Factors that Influence Short-term Learning of Visual-Tactile Associations: An Investigation of Behavioural Performance and the Associated Electrophysiological Mechanisms

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

Neuroplasticity is a mechanism whereby the brain changes its configuration and function through experience. Short-term learning (i.e. minutes to hours) is associated with early phases of neuroplasticity whereby the cortical responses increase to common stimuli, and underlies long-term learning (i.e. days to weeks). Tactile sensation is an important sense, therefore if it became compromised it would be valuable to have an understanding of the neural mechanisms that underlie tactile short-term learning, and other means to promote learning, such as the introduction of a second modality. Having more knowledge in the area of somatosensory learning could then provide the means leading to long-term learning and potential recovery of function after brain injury such as stroke. The focus of this thesis was to research the role of visual information on short-term somatosensory learning, and to understand the electrophysiological mechanisms that are associated with this modulation of learning within a single testing session.

The methodology consisted of learning Morse code tactile patterns corresponding to English letters, and was broken up into two experiments. The objective of the first experiment was to determine the functional benefit to performance of the temporal and spatial coupling of tactile and visual stimuli, and the second experiment was used to determine the electrophysiological mechanisms associated with the modulation of somatosensory processing by visual stimulation. Given that there is a quantifiable measurement of learning, we hypothesized that tactile-visual cross-modal coupling will increase the learning outcome and provide functional benefit. It has been shown (Eimer et al., 2001) that presenting a visual stimulus within the same spatial site as the corresponding tactile stimulus will enhance the measurable components, and better the behavioural performance (Ohara et al., 2006). The current results demonstrated that visual-tactile cross-modal association can have a positive effect on learning over a short period of time, and that presenting a visual stimulus prior to a tactile stimulus may be beneficial to performance during the early stages of learning. Also, the results from the second experiment demonstrated an elevated and prolonged tactile P100, and a noticeably absent N140 component when tactile information was presented before visual information. Further research, extending from this thesis, is needed to advance understanding of the performance and electrophysiological outcomes of visual-tactile cross-modal associations. The findings of this study give insight into the performance and electrophysiological effects involved with short-term somatosensory learning, specifically how the manipulation of a visual stimulus, both spatially and temporally, can affect tactile learning as indicated through behavioural performance, and affect the electrophysiological mechanisms involved with somatosensory processing.

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AMPA	∝-amino-3-hydroxy-5-methyl-4-isoxazole propionic acid
BOLD	Blood oxygen level-dependent
CRR	Correct response rate
DCML	Dorsal column-medial lemniscus pathway
EEG	Electroencephalography
ER	Error rate
ERP	Event-related potential
fMRI	Functional magnetic resonance imaging
LTP	Long-term potentiation
NMDA	*N*-methyl *D*-aspartate
SI	Primary somatosensory cortex
SII	Secondary somatosensory cortex
SCT	Spatially coupled-tactile first
SCV	Spatially coupled-visual first
SUT	Spatially uncoupled-tactile first
SUV	Spatially uncoupled-visual first
VPL	Ventral posterior lateral nucleus

Introduction

A considerable problem affecting the health of Canadians is stroke. Stroke is the third leading cause of death in Canada with one stroke occurring every ten minutes, and while 15% of stroke victims die, 40% are left with moderate to severe impairments (Heart and Stroke Foundation, 2008). Somatosensory impairments can occur if there is ischemia or hemorrhage to the middle or anterior cerebral arteries supplying the postcentral gyrus where the primary somatosensory cortex (SI) is situated. Damage to other areas such as the thalamus, the secondary somatosensory cortex (SII), and parietal association cortices could also hinder somatosensory function, as these structures are also involved with somatosensation. Somatosensory problems persisting after damage would be failure of tactile sensitivity and loss of conscious proprioception. Failure to recognize touch, pain or limb position can severely hinder independent living, and knowing that stroke victims may be left with these types of impairments makes inquiry into stroke rehabilitation a top priority for stroke research. The more that is known about the contributors to neurorehabilitation, the more can be done about making the healing process more efficient and specific to a patient's needs.

Neuroplasticity is the brain's ability to reorganize its cortex through synaptic modifications, ultimately changing its structure and function, thus making neuroplasticity an imperative mechanism for rehabilitation. There is collective verification (Hodzic et al., 2004; Pleger et al., 2001; Pleger et al., 2003) that short-term (i.e. minutes to hours) tactile learning is associated with detectable changes to the cortex. If the neural mechanisms underlying tactile short-term learning were well understood then this could lead to the foundation of tactile long-term learning and recovery. Characterizing the neural correlates of somatosensory processing and how additional aspects, such as task difficulty and coupling somatosensory with other modalities, is important in understanding the effects on tactile learning. This study investigated a short-term tactile learning paradigm and how it influences the somatosensory cortex within a single session. Tang et al. (2008) examined learning-related changes of a short-term vibrotactile discrimination paradigm. The authors found that presenting subjects with a tactile learning paradigm over successive training and testing blocks, helped to improve their behavioural performance as error rate and reaction time both decreased from one testing session to the next, showing that learning had occurred. Tang et al.'s (2008) study was focused on demonstrating the time course of visual-tactile learning as would be suitable for testing with fMRI (functional magnetic resonance imaging) and did not investigate the relationship between activation of the visual and somatosensory systems. How different sense modalities influence one another is referred to as cross-modal. Cross-modal effects can be very important for learning, as the manipulation of one modality can potentially affect the learning or performance outcome of another modality in tasks that are considered cross-modal. Therefore, to extend from the work of Tang et al. (2008) the studies is this thesis manipulated the relationship between the presentation of the pairs of visual and tactile stimuli, both temporally and spatially, and used electroencephalography (EEG) to investigate the cross-modal interaction between these systems with methodology similar to Tang et al. (2008). Results from this study will allow a better understanding of how activity in one sensory system may modulate activity in another due to cross-modal interactions, specifically how introducing a visual stimulus with a tactile stimulus will affect somatosensory learning. Understanding more about the cross-modal affects on learning could potentially be applied to rehabilitation because if it is known that introducing and manipulating a second modality can enhance the performance outcome of another modality and ultimately speed up the recovery process, this can be applied as multimodal tasks for rehabilitation.

Chapter 1: Review of relevant literature

1.1 Somatosensory cortex organization

Tactile stimulation is mediated by mechanoreceptors that detect a change in the form of the skin as an object contacts it. These receptors convert this mechanical tactile stimulation to action potentials, which conduct through cutaneous afferent fibers to the primary somatosensory cortex via the dorsal column-medial lemniscus pathway (DCML). In this pathway, first order neurons are comprised of large diameter cutaneous afferents that ascend through the ipsilateral spinal cord (dorsal) to synapse in the dorsal column nuclei in the medulla. Second order neurons originate here and their axons form the medial lemniscus that decussates to the contralateral side. These neurons project to and synapse with third order neurons in the ventral posterior lateral nucleus (VPL) of the thalamus which in turn project to the primary somatosensory cortex (SI), situated in the postcentral gyrus of the parietal lobe (as cited in Kandel, Schwartz & Jessell, 2000, p. 446).

SI is comprised of four Brodmann areas, 3a, 3b, 1, and 2. The majority of the fibre projections from the VPL end up in areas 3a and 3b of SI, which then project to areas 1 and 2, however, there are some direct connections between VPL and areas 1 and 2. For the purposes of touch sensation, the information is propelled to areas 3b and 1. SI is also important because it sends projections to Brodmann areas 5 and 7 of the posterior parietal cortex, which are also significant for sensory processing. Area 5 is involved with processing tactile information from the skin, along with proprioception from muscles and joints. Area 7 gathers tactile, visual and proprioceptive information in order to incorporate stereognosis and vision. Area 7 has also been found (Hyvarinen, 1981;

Hyvarinen, 1982) to have different functional parts, such as area 7a having purely visual and oculomotor responses, and area 7b being distinct in touch but also having vision represented together with somatosensory mechanisms. The information processing that occurs in areas 5 and 7 of the posterior parietal cortex travel to motor areas for the purposes of sensory initiation and the guidance of movement (as cited in Kandel et al., 2000, p. 452).

All four Brodmann areas of SI also connect to the secondary somatosensory cortex (SII) found on the bank of the lateral fissure. SII is important because it relays tactile information to the insular cortex that will innervate areas of the temporal lobe important for tactile memory. The rate and pattern of firing of SII neurons depends on the level of attention directed to the tactile stimuli. Thus SII controls the amount of tactile information to be sent to the temporal lobe for memory storage; not all information is stored, but only that which is behaviourally significant (as cited in Kandel et al., 2000, p. 452).

At the cellular level, the cortex of SI is arranged into vertical columns expanding from the cortical surface to the white matter below. The columns consist of six layers (labeled I, II, III, IV, V, and VI), and the neurons found within the columns all receive information from a common area of skin as well as respond to the same type of receptor. The neurons within the columns are aligned vertically and perpendicular to the cortical surface. Afferents ascending from the thalamus project to layer IV on the stellate cell neurons, which project upwards to the cortical surface. Pyramidal cells run parallel to the stellate cells and expand the thickness of the column as their dendrites are in contact with the axons of the stellate cells. Thus the sensory information travels vertically within the column, as well as out to subcortical nuclei; more specifically, layer VI relays back to the thalamus, while layers II and III project to other regions of cortex, and the subcortical regions receive input from layer V projections. Through the projections arising from the different layers of the cortex, information about a stimulus can be transmitted to other areas of the brain (Favorov & Kelly, 1994a; Favorov & Kelly, 1994b).

When touching an object or holding it in the hand, no single sensory receptor conveys all of the pertinent information about that object to the brain. The central nervous system must construct a perception of the object, using the discrete signals it receives from differing receptors that all sense a distinct attribute of the object. Mechanoreceptors, for the sense of touch, all have unique nerve terminals for differing types of sensation. The Meissner's corpuscles are small rapidly adapting receptors found in the superficial layer of the skin, and are important for detecting subtle mechanical sensations. The Merkel disk is the other small superficial receptor, but is slowly adapting to pressure put on the skin. It is because of these superficial receptors that humans are able to execute subtle tactile discrimination. There are two deep subcutaneous receptors known as the Pacinian corpuscle and the Ruffini endings, which are greater in size than the superficial mechanoreceptors. The Pacinian corpuscles are rapidly adapting to fast skin indentations such as vibrations, and the Ruffini endings are slowly adapting to stretch of the skin. The receptive field, the area of skin that activates a receptor, is different between superficial and deep receptors, in terms of shape and size. A cluster of 10-25 Meissner's corpuscles or Merkel disks sends afferent signals to a single dorsal root ganglion that innervates the superficial layer of skin. The receptive fields for these receptors range from 2 to 10 mm in diameter and are very localized. A single Pacinian corpuscle or Ruffini ending is found within the deep layers of skin tissue. The receptive fields for these receptors are large with no distinctive border, but there is a central area situated above the receptor where there is maximum sensitivity to touch. This allows the receptors to detect object properties from a global region of skin. Mechanoreceptors, depending on whether they are rapidly or slowly adapting, represent the intensity of a stimulus in different ways depending on the firing rate of action potentials. Slowly adapting receptors respond to pressure on the skin throughout the continuous application of the stimulus. As more pressure is applied, the firing rate of the neurons producing action potentials increases. Rapidly adapting receptors respond to the onset and offset of a stimulus, and the firing rate of a neuron is proportional to the speed of the stimulus on the skin. At the level of the cortex, the cortical neurons receive information about the pressure and rate of skin indentation from the slowly adapting and rapidly adapting neurons. Thus, the type of sensory modality and receptive field can define cortical neurons, much like mechanoreceptors, as each neuron receives afferents from mechanoreceptors in a particular region of the skin. The cortical neurons that are connected to the receptors become excited when the area of skin housing those receptors is touched. As mentioned, the neurons within a column of the cerebral cortex all gain input from the same areas of skin, and from one modality. In area 3b of SI, the modality is touch sensation, thus its primary input is from cutaneous mechanoreceptors. The column of cells representing a specific site of the skin is divided into two sections; one for input from rapidly adapting, and the other from slowly adapting. Area 1 neurons are also important for touch sensation with its main input from rapidly adapting receptors (as cited in Kandel et al., 2000, pp. 454-462; Vallbo et al., 1984; Vallbo et al., 1995).

Within the somatosensory cortex, columns of neurons are arranged topographically so that all Brodmann areas include an overall map of the body surface. The maps are arranged such that the proportion of a body part's representation in the brain is relative to the sensitivity of body part to touch. Areas such as the hand and mouth are represented more largely as they have an increased innervation density that is, there is more cortical tissue allotted to the processing of these regions of skin. There is a general arrangement of the sensory maps whereby the most caudal areas of skin are found more medially in the map, and as the map moves more lateral the representations are from the more rostral regions. A very important feature of cortical sensory maps is that they are not constant, but always changing depending on the individual's external environment and behavioural experiences. The process of plasticity leads to these changes (as cited in Kandel et al., 2000, pp. 459-462).

1.2 Plasticity

As described by Nudo (2006), "plasticity is the capability of the cerebral cortex to alter its functional organization as a result of experience", thus the brain is capable of physiological and anatomical changes. Plasticity, or neuroplasticity, occurs in both healthy and injured brains and is characterized by altered cortical maps, modulation of neurotransmitters, synaptogenesis, dendritic spine growth, and a change in synaptic strength. These physiological and anatomical changes can occur due to natural stimulation of the senses through acquisition of skills.

Neuroplasticity involves long-term potentiation (LTP), a long lasting strengthening of the communication between two neurons in response to a repeated stimulus. LTP is important for learning and memory, and is brought on through persistent changes at the level of the synapse. These synaptic changes come about by applying a repetitive stimulus that eventually allows for the growth of new proteins and an increase in the number of synaptic connections. Learning and memory take place at the level of the synapse, and requires that there be synthesis of synaptic connections, therefore increasing the synaptic strength of a neuron will allow for long-term memory to occur (as cited in Lundy-Ekman, 2007, pp. 72-74). However, LTP can also occur without any structural changes, but due to an increase in the amount of neurotransmitter released at the synaptic junction, lasting only a few hours.

