THE ASSESSMENT AND PROCESSING OF TACTILE SENSORY LEARNING

THE ASSESSMENT AND PROCESSING OF TACTILE SENSORY LEARNING

By

Steven Robert Passmore, Hons.B.Kin., M.S., D.C.

A Thesis

Submitted to the School of Graduate Studies

In Partial Fulfillment for the Requirements

for the Degree

Philosophae Doctorate

McMaster University

© Copyright by Steven Robert Passmore, 2012

PHILOSOPHAE DOCTORATE (2012)

McMaster University

(Kinesiology)

Hamilton, Ontario

TITLE: The assessment and processing of tactile

sensory learning

AUTHOR: Steven Robert Passmore, (Hons) B.Kin. (McMaster

University), M.S. (University of Nevada, Las Vegas), D.C.

(New York Chiropractic College)

SUPERVISOR: Professor Timothy D. Lee

NUMBER OF PAGES: xiv, 205

ABSTRACT

This dissertation examined perturbation effects during complex tactile information transmission. The four experiments provide evidence regarding sensory and information processing demands in early stages of complex tactile learning.

Experiment 1 established complex tactile learning behavioural performance.

Vibrotactile stimuli representing Morse code letters were communicated to participants with or without induced perturbation to the finger of letter reception. Response performance was measured and augmented feedback was provided retroactively.

Perturbation conditions lead to poor performance during tactile acquisition, but improved performance during application of knowledge.

Experiment 2 determined if the experiment 1 results demonstrated masking or response competition paradigms. Target "masking" is the reduced ability to detect or interpret a stimuli pattern by presentation of other information (Craig, 1985; Verrillo, 1985). Response competition is the competition or distraction from target response generation by secondary stimuli (Craig, 2000; Bolanowski et al., 2000). Experiment 2 tested response competition by spatially separating the perturbation and tactile information delivery sites.

Experiments 3 and 4 served to replicate behavioural acquisition data from experiments 1 and 2. They also extended the findings of the first two experiments by introducing neurophysiological measurement to reflect the changes associated with the two perturbation conditions. The study discerned whether the masking and response

competition paradigms from experiments 1 and 2 were predominantly impacting the peripheral or central information processing.

Results from the four studies collectively demonstrate that increased demands are placed on the sensory system during early stages of complex tactile learning when perturbation is spatially congruent with tactile information delivery. Experiments 1 and 2 revealed that attention does not supersede spatial location of perturbation, and perturbation location is paramount to yield sufficient interference to impede acquisition yet lead to enhanced knowledge retention and transfer. Experiments 3 and 4 determined that cortical information processing associated with complex tactile information acquisition are neurophysiologically differentiated when relative locations of meaningful and perturbation stimuli are congruent or spatially separated. The findings from this dissertation serve as an advancement of our understanding of masking and response competition phenomenon as they pertain to complex tactile learning.

ACKNOWLEDGEMENTS

I have been very fortunate in the undertaking of this dissertation. I have had positive influences, role models and reinforcement every step of the way. While I was at the helm of the preparation of the work conducted, many tremendous people helped me to stay on course and to enjoy the journey, not simply the end result.

My supervisor Dr. Tim Lee, provided this opportunity by graciously agreeing to continue to nurture my ongoing research curiosity. A curiosity I developed as an undergraduate research assistant in his lab many years ago. Tim has had a prolific career, and is highly admired by his peers. He is a well published, diligent scientist, and is a thoughtful and humble man. His balance of career, and the pleasures of his life, including Blues music, and golf have reminded me to strive for such equilibrium in my own career, and life. I am very grateful for his guidance and attention to detail, I know that having the strong academic foundation he helped to provide will allow me to continue to learn and grow.

Dr. Bernadette Murphy, kindly opened doors for me as a mentor and role model as a clinician scientist. Her knowledge of neurophysiological techniques and their applications was the precise fit I needed to be able to take my research questions to new heights. The knowledge and skillset she has helped me to develop are tools I now have the good fortune to apply on a daily basis. She is a colleague I look forward to collaborating with in the years to come as I continue to develop my research program at the University of Manitoba.

To my other committee members Dr. Jim Lyons, and Dr. Ramesh

Balasubramanium I wish to extend my sincere thanks for their feedback, and patience as
my dissertation has developed. I look forward to visiting, and sharing new research with
them at future conferences. I would also like to thank my external committee member

Dr. Heather Carnahan, and my thesis defence committee for sharing their insight and
lending your expertise to the final presentation, and preparation of this dissertation.

Without technical expertise, very few things run smoothly. I would like to acknowledge Dr. Heidi Haavik for teaching me how to interpret SEPs data from the other side of the planet (New Zealand). I would like to thank Bernadette, Heidi and Jess Bosse for their presentations, workshops, and the meetings we had regarding teaching me SEPs experimental design and application. I would like to thank Dr. Cheryl Glazebrook (my wife) for helping me to refine my E-prime programming skills so that my research creativity would not be limited by my programming abilities. I would like to thank Kenneth Clark Dickhout (my grandfather), and Bob Passmore (my father) for their informal lessons on tool use, soldering, and electrical circuitry over the years.

