0(31)	72
F (r)	66	0.7	0.9	76.9	34.8	39.3	5(22)*	80
M (r)	66	1.8*	1.7*	69.2	35.3	38.8	0(18)	83
F (l)	68	0.4	0.6	73.1	28.2	43.16	2(22)*	78
F (l)	71	0.4	0.6	53.9*	45.1	50.5	1(25)	80
F (r)	68	0.6	0.5	96.2	34.3	31.8	0(9)	63

Table 1: Subject information and cognitive scores; * indicates performance below age-based normative score. Stroop was not completed in one colour-blind subject. Age – years; biothesiometer – microns; SART – % correct nogo trials; Stroop – correct incongruent RT as % total RT; WCST – preservation errors (total errors); 3-back – % correct responses. [1](Arezzo, 1984) [2](Buxbaum et al, 2004) [3](Van der Elst et al, 2006 – interference scores calculated for verbal Stroop; no published norms for computerized manual response testing) [4](Barcelo & Knight, 2002) [5](Voelcker-Rehage, Stronge & Albert, 2006 – total % correct; no published norms for 3-back within older adults)

Session 2: Behavioural data

Despite a trend for worse performance during tactile stimulation with visual distraction (TTvv), no significant differences in force accuracy were found between conditions ($F_{2,12} = 2.52$; p = 0.1). Normalized as a percent of maximum force (Figure 9), TT was completed with 7.03% average error, VT 7.22%, and TTvv 8.30%.

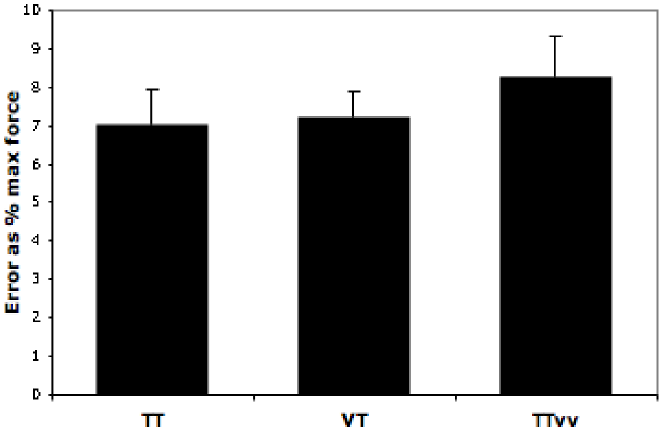

Figure 9: Older adult response error normalized as percent of individual subject maximum force. Standard error bars indicated. Conditions abbreviated as TT – tactile unimodal, 50 ms ISI; VT – simultaneous visual-tactile; TTvv – TT paired with concurrent visual-visual distraction.

4.3.2.2 Electrophysiological data

Peak amplitude:

One-way ANOVAs considering peak amplitude changes across condition revealed significant differences at CP3, CP4 and FCZ. At electrode site CP3, a significant effect of condition ($F_{2,16} = 4.01$; $p = 0.04$) and significant relevancy contrast between VT and TTvv ($F_{1,16} = 4.64$; $p = 0.05$) was observed for P100 amplitude. A post-hoc Tukey test found TT peak amplitude to be significantly less than TTvv, but not different from VT. A significant effect of condition ($F_{2,16} = 12.54$; $p = 0.0005$) and significant modality contrast between TT and VT, TTvv ($F_{1,16} = 23.42$; $p = 0.0002$) was found for N140 peak amplitude. Tukey's test showed TT amplitude to be significantly less negative than VT and TTvv. P230 peak amplitude measures displayed a significant effect of condition ($F_{2,16} = 14.42$; $p = 0.0003$) and significant relevancy and modality contrasts ($F_{1,16} = 5.28$, $p = 0.04$; $F_{1,16} = 23.55$, $p = 0.0002$ respectively). Tukey's test revealed TT amplitude to be significantly less than VT and TTvv. CP3 grand average waveforms are displayed in Figure 10 (A). Figure 10 group average bar graphs illustrate significant main and contrast effects at P100 (B), N140 (C) and P230 (D).