LTP is important for visual, motor and somatosensory learning, and the mechanism behind LTP is as follows (Luscher et al., 2000): due to a repeated stimulation, synapses that were once inactive now become active by calcium entering the postsynaptic neuron through NMDA receptors binding glutamate, an excitatory neurotransmitter. An increase in calcium allows for the phosphorylation of non-functional AMPA receptors, which can now be activated and inserted into the membrane of the postsynaptic neuron, creating new synapses. Continuing the stimulation, the postsynaptic neuron will develop a new dendritic spine and eventually more synapses, thus making the connections between neurons stronger, and increasing memory and learning capacity. These changes in synapses are what reorganize the cortical maps to disclose new functions.

Long-term potentiation can be broken up into an early phase and a late phase. By applying a single train of stimuli or repeatedly performing the same task, this induces the early phase that lasts from one to three hours. The features of the early phase are that it does not involve the structural changes of forming new proteins or synapses. What it represents is a functional change in the probability of neurotransmitter release caused by an increase in excitability due to the inhibition of inhibitory interneurons, allowing for the release of more neurotransmitter. Thus, with the probability of more transmitters being released, the synaptic junction between the pre-synaptic neuron and the post-synaptic neuron can be facilitated ultimately enhancing learning for the time being. The late phase of LTP is more persistent, and is brought on by four or more trains of stimuli causing it to last for a minimum of twenty-four hours. The late phase involves structural changes through protein synthesis and the formation of new synapses (as cited in Kandel et al., 2000, pp. 1262-1264).

1.3 Event-related potentials in the somatosensory cortex

An event-related potential (ERP) is known as "a potential related to cognitive or initiative processes" (Misulus, 1994) and is brought on by natural noninvasive stimuli. ERPs reflect the arrival of information to the brain, or movement execution that, by using scalp electrodes can reveal the electric field that is induced by the event of interest. Interpreting the results of ERP experiments is insightful because diverse receptors have different speeds of conduction, and they convey distinct stimulus properties, as well, they travel in anatomically segregated pathways through the peripheral nerve, spinal cord and brain (Regan, 1989). Therefore, analyzing the components of ERPs gives an understanding of the capabilities of the brain's afferent systems, making ERP traces helpful for clinical diagnosis as well as for research purposes.

Somatosensory potentials can be evoked by an electrical stimulus to a peripheral nerve generating a high-quality signal-to-noise ratio that allows precise timing of neural events. However, probing the somatosensory system this way does not allow for the stimulation of the sense receptors that would ordinarily respond to the stimuli, and so the sensitivity of the type of nerve fibers activated is undermined. Electrical stimulation applied directly to the nerve will induce a heterogeneous cluster of afferent fibers from muscles, joints, skin, and deep tissue, in addition to muscle efferents, all compromising the characteristics of the ERP. Natural stimulation of the somatosensory system permits true timing of sensory signals from sensory receptors to the cortex, and because it is purely the cutaneous afferent fibers being activated, natural stimuli provide a more intuitive understanding as to what is actually occurring within the brain's afferent system.

1.3.1 Somatosensory ERPs: The P100 and N140

Common somatosensory ERP components are the P100 and the N140 as found in many research experiments involving tactile-visual cross-modal tasks (Eimer & Driver, 2000; Eimer & Driver, 2001; Ohara et al., 2006).

The N140 is a negative amplitude component that peaks at approximately 140 ms post-stimulus and has been found to occur within the range of 120-180 ms (Yamashiro et al., 2008). The N140 component is believed to have multiple generators including bilateral generators within the secondary somatosensory cortices (Allison, McCarthy & Wood, 1992; Tarkka, Micheloyannis & Stokic, 1996). Furthermore, when studying the topography of the N140 under different concentrations of cognitive challenge that is, focusing attention towards or away from the stimulated hand, García-Larrea et al. (1995)

found that the N140 distribution became more symmetrical across the two hemispheres as the subjects' attention to their stimulated hand increased. As well, it was evident that the N140 amplitude increased in size as the spatial orientation of attention was concentrated on the stimulated area. Giaquinto and Fraioli (2003) also discovered that there was an enrichment of the N140 in stroke patients who were trained on spatial attention using cutaneous electrical stimuli.

Unlike the N140, the P100 is a positive amplitude component occurring approximately 100 ms after the onset of the stimulus with peak latency from 70-120 ms (Yamashiro et al., 2008). The P100 has been found (Tomberg at al., 2005) to be generated in the parietal cortex contralateral to the stimulated finger when using electrical brain mapping along with an attentional task of discriminating target tactile stimuli from non-target stimuli. More specifically, the P100 was generated in Brodmann's area 7b of the intraparietal cortex; an area accepting connection from Brodmann's area 5 which ultimately receives connections from somatosensory areas 3b and 1 responsible for somatosensation. The fact that area 7b receives connections from initial somatosensory processing centres indicates that this area, together with the P100, is important for higher-order processing of somatosensory stimuli, and is enhanced by attention. In fact, neurons in area 7 integrate tactile and vision that coincide within the same space (Kandel et al., 2000). Attention concerns the P100 when subjects concentrate on receiving a tactile stimulus compared to when the stimulus is unattended. In an attended situation the amplitude of the P100 increases and in addition, this amplitude value decreases as the stimulus duration increases in time (Spackman et al., 2006).

It is apparent that the N140 responds to spatial attention when tactile stimulation is applied to the hand, reflecting an increase in SII excitability. Like the N140, the amplitude of the P100 tends to increase when attention is applied to a tactile stimulus, but is affected by the stimulus duration, overall reflecting the excitability of parietal higher-order somatosensory processing.

1.3.2 Visual-tactile cross-modal somatosensory ERPs

It is often the case that an individual's environment has more than one modality influencing them at once; hence research has looked into how somatosensory ERPs can also be modulated by multimodal stimuli. Ohara et al. (2006) showed that a single tactile stimulus would affect the N140 differently when another task is performed. Subjects were to match two stimuli, the first condition involving two tactile stimuli and the second condition involving a tactile stimulus with a visual stimulus. With the ERPs being time-locked to the onset of the first stimulus, the bimodal matching task caused an increase in the N140 amplitude in comparison to the unimodal task. It has been proposed that the N140 is generated by sources within SII, thus as indicated by Ohara et al.'s (2006) results, the SII is suggested to be involved with higher order processing of cross-modal associations between tactile and visual modalities. Ohara et al. (2006) advocate that the P100 may be involved with differing activities than those of the N140 since the P100 was not modulated to a significant extent with the cross-modal matching task. The P100 could be involved in conveying information from the tactile to the visual modality, since its amplitude was enriched with a cross-modal control task that involved no matching of the two stimuli. From this study, the tactile N140 and P100 can be altered by cross-modal tasks involving the anticipation of a visual modality.

Attention is a factor that modulates somatosensory ERPs, consequently Eimer and Driver (2000) sought to test for cross-modal ties between touch and vision in response to endogenous spatial attention by having subjects detect a tactile or visual stimulus on an attended side while ignoring stimuli of the unattended side. The results indicated that when tactile stimuli were attended to there was an enhanced N140 that was largest in the tactile attended condition and less prominent in the condition where vision was the primary attended and touch was the secondary attended stimulus. Also, when vision was the attended modality, without touch, the N140 enhancement was not apparent. Similarly, spatial attention to touch was able to modulate visual ERPs lending evidence towards tactile-visual cross-modal connections in spatial attention. However, cross-modal ties from vision to touch were not apparent when attention was concentrated entirely on vision, but only when touch had some relevance, indicating that unless it is pertinent to cross-modal spatial attention, touch may be decoupled from visually dominant attention. These findings were not the same for visual modalities that were found to always be coupled to touch even when vision was not relevant to the tactile spatial attention.

Eimer et al. (2001) went a step further to determine how the tactile-visual cross-modal links would be affected under a different posture that is, with the hands crossed. They wanted to determine just how these cross-modal links are mediated, and proposed that if the cross-modal links between vision and touch are determined by initial hemispheric projections then their results would indicate that paying attention to a hand in the crossed position would still enhance visual ERPs on the same side as if the hand were uncrossed. In contrast, they stated that if cross-modal links from touch to vision are mediated by external locations that are common to the two modalities, then they expected that there would be elevated visual ERPs in the opposite side to that of uncrossed hands. They found that the visual ERPs (P1, N1, and P2, at occipital sites, and N1 at midline sites) were enhanced on the tactually attended side in the uncrossed condition, and analogous results took place in the crossed hands position where the attention to tactile stimulation enhanced the visual responses on the side where the attended hand was placed. This outcome indicates that cross-modal links between touch and vision are not mediated by hemispheric projections but rather by the immediacy of the visual stimulus to the position of the focused hand. However, these results were not found for the somatosensory ERP N140, which actually was absent or reversed when hands were crossed compared to uncrossed. The results of this study suggest that placing the hands in a crossed position cause a disturbance to attentional effects within touch, however the cross-modal effects upon vision were not disturbed.

The results of these studies signify that somatosensory ERPs can be altered by anticipation of a visual stimulus or even the spatial attention applied to touch. Also, that the cross-modal relations from touch to vision are controlled by common external locations of the two modalities. Hand posture also has significance in controlling somatosensory ERPs by downgrading or eliminating them when the hands are crossed, a feature that is quite the opposite for visual ERPs.

1.3.3 Other somatosensory event-related potentials

In addition to the N140 and P100 there are other ERPs that occur in response to tactile stimuli. The P300 is a late positive potential, widely distributed in response to attending to an oddball paradigm whereby target stimuli are presented randomly amongst constant non-target stimuli. The P300 has been found (Tarkka et al., 1996) to occur with bilateral representations in the medial temporal lobes, hippocampal or parahippocampal regions, and contralateral insular cortex, which is prominent in memory. Valeriani et al. (2001) also found there to be more than one generator of the P300, and similar to Tarkka et al. (1996) they found bilateral generators in the medial temporal areas, and in the contralateral temporal lobe. Although the P300 is generated in response to somatosensory stimuli it is not specific to this modality because it can also be elicited by auditory and visual stimuli. Much more is still to be learned about the P300 as a somatosensory evoked potential, as most studies concentrating on the P300 are designed around auditory and visual modalities as the primary stimuli.

Earlier somatosensory potentials have also been recorded (Josiassen et al., 1990) that include the N20, P30, P45, and N60, and have thought to be generated by prerolandic, postcentral and subcortical regions. They have been found to respond to attentional effects of the modality as early as the P30. The N20 however, is non-responsive to attentional effects suggesting that the gating of the subcortical thalamocortical connection is not regulated by attention to stimuli in the somatosensory modality. However, these early potentials were generated by direct stimulation to the median nerve, setting in motion unspecific fibers and bypassing the sensory receptors causing a reduction in the natural discrimination of the ERP signal. In a protocol involving genuine stimuli to the sensory receptors, somatosensory ERPs earlier than approximately 50-60 ms would not be expected. Reasoning behind the lack of early potentials may be due to a steady commencement with mechanical stimulations as opposed to an abrupt onset with electrical stimulation exciting complete nerve bundles instead of mechanoreceptors that would allocate receptor adaptation and conduction velocity affecting the overall timing (Schubert et al., 2008). The earliest reliable potential measured in response to tactile stimulation has been the P50, a positive deflection occurring 50 ms after initial stimulation. This was brought on by bilaterally stimulating the index fingers with Braille to test tactile spatial-selective attention and measured simultaneously with EEG and fMRI. The results indicate the P50 EEG tracing to be enhanced by spatial attention and that this amplification correlates with an enlargement in fMRI BOLD signal located in the contralateral SI (Schubert et al., 2008). The results also indicate a correlation between attention on early and late potentials (i.e. P100) with BOLD signal indicating that tactile spatial attention can improve processing in SI during an early course of the signal as well as during a later passage of the signal when higher cortical areas allow re-entrant feedback to SI.

1.3.4 Characteristics of tactile stimuli

When the sensory system receives tactile information from the environment it must sort out different traits about the stimulus to be correlated with the sensation of touch that is seen within an ERP tracing. Current somatosensory studies, eliciting an ERP response to natural stimuli within a lab setting, are mainly done through vibrotactile or punctate stimuli. Most protocols call for repeated stimuli, and these are easy to administer to the volar surface of the finger tip(s) (usually the index finger) where there are many sensory receptors. Punctate stimuli can be described as a ‘tap’ on the surface of the skin, usually driven by a single rod attached to a solenoid (Eimer & Driver, 2000; Eimer et al., 2001), or possibly many rods at once (Schubert et al., 2000). Contact time on the surface of the skin, as well as the intensity of the punctate stimulus can vary from one study to the next. A vibrating apparatus can induce vibrotactile stimuli, which can be custom-built for the purposes of the study. Vibrotactile stimulations can operate at a consistent frequency (Spackman et al., 2006), or in the case of tactile discrimination frequency studies can be done using different frequencies (Ohara et al., 2006;). Overall, these are methods in which somatosensory ERPs can be measured in response to natural tactile stimuli.

1.4 Evidence for adaptations to learning in the somatosensory cortex

1.4.1 Working memory

The capability of retaining and influencing information on the order of seconds, is known as working memory or short-term memory, and is a large contributor to learning because it is involved with cognitive processes such as attention, perception and action (Harris et al., 2002). Working memory tasks have been shown to involve the prefrontal cortex as the major contributor to managing what information is stored in memory. Kostopoulos et al. (2007) specifically found the midventrolateral prefrontal cortex to be involved with “active controlled retrieval processing” important for making understood tactile information stored in memory. They state that sensory information about a tactile stimulus is first administered in SI, which then contributes to the parietal opercular region for SII processing as well as the rostral inferior parietal lobe for an overall achievement of tactile perception. The secondary somatosensory regions are connected to the prefrontal cortex bidirectionally, thus the midventrolateral cortex can relay information with SII and the rostral inferior parietal lobe. Furthermore, Harris et al. (2002), when researching tactile memory, found that SI is not only involved with working memory for semantics but is fundamental in tactile working memory for the retention of sensory information. This implies that not only are SI neurons important for early somatosensory processing, but they also have a role in storing information contributing to working memory. It has also been suggested that in the same way SI is topographically organized for representing stimuli, these topographical regions contribute to the retention of sensory information as one stimulus can be compared to another by the retention of the memory trace over a delay period (Harris et al., 2001).