No graduate school experience is complete without your peers. I am grateful for the comradery of my McMaster office mates, and the memories I have from their day-to-day interactions. In our office it felt like everyday was Christmas, and we had the decorations to prove it! I am confident that yesterday's office mates are the colleagues and fellow Faculty members of tommorrow. Trips to the Phoenix, conferences across the continent, nights playing Euchre, I am fortunate to have trained alongside such intelligent,

creative, and well rounded people.

My experience in a laboratory setting was further enriched by my interactions with the University of Ontario, Institute of Technology students. Helping them to develop as students, helped me to develop as a mentor. Also to all of those who served as participants in my studies, research is truly not possible without the people willing to share their time in the name of advancing science.

Funding is a sometimes insurmountable barrier, that I have had the good fortune not to worry about thanks to the assistance of the research community, and my profession. I would like to acknowledge the support of McMaster University teaching and research assistantships, and the Ontario Graduate Scholarship program. New York Chiropractic College, provided selfless support of my academic development through their Fellowship program, of which I was the first and hopefully not the last Ph.D. student supported. The fellowship opportunity was brought to my attention by my clinical mentor and former colleague at the Buffalo Veterans Affairs Medical Center, Dr. Andrew Dunn. The support of New York Chiropractic College's research director Jeanmarie Burke, and vice president Michael Mestan have helped fascilitate the opportunity to disseminate my research findings at clinical conferences.

It was not my expectation to be able to attain, and commense a full time appointment as a Faculty member at a medical-doctoral university while still a graduate student, but thanks to Dr. Allan Gotlib and the Canadian Chiropractic Research Foundation, I was able to do that. The support of the chiropractic profession has been

unparalleled in creating career opportunities for chiropractors who pursue a terminal research degree. I have the remarkable priviledge and responsibility of a research focused academic appointment, and I am extremly grateful for the opportunity.

From the first day of my life, and all through my education including today, my parents Bob and Marcia Passmore, sister Amy Passmore and my grandparents have provided encouragement, celebrated accomplishments, and created an environment of love and support. They afforded me the life choices to follow my vision, and instilled me with a moral compass. It is the combined skillsets of interacting with people, public speaking, having the confidence to voice my opinion, self discipline and the dedication to never give up that I owe most to them.

I also would like to acknowledge the unwaivering support of my peer, colleague, wife, best friend and equal Dr. Cheryl Glazebrook. She supported my decision to pursue a Ph.D., and has provided her encouragement and expertise with every step of the journey. I have the great priviledge of being in a relationship with someone who truly understands the day-to-day struggles, and successes of my working and personal life, and I am honoured to be there for her too.

For the past two years, as I have been working on my dissertation, I have had my life enriched by the presence of a new little person, my son Reed. As he experiences the environment around him for the first time, I get to share and help him to understand the wonders of the world that in our adult life sometimes seem trivial. My journey through academia from 1997 (when I began my undergraduate studies) to 2010 (when Reed was

born), was a life with very little interaction with children. To quote Arcade Fire "I feel like I've been living in, a city with no children in it". I never realised how much I missed the perspective of a child in my day-to-day activities than when Reed entered my life.

Now with Reed's new "baby brother" and my second son Trent, a new chapter of my existence begins as my formal education draws to a close.

As I have been en route to completing my Ph.D., the balance of work, and recreation has been something I have tried to maintain. I have pursued my dream of gaining experience in the film industry, and am grateful to my partner in production Bill Reilly and all the cast and crew involved in projects by "Smalltown Pictures". Writing scripts, being on sets, attending film festivals, getting a distribution deal, and occassionally seeing a finished project on television were a reminder of how much the skills developed in academia parallel other creative ventures. I am also grateful for the "blue collar wisdom" provided by my friends and family from outside of the traditional academic route. Their friendship, fellowship, perspective and support has made a long journey far more enjoyable and enriched.

I also would like to voice my appreciation to those who create the art of our society. The painters, the authors, the filmakers and most specifically the musicians/songwriters who observe the world we live in, and publically share their perspectives. These are the people who create the soundtrack and atmosphere to our lives, and music has been a great source of sustainance and enjoyment while driving, processing data, writing and working on all other phases of the academic process. Music

echoed the mood of any given day as I completed the tasks I needed to.

In closing, I would like to thank the people who have left my life, the people who are still in it, and the people whom I have yet to meet. Those from the past and present have shaped me into the person I am today, those I will meet in the future will help me to continue to grow, and provide a new source of inspiration. Academic life is a constant influx and exit of people whom change out lives immensely. In conclusion I sincerely wish to share my gratitude for everyone who has ever had the curiosity to have a dream, and had the courage and ability to follow it.