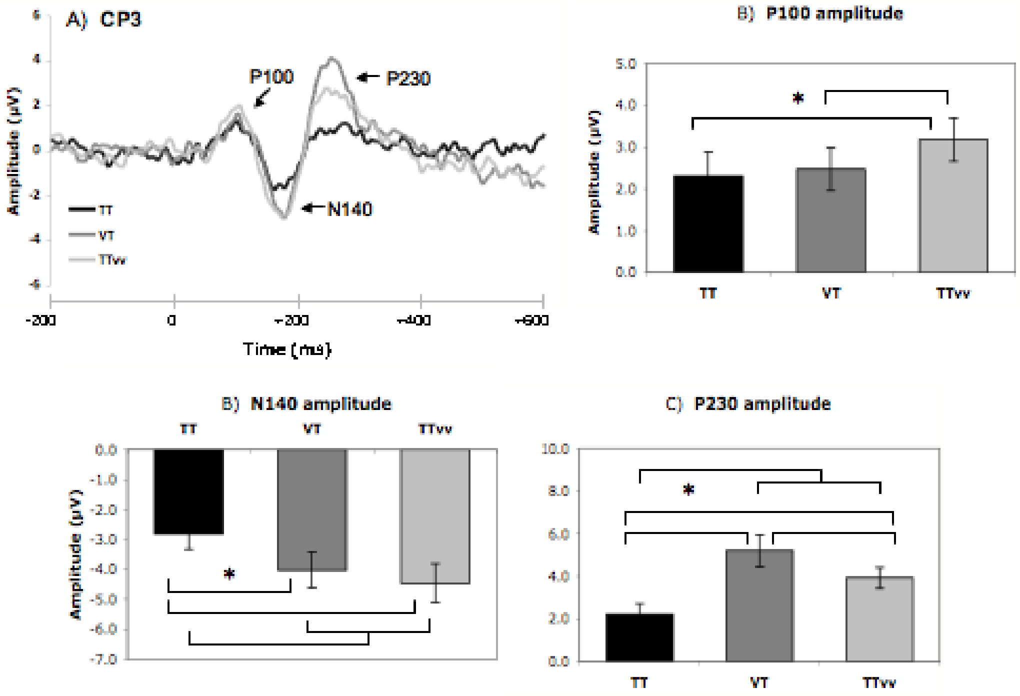

Figure 10: Older adult CP3 grand average waveforms (A). Group average bar graphs illustrating significantly modified P100 (B), N140 (C) and P230 (D) amplitude. Standard error bars indicated; all designated comparisons are significant. Conditions abbreviated as TT – tactile unimodal, 50 ms ISI; VT – simultaneous visual-tactile; TTvv – TT paired with concurrent visual-visual distraction.

There was no significant modulation of P50 amplitude at electrode site CP4. A significant relevancy contrast ($F_{1, 16} = 5.08$; $p = 0.04$) was found for P100 peak amplitude. An almost significant ($F_{2, 16} = 3.48$; $p = 0.055$) P100 trend of condition revealed TTvv amplitude higher than VT and TT. The main effect of condition was significant for N140 amplitude ($F_{2, 16} = 10.49$; $p = 0.001$). N140 modality contrast was also significant ($F_{1, 16} = 20.98$; $p = 0.0003$). Tukey’s test showed TT to have significantly less negative amplitude than VT and TTvv. P230 peak amplitudes showed a significant effect of condition ($F_{2, 16} = 11.35$; $p = 0.0009$) and significant relevancy and modality contrasts ($F_{1,16} = 5.58$, $p = 0.03$; $F_{1,16} = 17.11$, $p = 0.0008$ respectively). Tukey's test revealed TT amplitude to be significantly lower than, but not different from TTvv. CP4 grand average waveforms are displayed in Figure 11 (A). Figure 11 group average bar graphs illustrate significant main and contrast effects at P100 (B), N140 (C) and P230 (D).

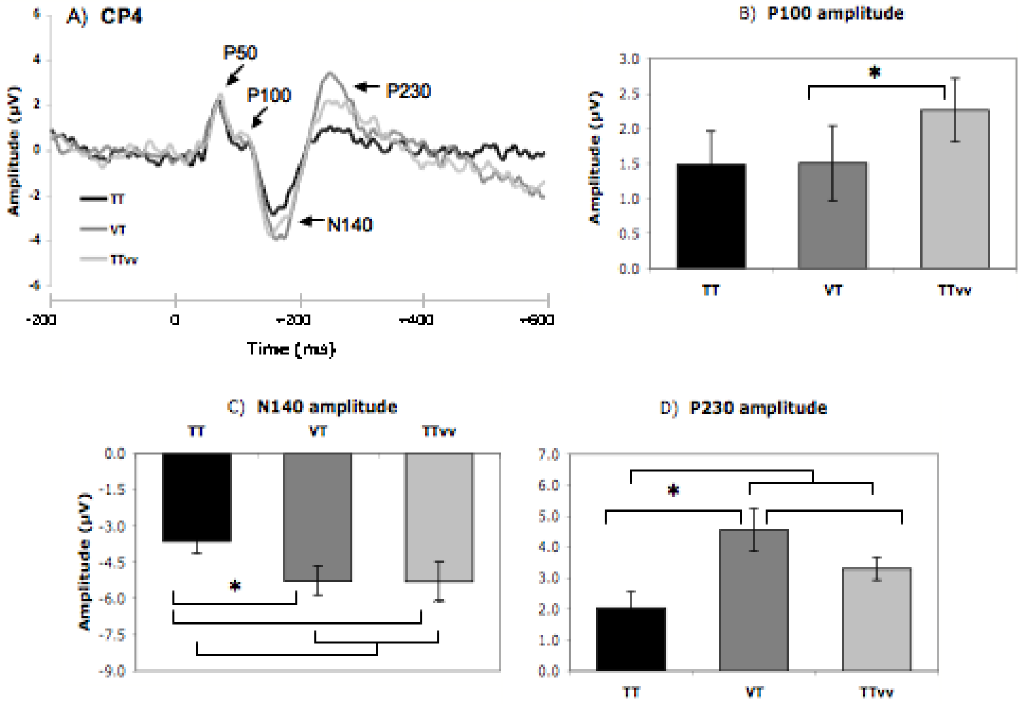

Figure 11: Older adult CP4 grand average waveforms (A). Group average bar graphs illustrating significantly modified P100 (B), N140 (C) and P230 (D) amplitude. Standard error bars indicated; all designated comparisons are significant. Conditions abbreviated as TT – tactile unimodal, 50 ms ISI; VT – simultaneous visual-tactile; TTvv – TT paired with concurrent visual-visual distraction.

N140 amplitude was not modulated at electrode site FCZ. A significant effect of condition ($F_{2,16} = 15.09$; $p = 0.0002$) and significant relevancy and modality contrasts ($F_{1,16} = 4.40$, $p = 0.05$; $F_{1,16} = 25.77$, $p = 0.0001$ respectively) were found for P230 amplitudes. Tukey's test revealed TT amplitude to be significantly lower than VT and TTvv. FCZ grand average waveforms (A) and associated N140 amplitude bar graph (B) are illustrated in Figure 12.