1.4.2 Short-term learning in the primary somatosensory cortex

Learning experiments involving the motor cortical regions show that skill learning is dependent upon the stage of acquisition that is, there is a fast learning stage where improvement is evident within the initial session, leading into a between-session slow learning stage where performance gains come from continued practice (Floyer-Lea & Matthews, 2005; Karni et al., 1995; Karni et al., 1998). This time course of plastic events is what establishes the location of skill acquisition in long-term memory. Similarly, understanding the neural mechanisms that underlie short-term tactile learning will allow a better understanding of the long-term learning of tactile stimuli.

There are studies that associate measurable cortical modifications as the result of tactile learning in the short-term. Hodzic et al. (2004) demonstrated that perceptual learning could be induced passively without the use of reinforcement or attention. By having subjects receive passive tactile coactivation to the index finger for a period of 3 hours, Hodzic et al. were able to use fMRI to measure a two-to-threefold expansion of the representation in contralateral SI and SII cortex. As well, there was a positive correlation between the enlargement of the represented area in SI and the performance of spatial discrimination; those participants who had the largest shift in cortical representation were the ones with the greatest improvement in performance. However, frequency discrimination performance decreased after the tactile passive coactivation bout, possibly suggesting that the best way to acquire new skills is to learn with attended effort as opposed to passively without attention. In similar studies (Pleger et al., 2001; Pleger et al., 2003) involving short-term, non-attended coactivation to the index finger, there were results parallel to those of Hodzic et al. (2003). A linear relationship developed between spatial discrimination threshold and cortical reorganization; subjects who demonstrated a large gain in spatial discrimination also had an enlarged representation of the corresponding stimulated finger within SI. Ragert et al. (2008) were able to demonstrate that perceptual learning takes place depending on the frequency of the tactile stimulation. When given a high frequency (20Hz) stimulus vs. a low frequency (1Hz) for 20 minutes, the high frequency was able to decrease two-point spatial discrimination and had lasting effects 24 hours later. The low frequency impaired performance. They related this increase and decrease in performance to long-term potentiation and long-term depression respectively which are mechanisms underlying cortical plasticity and learning. Much like the previous studies however, there was no attention involved with the task, which along with higher frequency stimulation could further the learning effects.

The present studies on short-term tactile learning are limited and need to be expanded because not much is known about this topic. An obvious factor that needs to be looked into is attention and its role in tactile learning as many of the present studies involve passive learning. Other possible inquiries include the physiological mechanisms driving an increase in learning, which would give insight into what is actually happening at the cortical level when acquisition occurs. As well, how tactile learning becomes affected by other modalities such as vision. These are all areas in which this study aspired to investigate.

Chapter 2: Research objectives and hypotheses

The aim of this thesis was twofold. The first aim was to determine if there is a functional benefit to tactile-visual coupling during tactile learning. Furthermore, presuming an interaction between vision and tactile stimuli, we wanted to determine how tactile-visual spatial attention, and stimulus order effects tactile learning. The second aim was to understand the electrophysiological mechanisms associated with the modulation of somatosensory processing by visual stimulation. Two separate experiments were conducted to address these objectives.

The objective of the first experiment was to determine the learning effects and functional benefit to performance of temporal manipulation and spatial coupling of tactile and visual stimuli during a tactile learning paradigm. Specifically, it was hypothesized that coupling vision with tactile stimuli will result in a decrease in the number of errors and reaction time (RT) from block-to-block until a learning curve is reached. Furthermore, it was hypothesized that presenting tactile and visual stimuli within the same spatial location as well as presenting a visual stimulus before a tactile stimulus, will be associated with an increase in performance, reflected by an increase in the rate of learning.

The objective of study two was to determine the electrophysiological mechanisms associated with the modulation of somatosensory processing by visual stimulation. It was hypothesized that presentation of the visual stimuli prior to the tactile stimuli would enhance somatosensory-related ERP amplitudes through bottom-up processing from visual to tactile processing streams, based on the work of Ohara et al. (2006).

It was further hypothesized that as the visual stimulus is paired with a tactile stimulus within the same spatial location, the amplitude of somatosensory-related ERPs will increase compared to when the visual stimulus is presented near the opposite hand not receiving the tactile stimulation. Evidence comes from Eimer et al. (2001) who found that visual stimuli with the tactile stimuli enhanced somatosensory ERPs, and that these cross-modal spatial relations between vision and touch are based on the common location that they share.

Chapter 3: Study One: Short-term learning of visual-tactile associations: An investigation of behavioural performance

Overview: Research looking into the cross-modal associations between vision and touch has determined much about the interaction between these two modalities; that they are dependent on sharing a similar location in space, that tactile effects can be decoupled if not relevant to a visually dominant task, and performance increases over a short timeframe when these two modalities are cross-modally presented. The current study investigated how vision affects somatosensory learning behaviourally, when learning was dependent upon the manipulation of the spatial location and temporal order of the stimuli. It was hypothesized that staging the two modalities within a common location, and preceding the tactile stimulus with a visual one, would boost performance representing an enhancement in learning. Participants were taxed with a Morse code learning paradigm, where they had to associate a visual letter of the English alphabet with a tactile dot/dash punctate stimulus on their left index finger. The task consisted of training and testing sessions to represent skill learning and skill assessment respectively. Four conditions were tested: two whereby spatial location of the visual stimulus was manipulated, and two whereby stimulus order was manipulated. The significant result was an elevated performance when the visual preceded the tactile stimulus during the early stages of learning. The overall conclusion was that tactile-visual learning can occur over a short period of time, and that early stages of learning may benefit from presenting the visual stimulus prior to the tactile stimulus.

3.1 Introduction

In a study done by Tang et al. (2008), it was shown that vibrotactile learning could increase within a single short-term (45 min) session. Specifically, the session involved participants learning a tactile version of Morse code; matching a dot/dash tactile pattern to a visual letter of the English alphabet, and consisted of marked training and testing components. What resulted was a training-reliant decrease in error rate and reaction time within a single session, which was also evident at retesting sessions. The authors advocate that the methodology used is fitting for evaluating neurological changes connected to short-term vibrotactile learning. Learning occurs at the junction between two neurons through the process of LTP, a component of neuroplasticity whereby repeated stimulation results in an increased firing rate between neurons to the point where new synapses are formed. These structural changes can last on the order of days to weeks, however the learning involved with Tang et al.'s (2008) study comes through the early phase of LTP. During this phase there are no structural changes, but a repeated stimulus results in an increase in the probability of neurotrasmitter released at the junction between two nerves by inhibiting inhibitory interneurons. This will result in a facilitation of the communication between the nerves that ultimately increases learning for the time being (a few hours). The authors focused on demonstrating the time course of the visual-tactile learning, however they did not investigate the relationship between activation of the visual and somatosensory systems. When two different systems interact and influence one another, they are known to have cross-modal associations. Cross-modal relationships can be very effective as one sensory system can modulate and have some bearing on learning and performance within the other system. The purpose of this study was to extend from the work of Tang et al. (2008) to investigate how vision affects somatosensory learning behaviourally when participants are taxed with a Morse code vibrotactile paradigm within a short-term session, and where learning, in this case the short-term effects due to early phase LTP, is dependent upon the cross-modal interactions between tactile and vision as they are manipulated spatially and temporally.

In a previous study on tactile-visual cross-modal associations, Ohara et al. (2006) looked at somatosensory discrimination based on the expectation of a previously paired visual stimulus. Their behavioural results indicated that there was enhanced performance when subjects had to discriminate between 2 stimuli in a cross-modal task (visual and tactile) compared to a unimodal task (tactile and tactile). They attributed this enhancement to top-down processing or the cognitive expectation of the visual stimulus when it was presented after the tactile stimulus, and that these cross-modal changes have their greatest effect in SII cortex where higher level processing occurs. Dionne et al. (2009) showed increased activation in SI during simultaneous visual-tactile stimulation compared to unimodal stimulation when all stimuli were relevant for a subsequent motor response. This is supportive of the possibility of bottom up effects of visual processing on the modulation of somatosensory information. Along the same lines, Meehan et al. (2009), when looking at intermodal spatiotemporal properties, determined that changes within the processing of early somatosensation were reflective of intermodal sensory gating, characteristic of bottom-up processing. Furthermore, it has been found (Eimer et al., 2001) that cross-modal links between somatosensory and vision are dependent upon the tactile and visual stimuli being presented within a common location in space. Thus, from these previous outcomes, it was hypothesized that when participants are presented with a Morse code vibrotactile paradigm that couples vision with tactile stimuli, this will cause learning to occur over time until a learning curve has been reached. Similarly, presenting a visual stimulus before a tactile stimulus would result in enhanced performance through sensory driven (bottom-up) processing as the visual stimulus primes the somatosensory system. Furthermore, presenting the visual and tactile stimuli within the same spatial location would also improve behavioural performance.

3.2 Materials and methods

3.2.1 Subjects

Twenty healthy volunteers were tested (13 females, 7 males; age range 19 to 33 years; average 24.25 years). Exclusion criteria were skilled knowledge of Morse code, or the presence of any neurological diseases. All subjects gave their informed consent to participate in the study, and the experimental procedures were approved by the Office of Research Ethics at the University of Waterloo.

3.2.2 Experimental procedure

Tactile Stimuli

Tactile stimuli were presented via a custom-built, vibrotactile device; a modified speaker mounted within a plastic box with a surface area large enough for the entire hand to rest. Participants were instructed to place their left index finger over a hole in the box approximately 1cm in diameter. Within the hole was a dowel attached to the center of the speaker’s diaphragm and placed flush with the hole. The dowel acted as a tactile hammer to present tactile patterns in the form of standardized Morse code stimuli. The stimuli were received by the volar surface of the left distal phalanx of the second digit. The tactile hammer was controlled by custom LabVIEW software (National Instruments; Austin, Texas, USA) producing stimulus waveforms that were converted to an analog signal (DAQCard 6024E, National Instruments, Austin, TX), which was then amplified (Bryston 2B-LP, Peterborough, Ontario, Canada). The vibrotactile stimuli consisted of short and long durations corresponding to the *dots* **(.)** (duration = 250ms) and *dashes* **(-)** (duration = 750ms) of standard Morse code, respectively (Table 1). The dots and dashes were arranged in combinations to represent Morse code letters corresponding to the English alphabet. The stimuli were delivered with an inter-element duration of 125 ms.

Manipulation of Task Difficulty

Tactile stimulus patterns were characterized as being either *easy* or *hard* depending on the complexity of the characteristic patterns. *Easy* letters are those with only one transition occurring between dots and dashes that take place at either the beginning or the end of the tactile pattern. The *hard* letters are those with more than one transition within the entire pattern (Table 1). The criteria for *easy* and *hard* patterns were in accordance to the method used by Tang et al. (2008). *Easy* patterns were verified by the early production of a learning curve, whereas the *hard* patterns resulted in a learning curve that progressed slower than that of the *easy* patterns. More specifically, the average reaction time and error rates were found to be greater for *hard* discriminations than *easy* ones. Four specific four letter sets (AYTV, BZPL, HEFC, IXOQ) were randomly selected prior to the study and all contained *easy* and *hard* discriminators in the ratio of 1:3 respectively. The *easy/hard* ratio, as put forth by Tang et al. (2008), was chosen in order to expand the discrimination challenge for each letter set, and allow for varying degrees of difficulty during testing.

Visual Stimuli

Visual stimuli were in the form of letters of the English alphabet that correspond to the tactile stimuli (Table 1). Participants had to learn the association between the tactile and the visual stimuli as the individual letters were precise identifiers for each tactile pattern. The letters were presented by way of a computer monitor placed in front of the subjects. In some cases the visual stimulus was coupled with the tactile stimulus by presenting the letter on the left side of the computer monitor screen, whereas in other cases the two modalities were not coupled and the visual letter was presented on the right side of the computer screen.

Response

In order to obtain behavioural data as a measurement of learning, subjects had to make a response using a plastic device outfitted with two buttons that were mapped to one of two responses: *match* and *no match*. The participants indicated their response by pressing one of the two buttons corresponding to the second and third digits of their right hand. Using the second digit indicated a *match* and using their third digit indicated *no match* between the tactile and visual stimuli presented. The response system was only utilized during the *testing* sessions of study one.

Behavioural Investigation

The design of this experiment consisted of skill acquisition followed by skill assessment, which represented *training* and *testing* segments respectively. There were four conditions: *spatially coupled-visual first (SCV), spatially coupled-tactile first (SCT), spatially uncoupled-visual first (SUV), and spatially uncoupled-tactile first (SUT)*. There were three training blocks, each one followed by a testing block for each of the four conditions so that the experimental period consisted of a total of twenty-four blocks (6 for each of the four experimental conditions) (Figure 1). By using training blocks followed by testing blocks, this allowed insight into short-term learning over consecutive blocks.

Training

The intention of the *training* sessions was so that subjects could learn the association between the Morse code tactile stimulus and the corresponding visual letter. *Training* involved subjects receiving a tactile dot-dash combination that matched with a corresponding visual stimulus (Table 1). There were four conditions, two whereby spatial location of the visual stimulus was manipulated, and two whereby stimulus order was manipulated, in which the stimuli are presented: *spatially coupled*, where the visual stimulus was presented on the left side of the computer monitor within the same spatial vicinity as the tactile stimulus; *spatially uncoupled*, where the visual stimulus was presented on the right side of the computer monitor within the opposite spatial location as the tactile stimulus; *visual first*, where the visual stimulus was presented 200 ms prior to the onset of the tactile stimulus; and *tactile fist*, where the tactile stimulus was presented prior to the visual stimulus, with 125 ms between the two stimuli.