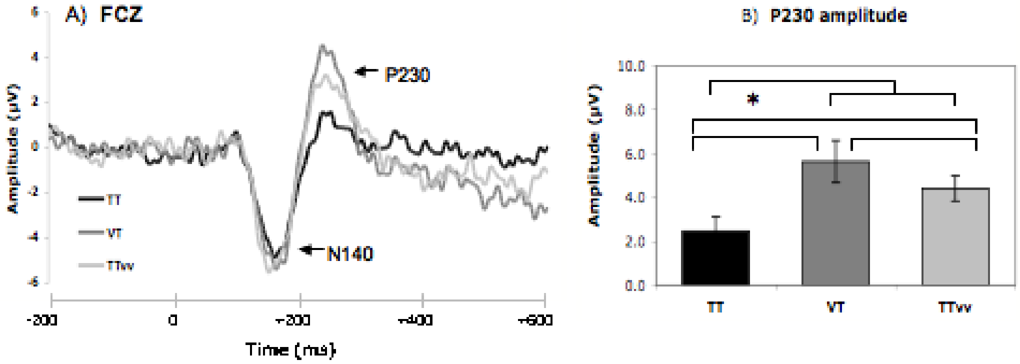

Figure 12: Older adult FCZ grand average waveforms (A). Group average bar graphs illustrating significantly modified N140 amplitude (B). Standard error bars indicated; all designated comparisons are significant. Conditions abbreviated as TT – tactile unimodal, 50 ms ISI; VT – simultaneous visual-tactile; TTvv – TT paired with concurrent visual-visual distraction.

Occipital site O1 was significantly modulated within TTvv stimulation. A t-test contrasting N1 amplitude following the first and second sets of stimuli found the potential less negative following the second stimulation than the first ($p = 0.05$). Figure 13 depicts O1 grand average waveforms for first and second stimuli sets within TTvv (A) and associated amplitude group average bar graph (B).

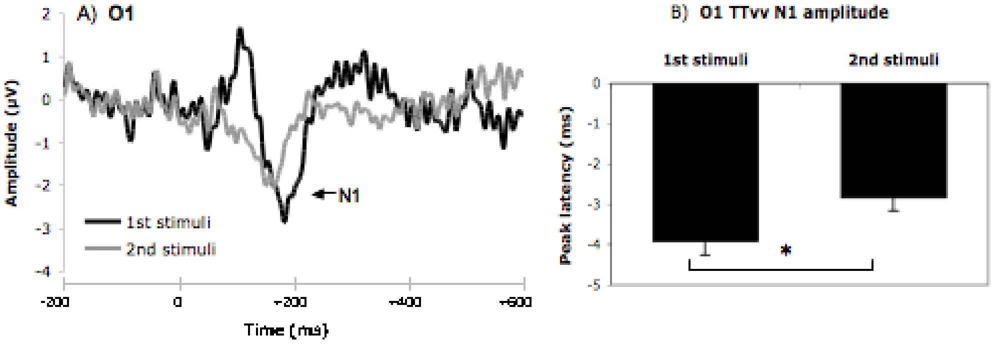

Figure 13: Older adult O1 grand average waveforms (A). Group average bar graphs illustrating significantly modified N1 amplitude (B). Standard error bars indicated; all designated comparisons are significant. Conditions abbreviated as TT – tactile unimodal, 50 ms ISI; VT – simultaneous visual-tactile; TTvv – TT paired with concurrent visual-visual distraction.

Latency:

One-way ANOVAs determining the effect of condition on peak amplitude latency revealed significance at CP3 and FCZ. At electrode site CP3 (Figure 14 A) only one relevancy contrast was found significant at N140 ($F_{1, 16} = 5.74$; $p = 0.03$). The main effect of condition was not significant for latencies at any potential. Latencies were similarly absent of significant modulation at site CP4. At electrode site FCZ (Figure 14 B), latencies were not modulated across condition at N140, but significance was found at P230 for condition ($F_{2, 16} = 3.70$; $p = 0.05$) and relevancy contrast ($F_{1, 16} = 4.77$; $p = 0.04$). Tukey's test did not reveal condition differences, although trends suggest TT N140 latency is later than TTvv, but not different from VT.

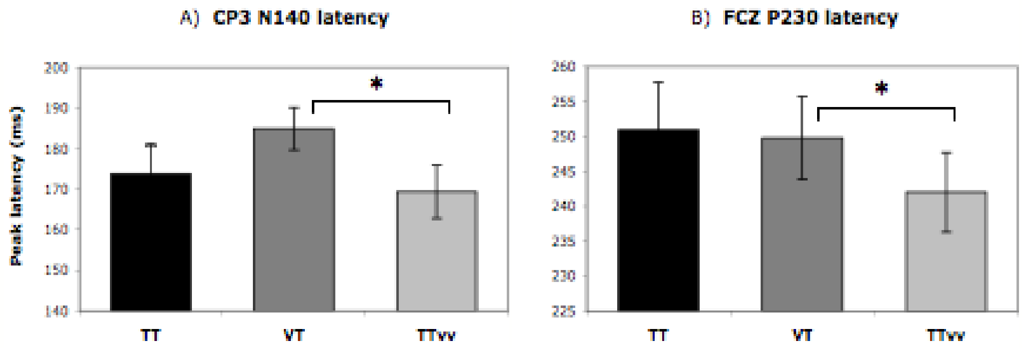

Figure 14: Group average latency of CP3 N140 (A) and FCZ P230 (B) peak latencies. Refer to Figure 10 and 12 for older adult CP3 and FCZ grand average waveforms. Standard error bars indicated; all designated comparisons are significant. Conditions abbreviated as TT – tactile unimodal, 50 ms ISI; VT – simultaneous visual-tactile; TTvv – TT paired with concurrent visual-visual distraction.

4.3.3 Contrasting data across age

To further consider the effects of healthy age-related cognitive decline, statistical analyses were conducted between experiments 1 and 2. Tracking somatosensory processing between healthy young and older adults will provide insight into this progression, and may prove useful in determining if low level priming or attentional components can be used to train motor behaviour.

4.3.3.1 Behavioural data

Error in response accuracy did not significantly differ between age groups during TT or VT conditions (Figure 15). However a one-tailed t-test found older adults performed with significantly less accuracy ($p = 0.05$) than younger adults when performance was paired with visual distraction.