The four *training* conditions are based on coupling a spatial location condition with a stimulus order condition, and each block consisted of four letters in the ratio of 1:3 representing *easy* vs. *hard* letters respectively. A ratio of 1:3 was used in order to maximize discrimination challenge as put forth by Tang et al. (2008). Throughout each of the four conditions of *training*, corresponding tactile and visual stimuli were presented every 5 seconds, for a total duration of 80 seconds so that each pair of stimuli are presented four times for a total of 16 stimuli per *training* block. The same 4 letters were presented randomly in each of the three training blocks. A different set of letters were assigned to be used in each *training* condition based on a balanced Latin square design such that all four training conditions were paired with each letter set an equal number of times across subjects. The same letter set that was trained was tested for learning effects during the *testing* phase. The importance of using such a design was confirmed by 1-way ANOVAs with letter set as the factor (AYTV, IXOQ, BZPL, HEFC) and number of errors for each test (block 1, block 2, block 3) as the dependent measure. Results indicated that letter set was significant for test blocks 1 and 2 ($F_{3,57} = 4.38$, $p = 0.0076$; $F_{3,57} = 3.16$, $p = 0.03$, respectively), but not test block 3 ($F_{3,57} = 1.43$, $p = 0.24$) (Appendix 1). This suggests that some letter sets were more difficult to learn initially but that after sufficient training, subjects learned each set equally well. Using the balanced Latin square design should have eliminated this as a potential confounding factor. Subjects were informed to pay attention to the visual and the tactile stimulation in order to learn the proper tactile pattern that matches with the appropriate letter. No response was required during the *training* session. See Figure 2 for the experimental time course of the *training* sessions.

Testing

The *testing* blocks determined if there were any functional benefits of manipulating spatial and tactile aspects of tactile-visual associations. It was predicted that learning will occur such that there will be an increase in the performance from one testing period to the next until a plateau in performance is reached. The purpose of the *testing* blocks was to evaluate the (collective) learning outcome of the *training* block(s). The *testing* blocks required the subjects to discriminate between matching (*meaningful*) and non-matching (*meaningless*) tactile-visual stimuli presented at random. The same 1:3 *easy* vs. *hard* patterns were presented as in the *training* block, within the center of the computer screen. There were a total of 32 stimulus pairs with a new pair presented every 5 seconds for a total time of 160 seconds per testing block. The tactile stimuli always preceded the visual stimulus as the visual stimulus acted as the ‘go’ signal for the response. A response was required whereby subjects had to press one of two buttons based on their decision of a *match* or *no match* between the tactile and visual stimuli, and were asked to create a response as quickly and accurately as possible. No performance feedback was given to the subjects at any time during the course of the experiment in order to prevent explicit learning. In order to determine a learning effect, reaction time (RT) was measured in milliseconds (ms) as well as the number or errors. A decrease in RT and the number of errors would be reflective of learning. Overall, study 1 took 48 minutes to complete (Figure 1). See Figure 3 for the experimental time course of the *testing* sessions.

3.2.3 Data aquisition

Behavioural performance measurements that were acquired were reaction time and accuracy when the participants would press one of two buttons; *match* or *no match*, during the *testing* phase. The behavioural performance measurements were collected by custom LabVIEW software (National Instruments; Austin, Texas, USA), and further processed using Microsoft Excel (Microsoft Corporation, Redmond, Washington, USA).

3.2.4 Data analysis

To test the hypothesis that tactile learning will occur across testing blocks, a 2-way analysis of variance (ANOVA) with condition (SCV, SCT, SUV, SUT) and test (block 1, block 2, block 3) as factors were performed on the number of errors made at each testing block, as well 2-way ANOVAs with condition and test as factors were performed on the reaction times. To test the hypothesis that the spatial location (visual stimulus coupled with tactile stimulus) and temporal order (visual stimulus presented before the tactile stimulus) have an effect on learning, separate 2-way ANOVAs with spatial location (coupled, uncoupled) and temporal order (*visual first*, *tactile first*) as factors were performed on the differences in the number of errors between *test blocks* 1 and 2, 2 and 3, and *test block*s 1 and 3. Similarly, 2-way ANOVAs with spatial location and temporal order as factors were performed on the differences in reaction time between *test blocks* 1 and 2, 2 and 3, and *test blocks* 1 and 3. Significant ANOVAs for all hypotheses were followed up with post hoc testing, which consisted of a Tukey test. All statistical tests were performed using SAS 9.1 (SAS Institute Inc., Cary, NC, USA).

3.3 Results

Figure 4 depicts the average number or errors and reaction time of the twenty subjects at each testing block. The ANOVA for the number of errors revealed a main effect of *test block* ($F_{2,\,38} = 32.12$, $p < 0.0001$) but not condition ($F_{3,\,57} = 0.39$, $p = 0.76$), suggesting that learning of the tactile-visual associations occurred over the session but that this was not influenced by the different conditions. Post hoc Tukey tests revealed *test block* one (mean = 6.8) to be significantly different than *test block*s 2 and 3 (means = 3.7 and 3.2 respectively). There was no interaction between test and condition ($p = 0.19$). The ANOVA for reaction time also had a significant main effect of test block ($F_{2,38} = 44.12$, $p < 0.0001$) but not condition ($F_{3,57} = 0.65$, $p = 0.59$). Post hoc tests revealed all test blocks to be significantly different from one another (test block 1 mean = 957.68 ms, test block 2 mean = 850.7 ms, test block 3 mean = 807.6 ms). There was no interaction effect between test and condition ($p = 0.32$).

In order to test the second hypothesis separate 2-way ANOVAs with spatial location (*coupled, uncoupled*) and temporal order (*visual first*, *tactile first*) as factors were performed on the differences in the number of errors, and the differences in reaction time between *test blocks* 1 and 2, 2 and 3, and *test blocks* 1 and 3. This analysis was performed, as there was a lot of variability between subjects in the performance on the first test block. Therefore, taking the differences normalizes the error results of each individual to themselves. The 2-way ANOVA on differences in the number of errors between *test blocks* 1 and 2 revealed a main effect of temporal order of the stimuli ($F_{1,19} = 4.52$, $p = 0.04$) but not spatial location ($F_{1,19} = 0.04$, $p = 0.84$) (Figures 5 & 6). Specifically, subjects improved to a larger degree following training where the visual stimulus was presented prior to the tactile stimulus (mean = 4.2), than when the tactile stimulus was presented prior to the visual stimulus (mean = 2.0). There was no interaction between spatial location and temporal order (p = 0.35) (Appendix 2). For the ANOVAs on the differences in errors between *test blocks* 2 and 3, and 1 and 3, there was neither a main effect of temporal order of the stimuli ($F_{1,19}$ = 1.01, p = 0.32 and $F_{1,19}$ = 2.25, p = 0.15, respectively) nor the spatial location ($F_{1,19}$ = 3.74, p = 0.07 and $F_{1,19}$ = 0.55, p = 0.47, respectively) (Figures 5 & 6), and no interaction between spatial location and temporal order (p = 0.78 and p = 0.44, respectively). The 2-way ANOVA on the differences in reaction time between test blocks 1 and 2 revealed a main effect of temporal order ($F_{1,19}$ = 5.40, p = 0.03) but not spatial location ($F_{1,19}$ = 0.00 p = 0.95). Specifically, subjects improved to a larger degree when visual was presented first (mean = 104.72 ms) than when the tactile stimulus was presented first (mean = 73.24 ms). There was no interaction between spatial location and temporal order (p = 0.93) (Figures 5 & 6). For the ANOVAs on the differences in reaction time between *test blocks* 2 and 3, and 1 and 3, there was neither a main effect of temporal order of the stimuli ($F_{1,19}$ = 1.17, p = 0.29 and $F_{1,19}$ = 1.28, p = 0.27, respectively) nor the spatial location ($F_{1,19}$ = 2.37, p = 0.14 and $F_{1,19}$ = 1.50, p = 0.24, respectively), and no interaction between spatial location and temporal order (p = 0.89 and p = 0.85, respectively) (Figures 5 & 6).

3.4 Discussion

In this study, behavioural effects of tactile-visual associative learning were measured. It was hypothesized that learning would develop from one test to the next until a learning curve is reached. It was also hypothesized that learning would develop more so by presenting the visual stimulus prior to and coupled with the tactile stimulus. Learning was measured by an increase in performance of error rate and reaction time. The main findings of this study were improved behavioural performance from one test session to the next, and when visual stimuli were presented prior to tactile stimuli in support of the hypothesis. The results of this study support the hypothesis that learning occurs across *test blocks*. As depicted in Figure 4, the average number of errors and reaction time for each condition decreases from one *test block* to the next, indicating that on average, the subjects are learning the associations between the tactile and the visual stimuli with each subsequent training session. The hypothesis that temporal manipulation of the stimuli will impact learning was only supported by the results for the differences in error and reaction time between test 1 and 2, and not tests 2 and 3 or 1 and 3. With that said, it was the visual presented first that made the impact on learning, and not so much the tactile presented first. Similarly, the hypothesis that having the tactile and visual stimuli spatially coupled would increase learning compared to when they were not coupled, was not made apparent. However, when looking at the means, they suggest that temporal order is greater for spatially coupled than spatially uncoupled for both test 1 and 2 difference, and test 1 and 3 differences (Figure 6).

The finding that tactile-visual association learning occurs from one *test block* to the next until a learning curve is reached replicates the results of Tang et al. (2008). They found an enhancement of behavioural performance as a result of consecutive test periods, as error rate and reaction time both decreased to form a learning curve. As shown in Figure 4, the average error rate and reaction time tracings decreased to form a learning curve by *test block* 3 much like Tang et al. (2008) as the training was very similar with the exception of the manipulation of visual and tactile stimuli. The purpose of Tang et al.

(2008) was to build a model capable of looking at the neural correlates of short-term tactile-visual associative learning. Tang's Morse code paradigm resulted in methodology suitable for achieving investigations into short-term tactile-visual learning, and so this methodology was used for the current study. Consequently, the performance results obtained were very much expected and are indicative that learning can and is occurring over a short period of time.

Temporal order of the modalities did have an effect on the early stages of learning, as visual presented before tactile stimuli resulted in the greatest performance change, a result that was hypothesized; *visual first* was expected to positively affect learning primarily through bottom up processing. Bottom up processing was demonstrated by Dionne et al. (2009) who conducted an fMRI investigation into the SI manipulation of bimodal (tactile + visual) versus unimodal stimulation. The SI BOLD signal was increased during the bimodal task, what they explained not to be driven by top-down higher order multimodal areas based on the results of their whole-brain analysis, but by the low-level sensory-to-sensory connectivity between somatosensory and visual processing locations; it was the bottom-up processing of incoming tactile and visual stimuli that caused the increased SI activity during the bimodal task. The source of their argument comes from the fact that attention was kept constant and so it could not account for the changes observed in SI, and that the changes had to be driven by bottom-up and not top-down processing. Furthermore, Meehan et al. (2009) used somatosensory evoked potentials (SEP) to test the intermodal (tactile and visual) influences within somatosensory processing within SI and to determine how spatiotemporal relationships between bimodal stimuli influence SI. Their results showed a decrease in the early SEP when the bimodal stimuli shared a greater spatial relationship, and an increase in the early SEP when the bimodal stimuli shared a greater temporal synchrony. The conclusion from their results characterizes intermodal somatosensory gating reflective of bottom-up processing as these changes take place in SI, the generator of the early SEP component.

In a task somewhat more similar to that used in the present study, Ohara et al. (2006) looked at a tactile-visual cross-modal task, they found that behavioural performance increased when the tactile stimulus was presented before the visual stimulus, a result they attributed to top-down processing caused by the cognitive expectation of the visual stimulus when it was presented after the tactile stimulus. Our results were only significant for the temporal differences between test 1 and 2, suggesting that vision presented before tactile does have more of a learning effect than tactile presented before vision, at least during the early stages. When asked whether they felt one condition was easier to learn over another, the number of subjects who found *tactile first* or *visual first* to be easier than the other, was quite similar. Four of the subjects found that when the tactile was presented first, this made it easier to learn the associations because it gave time to guess the letter before it appeared. Three individuals found it easiest to learn when the visual stimulus was presented before the tactile, and the other 13 individuals were indifferent as to what temporal order was easiest to learn, and felt the discrimination challenge to be similar across conditions. As the majority of subjects felt that there was no difference between *tactile first* and *visual first*, this is reflected in the results at the later stages of learning, where there was no significant difference between the two temporal orders.

It was found that spatial location does not significantly affect learning, and the proposition that having the two modalities within the same spatial vicinity would have the greatest learning outcome was not supported. Based on previous research (Spence et al., 2000 (Experiment 6); Eimer et al., 2001) cross-modal links between vision and touch are established on common external locations rather than anatomical hemispheric activation, and that sharing a familiar location would have the potential to influence activity in one another. Although the spatial location was found not to be significant, the mean results suggest what was hypothesized; that when the two stimuli are coupled together within the same spatial location, learning is improved more so than when they are uncoupled, and from the results on temporal order, this occurs more when the visual stimulus is presented first (Appendix 2). It could be that because attention was not directed specifically to a stimulated side as in an oddball paradigm, that the spatial location was not significant. Slight attention would be directed to the side where the visual stimulus lay, but participants were not focused completely to a certain side while ignoring the other. As the mean results are enhanced more so when the two modalities are coupled, this shows that cross-modal links may exist between vision and touch, and that they are more affected when the two senses have a spatial location in common.

A reasoning behind the findings of this study is the fact that learning strategy between subjects was not controlled for. Many individuals reported learning the dot/dash patterns by paying attention to the tactile sensation, whereas the majority of subjects would visualize the dots and dashes as they were receiving them. A couple of individuals would learn by judging the length of the pattern and compare it to the other pattern lengths within that letter set, what's more, some subjects would make a "musical tune" from the dots and dashes even though they could not hear due to white noise. Thus, each individual had a different way of remembering the associations between tactile and vision during the training sessions. By having subjects training with different strategies, some of the mentioned strategies may be better learning tactics than others, resulting in various individuals being better skilled at the task than others. However, because a particular learning approach was not assigned, the subjects were able to use the tactic that they felt was easiest for them in order to learn the task, therefore all subjects would have completed the associations between tactile and vision to the best of their ability. This was different than Ohara et al.'s (2006) study where all subjects were trained beforehand to ensure that they all used the same strategy for task performance. The participants in the Ohara et al. (2006) study were subjected to the task even before recording began as all subjects had to reach an 85% correct rate (CR) in order to move on with the actual recording of the task. Therefore, this would not so much be a measure of learning, but of discrimination as the task was already learned.