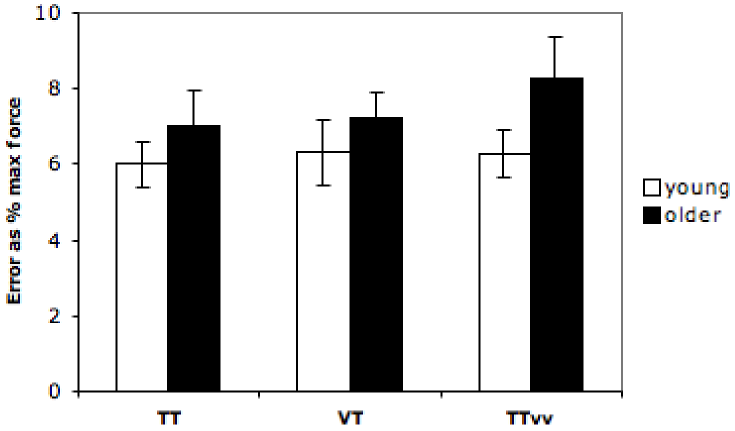

Figure 15: Performance error of young (white) and older (black) subjects; standard bars indicated. Significant accuracy differences indicated by *. Conditions abbreviated as TT – tactile unimodal, 50 ms ISI; VT – simultaneous visual-tactile; TTvv – TT paired with concurrent visual-visual distraction.

4.3.3.2 Electrophysiological data

Peak amplitude:

Mixed ANOVAs considering peak amplitude modulation with main effects of age and condition revealed significant interaction only at CP3 N140 ($F_{2, 32} = 4.83$; $p = 0.01$). Student’s t-tests to determine how peak amplitude within condition differed with age revealed no significant results, but suggest that crossmodal conditions drove the interaction (i.e. older adults presented with slightly more positive amplitudes at N140 during crossmodal stimulation than young adults, while measures were very similar between groups in the unimodal condition) (TT $p = 0.7$; VT $p = 0.1$; TTvv $p = 0.2$). Main effects of age were found significant at CP3 P100 ($F_{1, 30} = 7.28$; $p = 0.02$), and CP4 P50 ($F_{1, 24} = 4.67$; $p = 0.05$) and P100 ($F_{1, 27} = 6.15$; $p = 0.02$), all demonstrating higher ERP amplitudes in older than younger subjects. Main effects of condition were significant at CP3 P230 ($F_{2, 32} = 18.08$; $p < 0.0001$), CP4 N140 and P230 ($F_{2, 32} = 27.83$, $p < 0.0001$; $F_{2, 32} = 14.81$, $p < 0.0001$ respectively), and FCZ N140 ($F_{2, 32} = 6.12$; $p = 0.006$) and P230 ($F_{2, 30} = 17.90$; $p < 0.0001$). Grand average waveforms of both groups are superimposed in Figure 16.

Student's two-tailed t-tests contrasting N140 and P230 peak amplitude across age within difference waveforms supported the ANOVAs with significance only at N140. The difference between peak amplitude values during TT and VT conditions (TT subtracted from VT) was significantly different between age groups at CP3 ($p = 0.02$) and FCZ ($p = 0.04$). Comparing these results to waveform traces illustrates older adults to have more similar N140 peak amplitudes during TT and VT conditions; young adults present with more negative amplitudes during VT than TT, indicating a stronger effect of crossmodal modulation. A parallel non-significant trend also presented for peak amplitude differences across age in TTvv-TT difference waveforms. No significant differences were found comparing age groups between specific conditions. These findings suggest both young and older adult ERPs follow similar N140 and P230 modulation patterns during relevancy, but not crossmodal, manipulations.

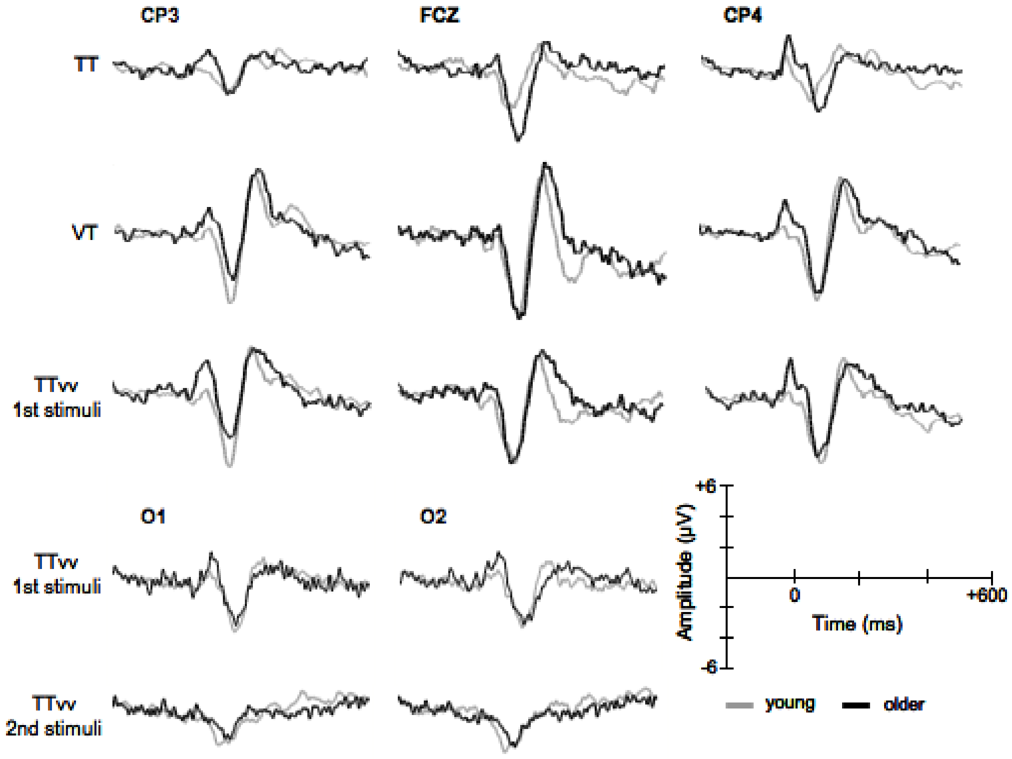

Figure 16: Grand average waveforms of young (grey) and older (black) adults. VT-TT difference waveforms between age groups are significantly different at CP3 and FCZ: older adults are less modulated by the addition of relevant visual stimulation than young adults. Conditions abbreviated as TT – tactile unimodal, 50 ms ISI; VT – simultaneous visual-tactile; TTvv – TT paired with concurrent visual-visual distraction.