During the initial stages of learning, when the visual modality was presented prior to the tactile modality, this was found to be a resource for learning. As this was what was hypothesized, it can be said that bottom-up processing is occurring at this stage whereby the visual system primes the somatosensory system. Learning at this stage is easily influenced as the stimuli are very new, therefore subjects would have used all of the information given to them (i.e. tactile and visual) in order to learn the task, however at later stages of learning, where there was found to be no benefit of temporal order, the visual stimulus may not have been as relevant for learning and may have even become a distractor to subjects. The thought behind this is that participants have known the

English alphabet their entire lives, and therefore did not feel challenged when receiving the letters as a visual resulting in them not having to concentrate as much visually to help them learn the tactile patterns. Research shows that focusing on task-relevant information and ignoring distracters is reflected in the enhancement and suppression of neural activity related to working memory, such that when there is an increased memory load a rise in performance is not dependent upon the enhancement of relevant information but the filtering of irrelevant information by neural suppression (Zanto and Gazzaley, 2009). Similarly, the focus on a single sensory modality results in behavioural decrements and decreased cortical activations responsible for processing unattended sensory stimuli, a strategy known as cross-modal deactivation (Mozolic et al., 2008). Thus it could be because of an increased memory load due to the novelty of the tactile stimuli, along with the expertise of the visual stimuli, that participants are concentrating more so on the tactile stimulus, and the visual stimulus becomes suppressed due to familiarity. However, the participants know that the visual stimulus is important to learning the task, and that is why at the subsequent testing blocks, the tactile first condition does not become significant over the visual first condition, but there simply becomes no difference between the temporal order of the two modalities.

Different testing strategies were also used between this study and the previous ones on cross-modal associations between vision and touch. Previous studies (Eimer and Driver, 2000; Eimer et al., 2001; Ohara et al, 2006) all used an oddball paradigm where subjects differentiate between target and non-target stimuli. The methodology used here was that of associative learning whereby subjects have to correlate between two modalities. The differences between a cross-modal task that involves choosing to attend to one type of stimulus while ignoring the other type, and a cross-modal task where information from both modalities is required, may account for differences between the previous studies and this one.

This study determined the behavioural effects of introducing a visual stimulus to a tactile learning paradigm, and how alterations to the visual modality affect tactile learning. As predicted from Tang et al. (2008), learning occurred over subsequent testing sessions as subjects acquired the knowledge to recognize the associations between the tactile and visual stimuli. It was also shown that presenting the visual stimulus prior to the tactile stimulus was beneficial to performance at least during the initial stages of learning. This became indifferent by the final testing stage. Also, contrary to the hypothesis, having the visual and tactile stimuli within the same spatial vicinity did not improve performance. In summary, during the early stage of a cross-modal learning paradigm, presenting a visual stimulus prior to a tactile stimulus can results in enhanced learning due to bottom-up processing.

It is also important to determine what is occurring at the level of the cortex, specifically what is happening to the somatosensory ERP traces due to cross-modal links between vision and touch as the visual stimulus is manipulated. An encephalography approach will give insight into the latency and amplitude alterations to the somatosensory ERP, brought on by making temporal and spatial manipulations to one of the modalities within a cross-modal pair. Study two addresses this topic.

Easy		Hard					
A	____	C	_·_·	Y	_·__	X	_··_
B	_···	E	··__	L	·_··	Z	__··
H	····	F	··_·	P	·__·	O	__··_
I	___·	T	·_·_	Q	__·_	V	··__·

Table 1: Morse code letters and their corresponding dot and dash patterns

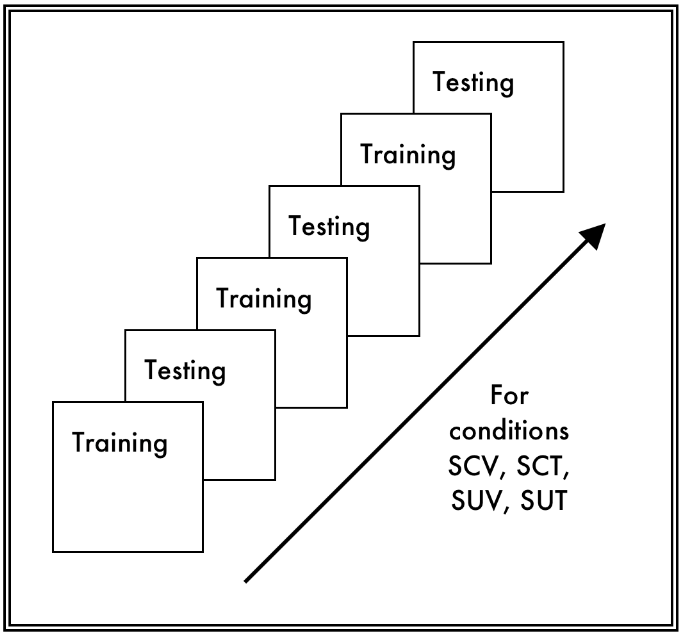

Figure 1: Study one blocking procedure

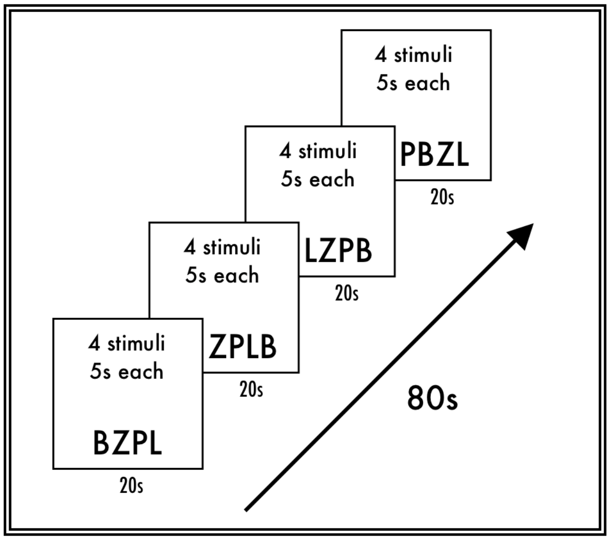

Figure 2: Study one training procedure

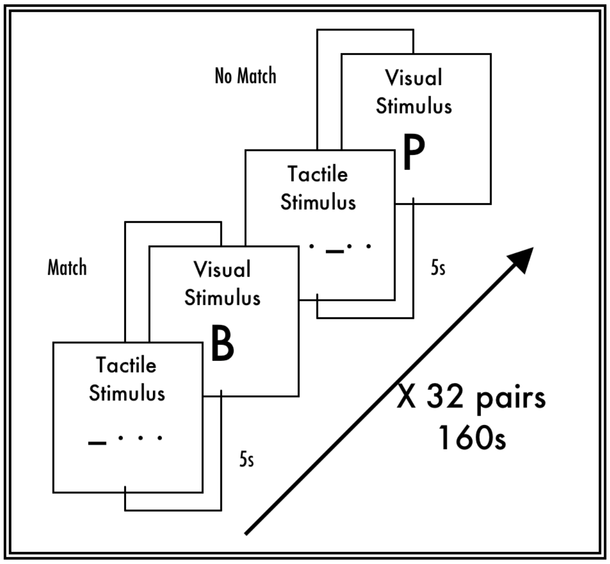

Figure 3: Study one testing procedure

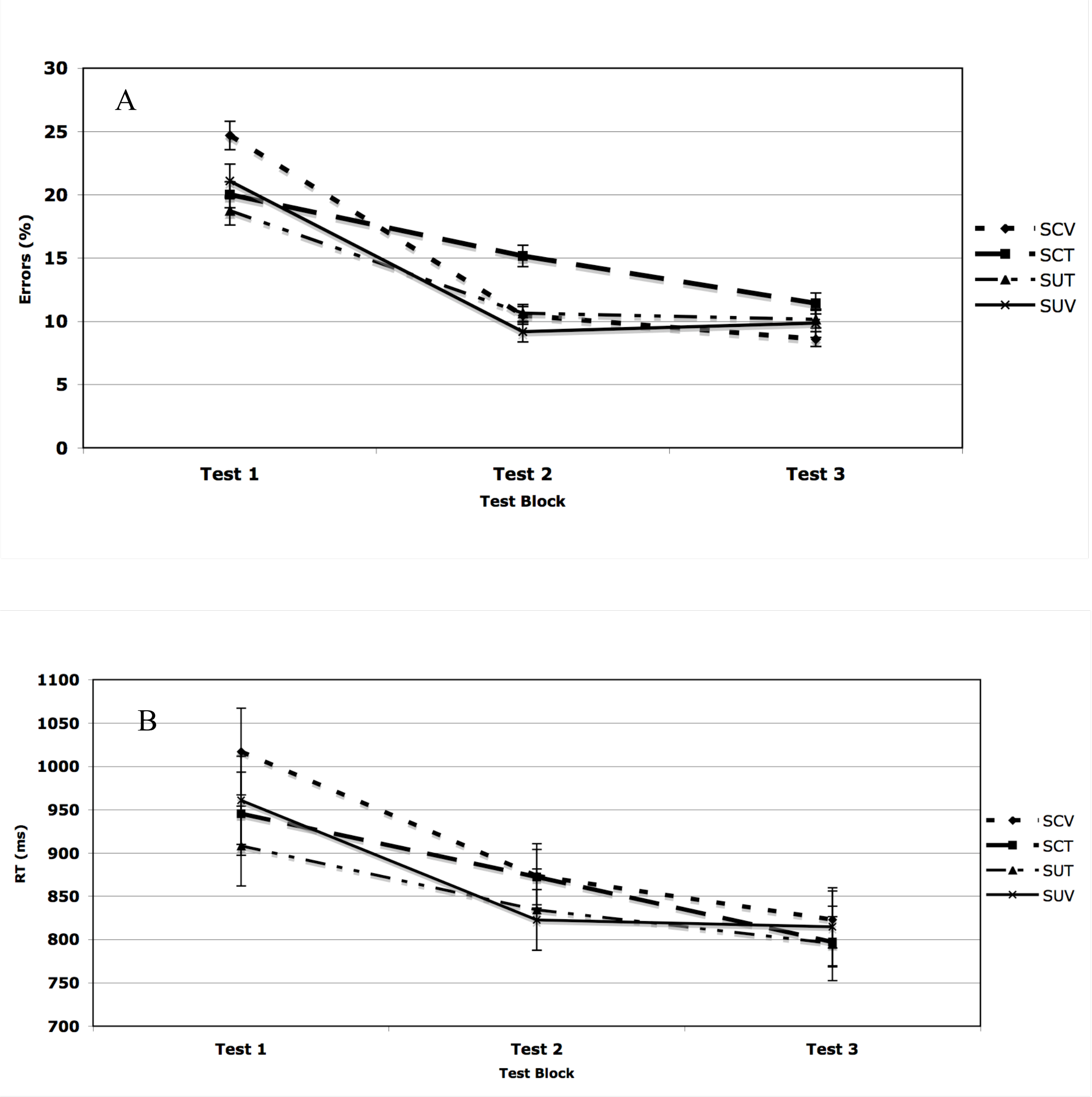

Figure 4: (A) Average (N = 20) number or errors, as a percentage of the number of Test stimuli (32), at each test block (B) Average (N = 20) reaction time at each test block.

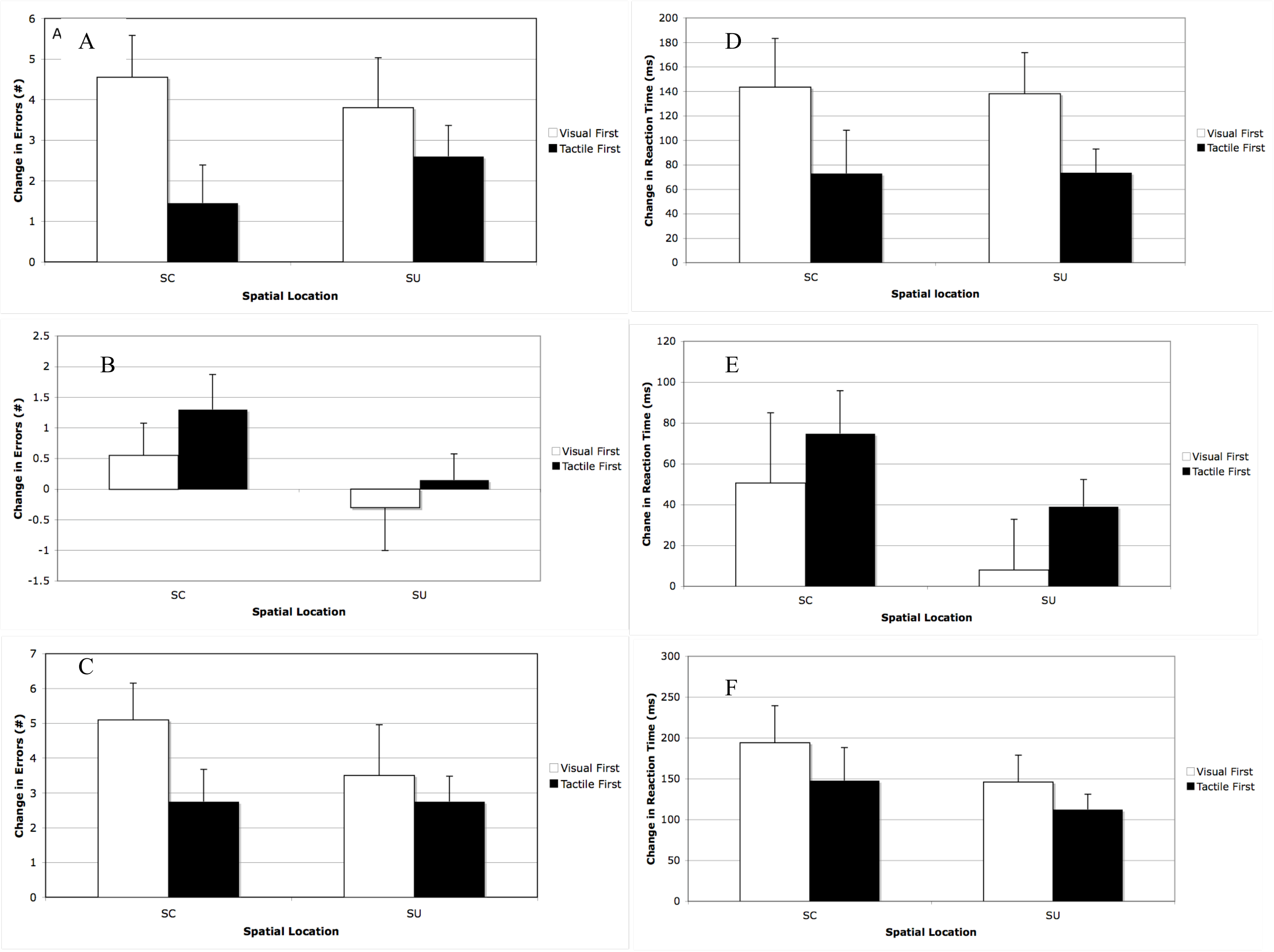

Figure 5: The average (N = 20) change in the number of errors between tests 1 & 2 (A), 2 & 3 (B), and tests 1 & 3 (C) for temporal order (visual first and tactile first) at spatial location (coupled (SC) and uncoupled (SU)). The average (N=20) change in reaction time between tests 1 & 2 (D), 2 & 3 (E), and test 1 & 3 (F) for temporal order at spatial location.

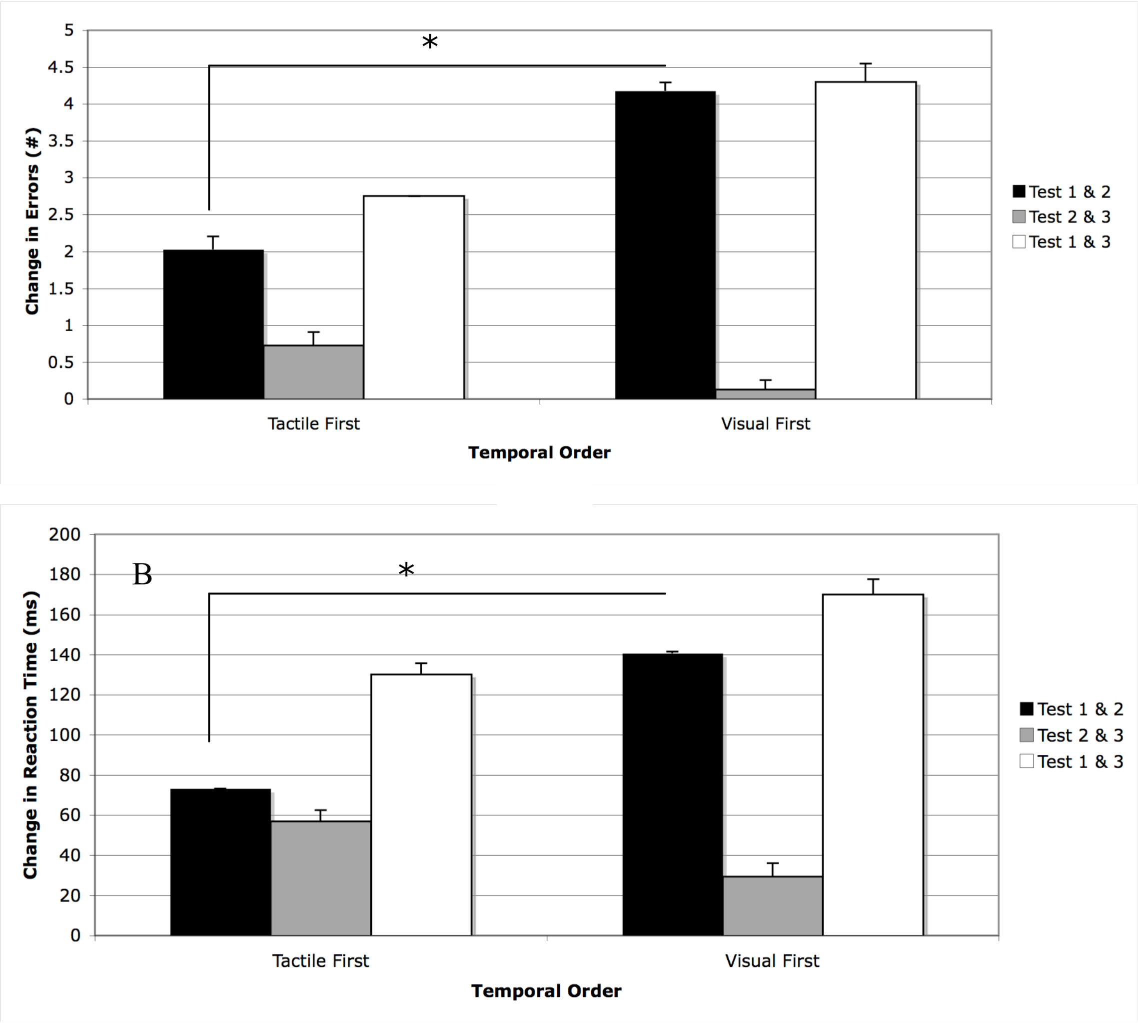

Figure 6: The change in the number of errors (A) and change in reaction time (B) at temporal conditions tactile first and visual first taken by collapsing across spatial location (coupled and uncoupled) for the differences between tests 1 &2, 2&3, and tests 1 & 3.

Chapter 4: Study Two: Visual-tactile associations: An investigation of electrophysiological mechanisms

Overview: The influence of different modalities on one another may also be represented at the level of the cortex as cross-modal relations between vision and touch show event related potential enhancements when these two modalities are represented cross-modally. The intent of this current study was to investigate changes to somatosensory-related ERPs in response to the manipulation of temporal order and spatial location of the modalities. It was hypothesized that preceding a tactile stimulus with a visual one, and having the two modalities coupled within a common spatial location, would result in an enhancement of the somatosensory related ERPs. Participants were given a Morse code paradigm and had to pay attention to the associations between a visual letter of the English alphabet, and a tactile dot/dash punctate stimulus on their left index finger. Because leaning was not to be measured, it was made impossible due to the number of stimuli. Four conditions were tested: two whereby spatial location of the visual stimulus was manipulated, and two whereby stimulus order was manipulated. The lack of spatial location, in study one, affecting the cross-modal interaction was noted, causing a collapse across the spatial differences and making the temporal order a primary concern. The main findings were a significant P100 amplitude and latency in conditions where the tactile stimulus was presented before the visual, as well as a noticeably absent N140 amplitude in the same condition, concluding that presenting a tactile stimulus prior to a visual one may have an attentional effect on the P100, however further research is needed.

4.1 Introduction

The importance of this study was to see how the manipulation of the visual stimulus, as in study one, would affect the somatosensory tactile ERPs. Eimer and Driver (2000) determined the existence of cross-modal links between vision and touch in a study where subjects were responsible for detecting a tactile or visual target on an attended side, altogether ignoring stimuli of an irrelevant modality on the unattended side. When compared with unattended stimuli, tactile stimuli at attended locations elicited enhanced negativity of the ERP in all conditions where tactile sensation was relevant, giving notion to the fact that cross-modal links do exist between vision and touch. Eimer et al. (2001) also found these links to exist as tactile ERPs were enhanced when the tactile and visual stimuli shared common external locations. Ohara et al. (2006) looked at somatosensory discrimination based on the expectation of a previously paired visual stimulus. ERP results indicate an enhancement when subjects had to discriminate between a cross-modal task (visual and tactile) rather than a unimodal task (tactile and tactile). They contribute this enhancement to top-down processing or the cognitive expectation of the visual stimulus when it was presented after the tactile stimulus. From these previous results, the initial hypothesis was that presenting the visual and tactile stimuli within the same spatial location would enhance the amplitude of the somatosensory ERPs, and that introducing the visual stimuli before the tactile stimuli will enhance the ERP amplitudes through bottom-up processing from visual to tactile, based on Ohara et al. (2006). The results from study one specifically found behavioural evidence that temporal order of the tactile and visual stimuli had a beneficial effect to learning during the initial stages. The importance of study two was to expand from the results of study one and provide an ERP experiment that would investigate the underlying mechanisms involved with the cross-modal associations with vision and touch.

4.2 Materials and methods

4.2.1 Subjects

Twelve healthy volunteers were tested (9 females, 3 males; age range 20 to 36 years; average 23.67 years). Exclusion criteria were skilled knowledge of Morse code, or the presence of any neurological diseases. All subjects gave their informed consent to participate in the study, and the experimental procedures were approved by the Office of Research Ethics at the University of Waterloo.

4.2.2 Experimental procedure

This study was designed to test the ERP response of somatosensory-visual associations based on spatial location and stimulus order. It was anticipated that coupling visual with tactile stimuli, and presenting the visual stimuli prior to the tactile stimuli, would enhance the somatosensory ERPs.

The same four conditions as in study one (*SCV, SCT, SUV, SUT*) were presented, including additional conditions, *tactile only* and *visual only*. In the *tactile only* condition subjects received tactile stimulation, in the form of Morse code patterns, without any associated visual letters to represent the patterns. Subjects were required to look at a marker in the middle of the computer monitor as they received stimulations, and pay attention to the tactile patterns without relating the patterns to a corresponding letter. This allowed for a baseline measurement of the somatosensory ERPs to tactile patterns alone, and was used as a comparison to when the visual stimuli were introduced. Similar to the *tactile only* condition, the *visual only* condition involved visual stimuli in the absence of tactile stimuli, allowing for a baseline measurement of visual ERPs.

All six conditions were presented based on a Latin Square design, and each condition was presented in two blocks of 50 stimuli, with each condition presented once before being presented a second time. Approximately 600 stimuli were needed to obtain around 100 artifact-free (free of eye blinks and large muscle movements) trials to average for each condition. All letters of the English alphabet were presented at random so that learning would not occur.

In order to keep the participants motivated, a pseudo test, similar to study one (Figure 3), was implemented after every two conditions, however no behavioural performance data was collected.

Participants received 70 dB of white noise (70 dB; Stim2, Neuroscan, Compumedics USA, Ltd. Corporation, Charlotte, NC, USA) throughout the experiment, to avoid any vibrotactile tracking by means of audition. See Figure 7 for the overall experimental design.

4.2.3 Data acquisition

Electroencephalographic (EEG) data was recorded from 32 electrode sites (Acti-cap, Brain Products, Germany) in accordance with the international 10-20 system for electrode placement, and were referenced to AFZ for collection and then re-referenced to linked mastoid electrodes in the analysis phase. All channel recordings had impedances of 5 kΩ or less. EEG was amplified (20,000x), filtered (1-100 Hz) and digitized (500

Hz) (Synamps2, NeuroScan 4.3, Compumedics, Charlotte, North Carolina, USA) before being stored for off-line analysis. Any EEG that contained ocular and/or movement artifacts was excluded by the experimenter from the analysis process by first visually inspecting it and then manually eliminating those components consistent with topographies for eye blinks and movements. ERPs were extracted by averaging together epochs time locked to the presentation of the tactile stimulus (-100 to 1000 ms). ERPs were baseline corrected post-stimulus and filtered using a bandpass filter (1-30 Hz). Approximately 80 artifact free stimuli were then used to derive the ERPs for each subject and condition.

4.2.4 Data Analysis

The results from study one concluded that spatial location does not affect tactile-visual associated learning, therefore for the analysis of study two results, the four conditions were collapsed into two based on temporal order (*visual first*, *tactile first*), which had shown an effect in study one for the initial stages of learning. A one-way repeated measures ANOVA was used to test the effects of the conditions (*tactile only*, *tactile first*, and *visual first*) on each of the ERP amplitudes and latencies of the expected components (P60, N80, P100, and N140) at electrode sites CP4, FZ, CZ, PZ. It was hypothesized that ERP amplitudes would be influenced by the order of stimulus presentation that is, an enhancement of the associated somatosensory ERPs as vision precedes tactile. Significant ANOVAs were followed up with a Tukey post hoc test. Subjects were excluded from the ANOVAs if they did not present a particular component in either two or more of the conditions. All statistical tests were performed using SAS 9.1 (SAS Institute Inc., Cary, NC, USA).

4.3 Results

P60 & N80

The P60 was quantified at the CP4 location because this is where it was maximal overlying the contralateral SI. Average amplitudes were 1.3μV, 0.9μV and 0.7μV for the *tactile only*, *visual first*, and *tactile first* conditions, respectively. The average latencies were 62.18ms, 55.09ms, and 54.36ms for the *visual first*, *tactile only*, and *tactile first* conditions, respectively. Although at electrode site CP4, the P60 ERP was apparent, there was no significant effect of task condition on either the amplitude ($F_{2,20} = 0.86$, $p = 0.44$) or the latency ($F_{2,20} = 0.84$, $p = 0.45$). At electrode site CP4, the N80 ERP was apparent however, there was no significant effect of task condition on either the amplitude ($F_{2,20} = 2.38$, $p = 0.12$) or the latency ($F_{2,20} = 0.94$, $p = 0.41$).