Latency:

Mixed ANOVAs to determine significant interactions between age and condition on peak amplitude latencies revealed an effect at CP4 N140 ($F_{2,\,32} = 9.56$; $p = 0.0006$). Follow-up t-tests found significance at TT ($p = 0.004$) but not VT or TTvv, revealing older adults present with delayed latencies (170 ms) beyond young adults (142 ms) only within the unimodal condition. T-tests within TTvv stimulation found O2 N1 onset within younger adults to occur significantly earlier (142 ms) than in older adults (167 ms) following the second set of stimuli ($p = 0.03$).

Difference score t-tests between TT-VT ($p = 0.001$) and TT-TTvv ($p = 0.01$) at N140 were both significant. In addition, P230 VT comparisons were significant at FCZ (p = 0.02) and almost significant at CP4 (p = 0.056), suggesting that older adult P230 amplitude peaked slightly later than in young adults. P230 TT-TTvv difference score was also found significant at CP3 (p = 0.05). These difference scores allow specific comparisons of the amount of modulation associated with modality or relevancy manipulation. N140 and P230 scores suggest there is less of a latency shift between unimodal and visual distractor conditions within older adults.

Topographical maps:

Topographical maps are included to provide qualitative support for activation regions of each tactile ERP component. Later potentials, N140 and P230 especially, are likely sourced by multiple generators, and as such it is difficult to conclusively interpret cortical distribution from these maps. EEG data from all recorded sites, averaged across selected time epochs, were collapsed into images illustrating general activation ranges. Time windows were selected based on group average peak amplitude latencies, and are thus slightly different between age groups: young adults P50 54-64 ms, P100 100-110 ms, N140 160-180 ms, P230 224-244 ms; older adults P50 64-74 ms, P100 100-110 ms, N140 160-180 ms, P230 240-260 ms. P50 (Figure 17 A) representing contralateral SI activation appears minimal within young adults, but is clearly evident in older adults. P100 (Figure 17 B) is similarly largely absent within young adults, but appears most localized to somatosensory and parietal regions within older adults. The limited distribution of early potentials in younger subjects may be indicative of a general baseline shift or simply be relative to early disinhibition in older subjects. Cortical activity corresponding to N140 (Figure 17 C) is widespread but appears focused within contralateral prefrontal regions and highest during VT for both age groups. P230 (Figure 17 D) also correlates with widespread activity, with ipsilateral fronto-parietal activation especially high in both groups during VT.

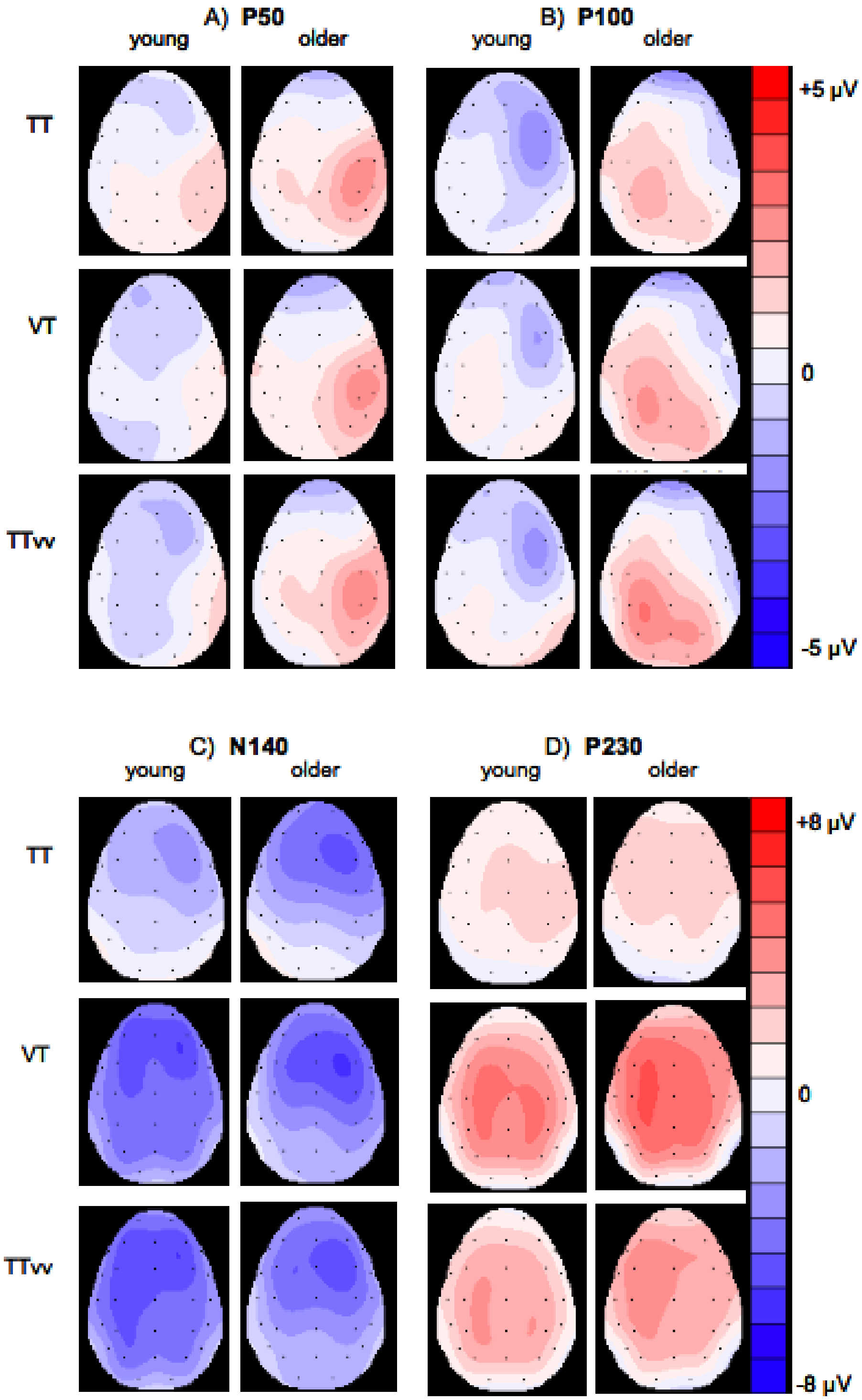

Figure 17: 32 electrode sites averaged across P50 (A), P100 (B), N140 (C) and P230 (D) epochs to subjectively represent neural correlates underlying each potential. Red signifies positive, blue negative activation; note different scale ranges for early (+/-5 µV) and late (+/-8 µV) potentials. Conditions abbreviated as TT – tactile unimodal, 50 ms ISI; VT – simultaneous visual-tactile; TTvv – TT paired with concurrent visual-visual distraction.

4.4 Discussion

This thesis addressed three main objectives in an attempt to expand crossmodal research to include the effects of healthy age-related cortical changes. Of primary consequence was the ability for visual-tactile stimulation to facilitate somatosensory activity, above that of unimodal tactile stimulation. This effect was consistent across age. Secondly, we considered the impact of aging on stimulus processing countered with irrelevant crossmodal distraction. Interestingly, both young and older subjects processed task-relevant stimuli with similar distribution. However, when ERPs were time-locked to the irrelevant stimuli, associated decrements were observed within older adults. Lastly, potential functional significance of somatosensory modulation was explored by the requirement of a sensory-guided movement in response to relevant stimulation. Although young adults performed equally regardless of modality or relevancy, older subjects tended to lose accuracy when faced with distraction. These findings are discussed in detail below.

As predicted, the presence of simultaneous task-relevant visual and tactile stimulation facilitated somatosensory and associated networks. This effect was consistent across age and most evident within later post-perceptual tactile ERP amplitudes. Cortical enhancement of such components enables more efficient sensory processing, and more information to be extracted from stimuli for related sensory-guided activation. Within healthy young adults, N140 peaked earlier following tactile unimodal stimulation than relevant crossmodal stimulation. This shift in latency was most apparent at electrode sites contralateral to tactile stimulation and is perhaps related to processing efficiency. Younger adults may have found the unimodal condition easiest to complete because direct comparisons between stimuli could aid responses. The addition of a second modality and the requirement to judge stimuli simultaneously may have required more focused attention, prompting a slight processing delay in SII-frontal networks. In comparison, older adults did not present with any latency shifts from unimodal to crossmodal stimulation. Perhaps the experimental task proved challenging enough to require extra focal attention at all levels, or perhaps latencies were indicative of globally slowed cognitive processing. Although not temporally sensitive, an fMRI study by Rissman, Gazzaley and D'Esposito (2009) reports that activation and behavioural patterns of young adults begin to mimic those of aged adults when faced with high cognitive load. It's possible within the current study that while crossmodal stimulation was not behaviourally taxing for younger adults, it was sufficient to slightly increase cognitive effort, requiring additional attentional demand and top-down contribution. Post-perceptual networks of somatosensory association and frontal regions were similarly affected across age, although younger adults showed greater modality modulation of N140 (augmented with crossmodal stimulation). This again may be indicative that older subjects were generally more attentive and demanding of cortical regions within both unimodal and relevant crossmodal conditions.

Overall across age, early P50 and P100 components were not modulated between relevant unimodal and relevant crossmodal stimulation. As in the pilot study, tactile components within SI and SII were likely unaffected by the presence of vision because processing speed was too early to accommodate visual input (Driver & Noesselt, 2008). Perhaps because of general disinhibition associated with healthy aging, older subjects presented with increased P50 and P100 amplitudes compared to the younger group. Typically with healthy aging an increased amount of background noise is processed; the amplification of early stimulus-dependent potentials increases the signal-to-noise ratio and permits relatively more sensitive sensory processing (Hillyard, Vogel & Luck, 1998).

Task-relevancy manipulations produced different results than expected. The presence of a salient visual stimulus facilitated tactile ERPs above unimodal stimulation within both age groups. Younger adults were especially not affected by crossmodal relevancy, as all amplitudes were statistically facilitated to the same extent in visual-relevant and visual-irrelevant conditions. This was contrary to our original hypothesis that younger adults would successfully ignore vision, allowing tactile ERPs to reflect unimodal instead of crossmodal levels. However, given that performance ability was unchanged across tasks, it is quite possible that the conditions did not adequately tax attentional capacities of healthy young adults.

Neural correlates of the P100 component were amplified above unimodal presentation following irrelevant visual stimulation within older adults. Non-significant trends also revealed visual-irrelevant P100 amplitudes higher than those measured within relevant crossmodal stimulation. This modulation of the secondary somatosensory cortex was opposite than predicted, but may be representative of additional concentration on vibrotactile stimulation in the presence of visual distraction. Preuschhof and colleagues (2010) suggest that within dual stimulation paradigms, SII modulation is dependent on the amount of conscious attention and mental comparisons made between a current stimulus and average stimulation amplitude. Integrating current and prior information can help encode degraded or noisy stimuli, a method that may have strengthened tactile information experienced under visual distraction. Perhaps increasing task difficulty with irrelevant stimuli prompted older subjects to use an altered behavioural strategy revolving around relative amplitude differences instead of absolute value summations.