P100

The P100 amplitude, at CP4, showed a significant change ($F_{2,18} = 7.45$, $p = 0.004$), and post hoc analysis (Tukey test) confirms that contrary to the hypothesis the *tactile first* condition had the greatest amplitude (mean = 2.9 μV) and was significantly greater than either the *tactile only* (mean = 1.2μV) or *visual first* (mean = 0.5μV) conditions (Figures 8 & 10). The topography graph (Figure 10) of the P100 at electrode site CP4 shows a similar distribution across conditions. There is a positive bilateral spread across the parietal region, but perhaps the greatest difference between the conditions is the large positive midline within the *tactile first* condition. This main difference coincides with the ERP trace. The P100 latency, at CP4, was also significant ($F_{2,18} = 7.91$, $p = 0.0034$), and post hoc analysis (Tukey test) showed that the P100 latency in the *tactile only* condition was significantly different (mean = 71.2ms) than either *tactile first* (mean = 141.4ms) or *visual first* (mean = 117.2ms) (Figures 8 & 10). At electrode site FZ the P100 latency was significant ($F_{2,22} = 11.09$, $p = 0.0005$), and a Tukey test showed that the *tactile only* condition (mean = 55.67ms) was significantly different from *tactile first* and *visual first* conditions (means = 117.67 and 101.17 ms respectively) showing that the frontal distribution only emerges under the bimodal conditions. Also at CZ P100 amplitude was significant ($F_{2,22} = 6.11$, $p = 0.008$), with *tactile first* (mean = 3.7µV) being significantly different from both of the other conditions (*visual first* mean = 1.8µV, and *tactile only* mean = 1.6µV) as shown by the Tukey test. The P100 latency was also significant ($F_{2,22} = 5.59$, $p = 0.01$) with *tactile first* (mean = 126ms) being significantly different than *tactile only* (mean = 86ms) as shown by the Tukey test.

N140

The N140 ERP was determined to be significant ($F_{2,18} = 3.91$, $p = 0.04$) in amplitude at the CP4 electrode site. Furthermore, post hoc analysis (Tukey test) showed that the *tactile first* (mean = -0.7µV) condition was significantly different from the *tactile only* (mean = -2.2µV) condition, but not significantly different than the *visual first* (mean = -1.8µV) (Figures 9 & 10). The topographical distribution (Figure 10) for the N140 at electrode site CP4 has similar distribution across the *tactile only* and *visual first* conditions. The greatest negativities are apparent within the frontal region. At electrode site FZ the N140 latency was significant ($F_{2,18} = 5.89$, $p = 0.01$) and Tukey test showed *tactile first* (mean = 172.8ms) to be significantly different from the *tactile only* condition (mean = 98ms).

4.4 Discussion

In this study, the electroencephalographic response to tactile-visual associations was measured. It was hypothesized that presenting the visual stimulus prior to the tactile as well as the presentation of the visual stimulus within the same spatial location as the tactile modality would enhance the somatosensory ERPs. However, due to the results of study one where spatial location of the tactile-visual association was found not to be significant, the results of study two are based on the collapsed effect of temporal order. Thus, combining the two conditions whereby tactile was presented first (SUT + SCT) and visual was presented first (SUV + SCV) gives results based on temporal order only (*tactile first* vs. *visual first*). The main findings of this study were a significantly enhanced P100 amplitude and latency, at electrode site CP4, in the *tactile first* condition over the other two conditions and to the point where the N140 was not present in this condition.

There were no significant effects of the modality manipulations on P60 amplitude suggesting that there were no differences at the early stages of processing between conditions. This is similar to other experiments (Eimer and Driver, 2000; Eimer et al., 2001; Ohara et al., 2006) on the cross-modal relations between vision and touch, and is representative of a lack of higher order activity at an early stage.

At electrode site CP4, situated over the primary somatosensory cortex, the P100 was found to have a significant amplitude change in the *tactile first* condition over *tactile only* and *visual first*. This result is opposite to that hypothesized whereby the *visual* first condition would result in the significant amplitude difference. Ohara et al. (2006) found P100 to have a significantly higher amplitude during a tactile-visual cross-modal control tasks compared to tactile-tactile unimodal control tasks, and no significant change in the tactile-visual cross-modal delayed matching-to-sample task over the tactile-tactile unimodal delayed matching-to-sample task. They state from their results that the P100 may only be involved in the transfer of cross-modal information. However the difference in comparison to the present study is the level of challenge. Ohara et al. (2006) used a matching task where subjects had to distinguish between two modalities each with two levels of information, whereas the subjects in the present study had to distinguish between 26 different dot/dash patterns and their corresponding letters. Also, the Ohara et al. (2006) methodology had subjects already exposed to the task before recording, therefore the task to them was not novel, as in this case. As a result the enhancement of the P100 in the *tactile first condition*, and the suppression of the P100 in the visual-first condition, may be due to the focus on learning the tactile patterns and finding the visual letters as a distractor because they are already learned through experience. Different subjects than those from study one participated in study two because measuring learning was not the goal of this study, but to determine the mechanism behind tactile-visual interactions. Therefore, the task would be novel to these subjects resulting in the visual stimulus as a distractor. Although this study was not measuring learning, subjects did not know this, and were given a testing session just so they would pay attention to the task.

However, they could have been using learning strategies similar to the subjects in study one, where all learning strategies involved focus on the tactile pattern in order to learn the task. Whether it was concentrating on the tactile stimulation, visualizing the dot/dash patterns or trying to judge the length of the patterns, focus would have been on the tactile and not the visual. Even though the tasks were identical for both the *tactile first* and *visual first* conditions (they both involved the twenty-six letters of the English alphabet), the task may have been more difficult when the tactile was presented first because when given a tactile pattern it would be hard to distinguish it as a letter from the other twenty-five patterns representing a letter because there is more information given and harder to keep the patterns of dots and dashes in mind. Whereas when given a visual letter first, subjects are already familiar with it and wouldn't find it a challenge to know what letter is presented. The P100 is known to increase in amplitude when subjects concentrate on receiving a tactile stimulus (Spackman et al., 2006), and this can account for the great increase in the P100 amplitude when the tactile dot/dash pattern is presented first, as there is great concentration to try and learn this novel task. In relation to Dionne et al. (2009), who purposely kept the attentional requirements within their bimodal task the same in order for the relevance of the modalities to be equal, the attentional demands between the different modalities within the current task was not equal, and the relevance of the tactile stimuli seemed to be greater than the visual.

An unexpected result that was not hypothesized was a change in the latency of the P100 at electrode CP4. The *tactile first* and *visual first* were both found to be significantly different from *tactile only*. This could be due to a sustained focus on learning the tactile pattern because as previously mentioned it was a difficult task.

The N140 amplitude also does not support the hypothesis that *visual first* would enhance amplitude, as the *tactile first condition* was the only condition found to be significantly different from the *tactile only* condition. The N140 has been shown to increase in amplitude the more attention there is concentrated on the stimulated hand (Garcia-Larrea et al., 1995). From this, it can only be suggested that subjects were not concentrating on their stimulated finger during the *tactile first* condition, as in this condition the N140 is absent. This seems unlikely, as was mentioned previously through subjects' learning strategies that all attention was focused on the tactile stimulus. It could be that because the tactile stimulus is focused on intently, as represented by the enlarged and prolonged P100, that the P100 overthrows the N140. This could imply that cross-modal associations are not occurring, as it is just the somatosensory stimulus getting processed, whereas the visual stimulus is being ignored. This could all be due to the difficulty of the task.

Certainly, more research is needed to investigate the precise mechanisms driving these tactile-visual cross-modal interactions. Possible future directions are mentioned in the next section of this thesis.