Later components within grand average waveforms of crossmodal conditions were similar across age, however reduced variability between subjects enabled statistical significance within the older adult group. Specific to younger adults, N140 amplitude was facilitated above unimodal stimulation but not different from relevant crossmodal stimulation. This facilitation was significant at electrode sites over somatosensory cortex, but absent at frontal site FCZ. N140 amplitudes at FCZ were very similar across all conditions in older adults. Within the older group, separate from young adults, N140 latency displayed a relevancy effect at CP3 ipsilateral to tactile stimulation. With visual distraction, N140 peaked earlier than with relevant crossmodal stimuli; this was also the case for P230 latency at FCZ in older adults. These results seem counterintuitive given the predicted effect of distraction on tactile latencies, however they may suggest that older adults were able to process post-perceptual tactile stimuli equally beyond initial visual saliency. As N140 and P230 peaks were not different from peaks following tactile unimodal stimulation, age-related relevancy effects may be most obvious within the irrelevant modality itself (i.e. within visual and not tactile ERPs).

Particularly within the older group, P230 modulation was most sensitive to task relevancy. Neural correlates of P230 responded in graded fashion to modality and relevancy: unimodal activation was smaller than visual-irrelevant excitation, which in turn was smaller (although sometimes non-significantly) than facilitation following simultaneous relevant crossmodal stimulation. P230 is a relatively unreported inflection within tactile ERPs. Following the progression of sensory information, it is assumed frontal and sensory association networks source this peak, however generators and neural correlates are unknown. A similar frontal peak (236 ms onset) recorded during visual stimulation was reportedly modulated by the presence of task-irrelevant sound (Fiebelkorn, Foxe & Molholm, 2010). Fiebelkorn and colleagues considered this modulation (but not component) partially representative of ‘stimulus-driven spread of attention’ accompanied by a bias to process stimuli as a whole object, even when presented in separate features. P230 also matches temporal reports (220-250 ms post-stimulus) of the progression of attention to task-irrelevant visual features (Schoenfeld et al, 2003). No literature has specifically linked P230 to somatosensory processing, however based on current findings later tactile ERP components may be representative of attention and task-dependent selection of stimuli beyond initial perceptual processing.

With the exception of the frontal N140 component, tactile ERPs were modulated in very similar patterns across age. This is perhaps because volunteers for the older subject group were unknowingly selected from a relatively homogeneous sample experiencing few adverse effects of aging. The expected degradation of PFC connections and inability to suppress irrelevant stimulation does not appear to have advanced to a stage warranting functional impairment in these subjects. Although suppression decrements within older adults do not always translate to universal decline in cognitive performance (Gazzaley et al, 2005b), observable shifts in neural activity may not only be characteristic of low functional abilities (Zanto & Gazzaley, 2009). Considering unimodal studies, sufficient suppression deficits correlate to poor working memory ability, while older adults with high working memory performance present with ERP traces more similar to those of young adults (Gazzaley et al, 2005b). Although working memory and sensorimotor performance entail quite different task requirements, the general finding of similar task-relevant ERP waveforms between healthy aged and young adults is consistent. Perhaps changes in cortical activity patterns following distraction are more easily evident when dissociating between relevant and irrelevant sensory ERPs; healthy older adults maintain task-relevant demands, but falter specifically with irrelevant stimulation.

Behaviourally, visual distraction did not impact motor performance of younger adults. Contrary to expectation, facilitation of somatosensory networks following relevant crossmodal stimulation did not translate to improved motor performance in either age group. It is likely that all experimental conditions were well within the bounds of the attentional capacities of healthy young adults. General performance accuracy tended to be slightly worse in older subjects, however this could be due to age-related limitations in fine motor control of force (Voelcker-Rehage, Stronge & Albert 2006). Across conditions, a non-significant trend revealed older adults performed least accurately following visual distraction. Comparing behavioural results between young and older adults finds ability to perform the task with irrelevant distraction to be significantly worse in the older group. Post-hoc analysis of occipital electrodes in the visual distractor condition may help explain these behavioural differences across age. As a potential confound, it should be noted that variability within recorded visual ERPs, especially within older adults, was high. As such EEG noise unrelated to stimulation may contribute to N1 shifts that are subsequently inferred as modulation. Post-hoc explanations are offered to support behavioural data, but are open to interpretation. Within younger adults, the N1 component was delayed following the first set of visual-tactile stimulation compared to the second set of stimuli. This suggests subjects were initially drawn to the sudden visual stimulus, but that attention was successfully disengaged upon the second presentation. Following the second stimuli, N1 peak latency in young adults was significantly earlier than the latency within older adults. This could be representative of a generalized processing speed decline with age. Older adults presented with similar latencies across both visual distraction sets, but with reduced N1 amplitude following the second stimuli. These results match data from Gazzaley and colleagues (2008): subjects were presented with two types of visual stimuli and instructed which to attend and which to ignore. Grand average visual ERP waveforms illustrate reduced N1 amplitude in older adults following ignored stimuli compared to attended stimuli. Gazzaley and colleagues do not explicitly discuss this modulation because N1 amplitude was not shifted across conditions within young adults (which also matches our findings). Such post-perceptual amplitude modulation may be indicative of an altered behavioural strategy involving conscious stimulus selection after all incoming information is initially processed. Perhaps the older group was sufficiently distracted at the onset of each salient visual stimulus, but that a motivated attempt was made to ignore vision in the second set. This effort proved somewhat inadequate, as motor performance still tended to be less accurate and was conceivably more influenced by distraction.

Prior research has suggested that the ability to engage crossmodal selective attention is preserved with aging, despite the fact that older adults may be more prone to distraction (Hugenschmidt et al, 2009). Distractibility associated with healthy aging may not be a reliable measure of attentional ability, provided that some studies report older adults are not differentially affected by exogenous attentional capture regardless of increased general processing (Hugenschmidt et al, 2009). A limited ability to suppress irrelevant stimulation could result in additional processing of background noise, yet a more conscious effort at ignoring distraction and focusing on stimuli of interest could permit appropriate sensory modulation. Increased distractibility may be instead related to a shift in bottom-up capacities. This explanation matches our results, as relative modulation within tactile ERPs was very similar across age and the main difference appeared with exogenous attention pull towards secondary visual distractors. Indeed across many situations cortical activity within older adults is found to be higher, revealing increased baseline measures of conscious cognitive control. Older adults may simply work harder to achieve the same behavioural results as younger adults.

In summary, these experiments suggest that visual-tactile crossmodal stimulation is facilitatory to somatosensory activation in both healthy young and older adults. This modulation is especially apparent within later tactile ERPs inferred to represent secondary somatosensory, association, and frontal regions. Changes in attentional focus or task strategy may contribute to observed latency shifts of these later potentials, differentially affecting stimulus processing across age. Contrasting relevant visual-tactile stimulation to task-relevant vibration with visual distraction reveals that both age groups process relevant stimuli with very similar cortical activation. Age-related decrements become evident when activity related to the irrelevant vision is considered. It appears as though older adults are repeatedly drawn to salient visual cues, requiring a focused effort to remove and reorient attention to task demands. Younger adults retain processing efficiency, and effectively suppress irrelevant stimuli. Although all older subjects in this study have seemingly ‘successfully’ aged, this slight degradation negatively impacts sensorimotor translations, producing very mild behavioural deficits. Despite the lack of performance improvement following somatosensory facilitation (no low-level priming advantage), these results could suggest that tailoring attentional strategies be beneficial to function.

Chapter 5: General discussion

5.1 Limitations and future directions

Temporal constraints and the amount of stimuli required to average ERPs placed limitations on the number of conditions included within these experiments. Generally, attention-based studies should not necessitate subjects to focus for lengths exceeding 40 minutes, as fatigue and waning vigilance become confounding effects. Visual processing comparisons would be advantageous, especially to consider the effects of irrelevant vision across age, but an additional unimodal visual condition would have increased collection by 10 minutes. It was hypothesized that visual distraction would elicit significant changes within tactile ERPs, however in light of our findings, perhaps age-related and relevancy modulation would have been best observed with a more extensive analysis of visual ERPs. The task relevancy of vision was manipulated instead of vibration because past research suggests tactile stimuli can be effectively decoupled from sensory processing if it is continually irrelevant. As vision is typically the more dominant sense, it was predicted that stimulus saliency would be attentionally demanding even in task-irrelevant conditions, sufficient to alter tactile processing.

Additionally, given that older adults presented with age-related delayed N140 latencies in all conditions, it would be interesting to compare findings to single stimulation trials. Practice blocks did present single visual or tactile stimulation, however these trials did not yield enough EEG data for analysis. Contrasting ERP latencies between single and double stimulation may more concisely reveal that task difficulty and cognitive effort modulates N140 substrates. Within younger adults, N140 is delayed following crossmodal stimulation, perhaps because integrating stimuli is more demanding than processing unimodal stimuli. Perhaps older adults would present with earlier N140 latencies during single stimulation, as it is less cognitively demanding, but that even simple dual stimulation requirements exceed some processing capacities.

Participants across both age groups were primarily of homogenous nature. Younger adults were all university educated, however as the task was sufficiently novel, it is assumed data is generalizable and representative of the healthy young adult population. The older adults were recruited through the University of Waterloo's Research and Aging Pool, and subsequently most were from very similar health or research related backgrounds, physically active and highly educated. Subjects within this group have aged 'successfully' with minimal apparent functional decline; this limited our hypothesized ability to correlate poor cognitive test performance with ERP measures. This also could explain the limited impact distracting vision appeared to have on tactile processing; perhaps this group of older adults could still adequately ignore irrelevant task demands. Validating these experiments should involve a more heterogeneous sample population.

Response requirements within the experimental protocol were novel and without direct translation to real-life situations. Although it is difficult to design a task necessitating attention and integration of stimuli (most paradigms are based within target detection or match-to-sample), it would perhaps be more beneficial to include motor responses that mimic functional or rehabilitative behaviours. Alternatively, perhaps using a different response device with more obvious gradations to judge stimulus amplitude, or a measure more sensitive to relative shifts in individual data, would have provided more objective results. Ideally, EEG data recorded in conjunction with functionally-relevant stimulation and task demands would provide the most informative analysis of sensorimotor translations.

Lastly, as tactile ERP component P230 appeared most sensitive to task-relevancy across age, it would be intriguing to further investigate its neural correlates. Little is reported on this potential, especially when time-locked to somatosensory stimulation. Replicating a similar fMRI-compatible paradigm could provide a better indication of source generators and regional areas of activity. It would be interesting to observe if cortical patterns shift with the type of modality input, or if the potential is less modality-specific and more reliant on task demands. If frontal regions are involved as expected, extension to older adults with known PFC decline would also be an interesting analysis.

Continuing research within the sensorimotor realm of aging participants will ideally build support for optimal rehabilitation techniques. It is imperative that these studies involve representative age-matched controls, as the progression of structural and chemical cortical changes shift sensory processing from typical younger adult standards. To discover a method of stimulation that optimally facilitates sensory regions to allow functional motor improvement could be advantageous for recovery of impaired motor control. Perhaps attention-based and crossmodal low-level priming can contribute to the development of these techniques.

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