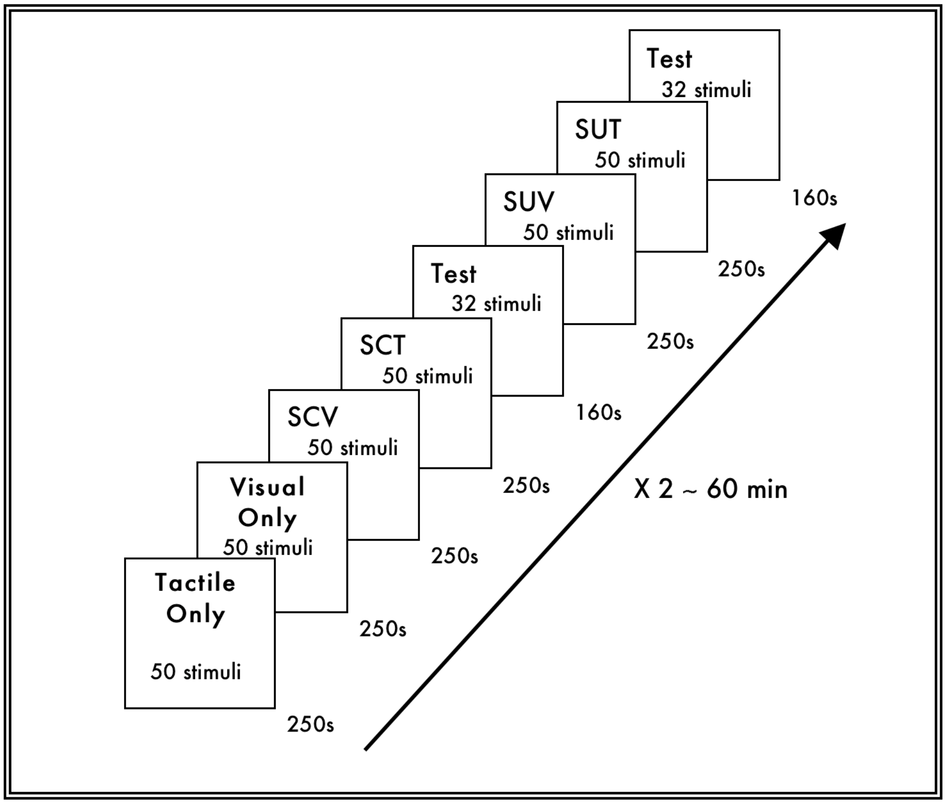

Figure 7: Study two experimental design

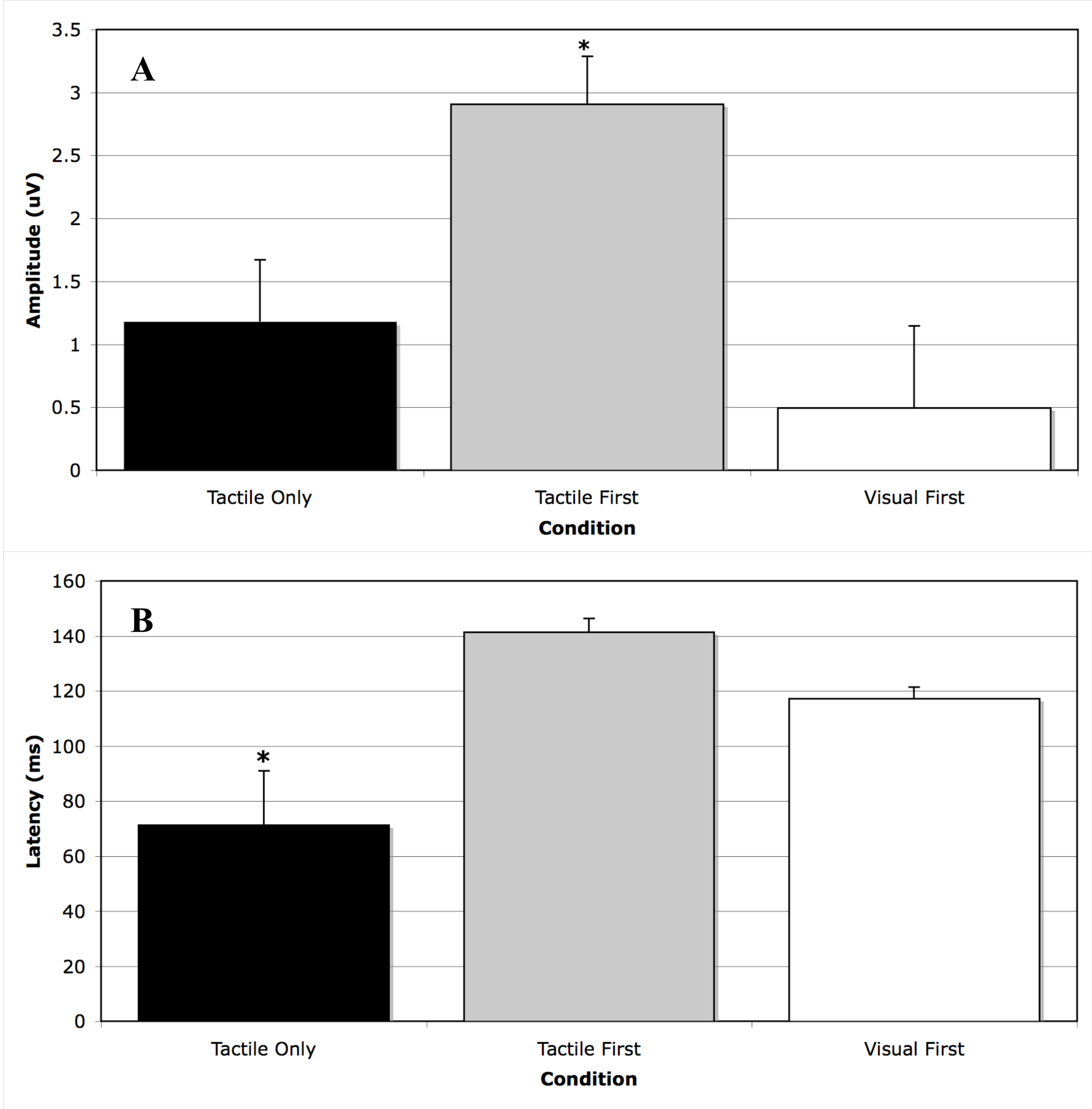

Figure 8: Mean P100 ERP amplitudes (A) and latencies (B) at electrode site CP4

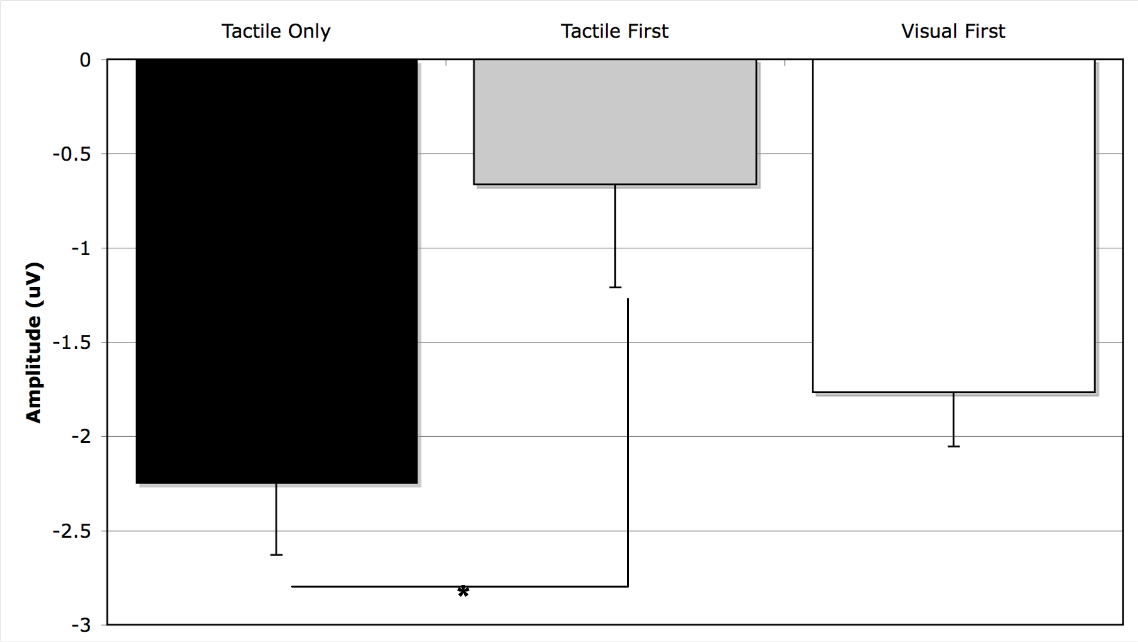

Figure 9: Mean N140 amplitudes at electrode site CP4

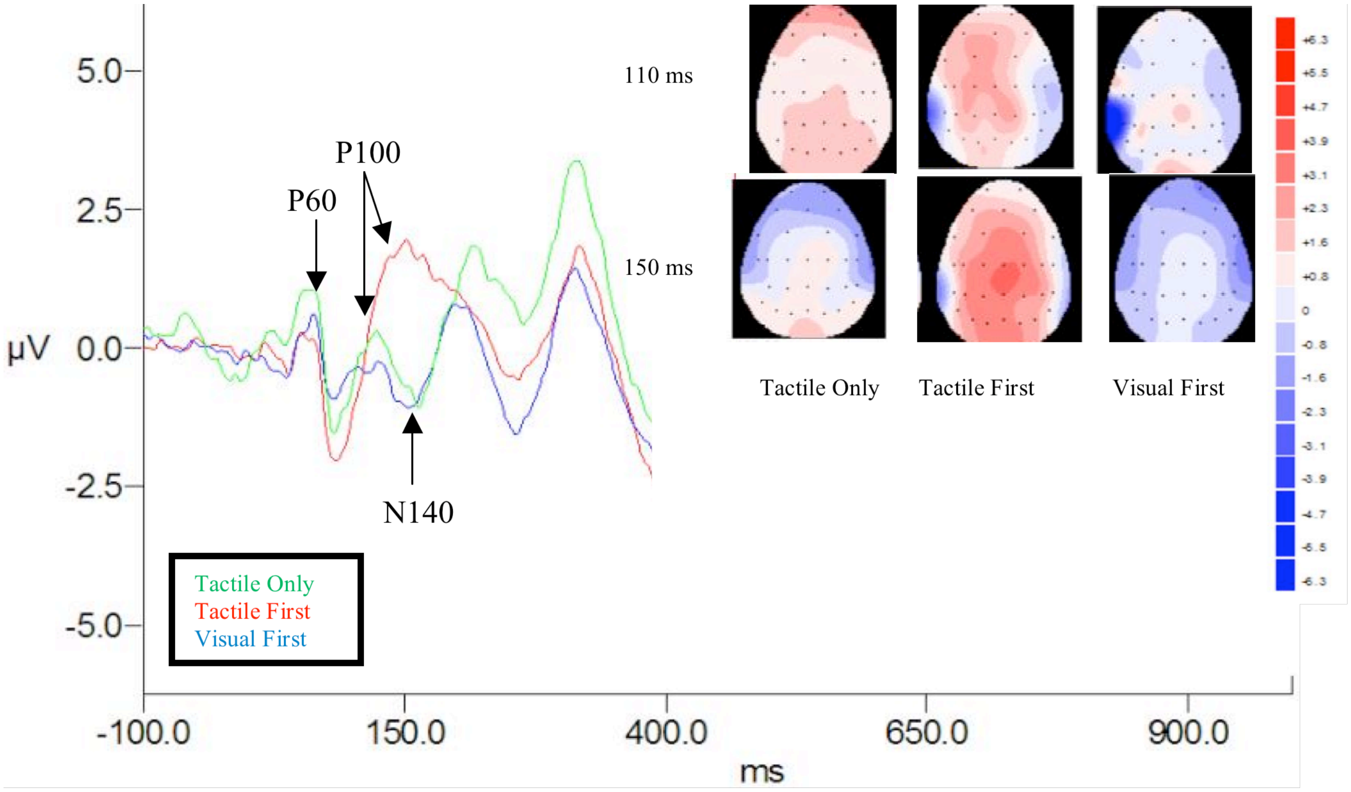

Figure 10: Grand-averaged somatosensory ERPs elicited at electrode site CP4 in the Tactile Only, Tactile First, and Visual First conditions, by tactile stimuli to the left index finger.

Chapter 5: General discussion

5.1 Limitations and future directions

The two studies that made up this thesis involved visual stimuli consisting of letters of the English alphabet. Although consistent with the idea of Morse code and the previous study (Tang et al., 2008) on which this research extended from, the letters would have been too familiarized by the participants through life-long exposure. As a result, the visual stimulus may well have been treated as irrelevant during a cross-modal task where both types of stimuli were important for performance. Previous studies (Eimer and Driver, 2000; Eimer et al., 2001) of cross-modal relationships between vision and touch all involved a task where concentration was focused on a single modality while ignoring the other (oddball paradigm). Thus, it would be appealing to perform this task with visual stimuli completely novel to the participants such that concentration would be required equally upon both modalities. If this were the case, it could be predicted that spatial location may have a learning effect because participants would have to concentrate on the visual stimulus without ignoring it or treating it as a distractor. If the novel visual stimulus is coupled with the tactile stimulus within the same spatial location this could enhance performance because cross-modal associations are mediated by external locations that are common between the modalities (Eimer et al., 2001). Similarly, the temporal order may find conditions in which vision is presented first to be beneficial to performance, as vision would be equally important to the task, and the visual stimulus would then prime the somatosensory with information that is imperative for the somatosensory learning.

It would also be important to conduct further studies into the electrophysiological mechanisms behind tactile-visual cross-modal associations. Study two attempted to look at this however, similar to study one, the task involved a visual stimulus that was too familiar to participants, which could have caused it to be treated as a distractor and become irrelevant to the task. The task may also have been too challenging (with 26 different dot/dash patterns to distinguish) which may have resulted in an elevated and prolonged P100 during the *tactile first* condition, due to attention focused on the tactile stimulus alone. It would be interesting to conduct a study whereby a fewer number of stimuli pairs are presented to make the task easier and allow the focus to be equal between modalities, therefore, the P100 amplitude and latency may diminish over time and the N140 may become present.

5.2 Conclusion

Overall, the results of this thesis provide evidence for cross-modal relationships between vision and somatosensation, as they are manipulated both spatially and temporally. Specifically, that a common spatial location between the two modalities may not be required to enhance learning, and the presentation of the visual stimulus prior to the tactile stimulus may enhance learning at the beginning stages. Reasoning for these results may be the familiarity of the visual stimulus causing it to be more of a distractor than an aid to the task. The findings also elucidate possible mechanisms that underlie temporal modulation, but give rationale into continued investigation into the factors that influence cross-modal associations between vision and touch.

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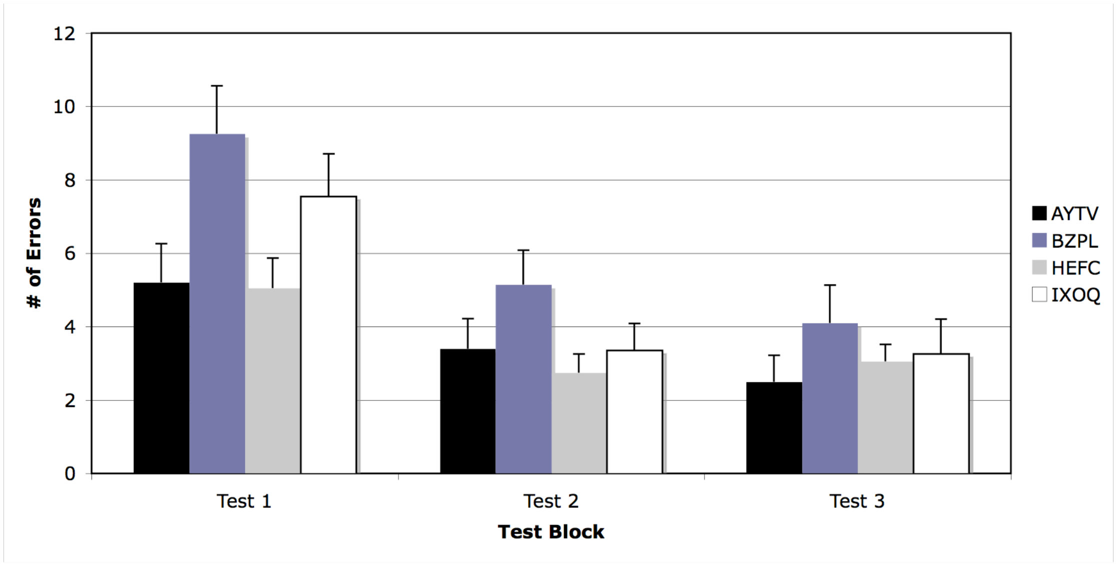
Appendices

Appendix 1

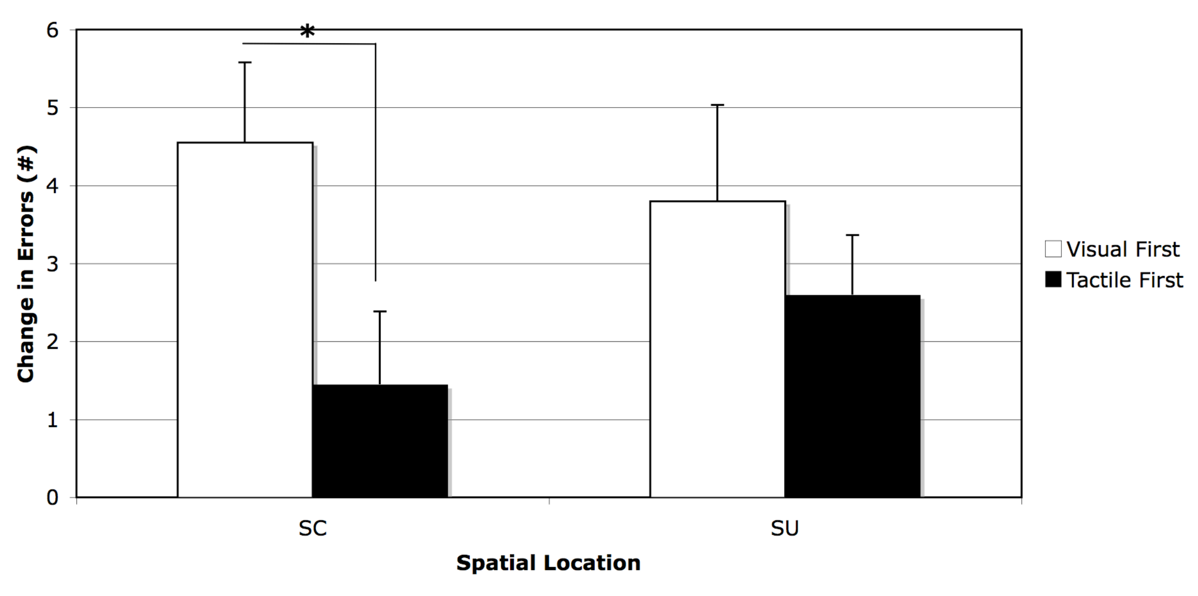
For study one a different set of letters were assigned to be used in each *training* condition based on a balanced Latin square design such that all four training conditions were paired with each letter set an equal number of times across subjects. The same letter set that was trained was tested for learning effects during the *testing* phase. The importance of using such a design was confirmed by 1-way ANOVAs with letter set as the factor (AYTV, IXOQ, BZPL, HEFC) and number of errors for each test (block 1, block 2, block 3) as the dependent measure. Results indicated that letter set was significant for test blocks 1 and 2 ($F_{3,57} = 4.38$, $p = 0.0076$; $F_{3,57} = 3.16$, $p = 0.03$, respectively), but not test block 3 ($F_{3,57} = 1.43$, $p = 0.24$).



Appendix 1 Figure: Study one's mean (N = 20) number of errors per letter set at each testing block.

Appendix 2

Although the 2-way ANOVA on the differences in the number of errors between *test blocks* 1 and 2 revealed that there was no interaction between spatial location and temporal order (p = 0.35), Figure 5A seems to show that the effect of temporal order is driven by one spatial location. However, the post hoc Tukey test does not directly test this in the 2-way ANOVA, therefore separate 1-way ANOVAs for each spatial location were used to test the effect of temporal order on the number of errors made on the difference between test blocks 1 and 2. The results conclude that temporal order is significant when the stimuli are spatially coupled ($F_{1,19} = 8.08$, p = 0.01), however temporal order is not significant when the tactile and visual stimuli are uncoupled ($F_{1,19} = 0.51$, p = 0.48).



Appendix 2 Figure: The average (N = 20) change in the number of errors between tests 1 and 2 for temporal order at specific spatial locations.