TABLE OF CONTENTS

ABSTRACT	iii
ACKNOWLEDGEMENTS	v
TABLE OF CONTENTS	
LIST OF TABLES AND FIGURES	xiv
LIST OF ALL ABBREVIATIONS AND SYMBOLS	xvi
DECLARATION OF ACADEMIC ACHIEVEMENT	xix
PREAMBLE	1
GENERAL INTRODUCTION	3
1.1 The tactile sense - reception, perception, communication and perturbation	3
Mechanical Tactile Detection & Processing	5
Tactile Attention	7
Tactile Memory	12
Short term/working memory	13
Memory for complex information	14
Tactile Learning and Communication	16
Tactile Masking	26
History of Tactile Masking	26
Target Stimulus Properties versus Mask Stimulus Properties	28
Tactile Summation/Enhancement/Negative Masking	33
History of Tactile Summation/Enhancement/Negative Masking	34
Target Stimulus Properties versus Negative Mask Stimulus Properties	35
Conclusion	36
SOMATOSENSORY EVOKED POTENTIALS REVIEW	38
1.2 The origin, and application of somatosensory evoked potentials as a	
neurophysiological investigative technique	40
Origins of Somatosensory Evoked Potentials	
Parameters for SEP generation & recording of waveforms	
SEP peak nomenclature, interpretation and generators	
The N18 Peak	
The N20 Peak	
The N24 peak	
The N30 Peak	
Utilization and Application of SEPs	
Clinical	
SEPs Study Design and Concurrent Cortical Representation	
Control/pretest SEPs then SEPs concurrent with an experimental task	
SEPs Tactile Masking/Pain Studies	
SEPs Design (Pre and Post) and Neural Reorganization/Neuroplasticity	
Conclusion	62

1.3 The perturbation of complex tactile learning	63
References	70
DOCUMENT ONE	104
Experiment 1	114
Method	114
Participants	114
Apparatus and materials	115
Design.	117
Procedure.	117
Analysis	120
Results	121
Sensory testing.	121
Acquisition	122
Retention.	122
Transfer	123
Discussion	124
Experiment 2	127
Method	
Participants	
Apparatus, materials, design, procedure and analysis	
Analysis	
Results	
Sensory testing.	
Acquisition	
Retention	
Transfer	
Discussion	
General Discussion	
Masking not Response Competition	
Summation/Enhancement.	
Future directions	137
Conclusion	
Acknowledgements	
References	
DOCUMENT TWO	
Abstract	
Experiment 1	
Method	
Participants	
Design.	
Apparatus and materials	
**	
Vibrotactile task.	
Non task specific perturbation (induced paresthesia)	164

SEP stimulation and recording.	166
Data Analysis	
Sensory data analysis.	
Behavioral data analysis.	168
SEP data analysis.	
Results	169
Sensory testing.	169
Behavioral performance	169
SEP amplitude	170
Discussion	170
Experiment 2	171
Method	172
Participants	172
Apparatus, materials, design, procedure and analysis.	173
Results	173
Behavioral performance	174
SEP amplitude	174
Discussion	175
General Discussion	176
Acknowledgements	181
References	182
GENERAL CONCLUSION	195
References	203

LIST OF TABLES AND FIGURES

INTRODUCTION

Table 1	Mechanoreceptors*/Tactile Reception Channels**.	97
Figure 1	Item "1" is the Morse code representation of the letter "P", while item "2" is the Braille representation of the letter "P".	100
Figure 2	Adapted from Neal and Fields (2010). Peripheral nerve innervation regions on the anterior and posterior skin surface of the hand.	101
Figure 3	White dots represent active pins, and black dots represent inactive pins. Sequence "1" presents: a forward "energy" mask (1A), a period of tactile silence (1B), the letter "T" (1C), a period of tactile silence (1D), a backward "energy" mask (1E). Sequence "2" presents a forward "pattern" mask (2A), a period of tactile silence (2B), the letter "T" (2C), a period of tactile silence (2D), a backward "pattern" mask (2E). The amount of time that cells 1B, and 2B are presented for determine the duration of stimulus onset asynchrony (SOA) for forward masking. The SOA for backward masking is the duration of time that cells 1D and 2D are presented.	102
Figure 4	Adapted from Gescheider, Verrillo and Pelli (1991). The right half of the illustration demonstrates a 730ms "pedestal" where a 300Hz vibrotactile stimulus was presented, this results in a high pedestal. The left half of the illustration has an additional 300ms 300Hz signal embedded within the 730ms 300Hz "pedestal" stimulus, this lowers the pedestal. Participants were challenged to identify when a signal was embedded within the "pedestal" stimuli. When the pedestal and signal were presented together the detection threshold (pedestal to overcome) was lowered (negative masking).	103
DOCUMENT	1	
Table 1	Mean Total Response Times (TRT in Milliseconds) by Condition During Acquisition in Experiments 1 and 2.	146
Table 2	Mean Total Response Times (TRT in Milliseconds) by Condition During Retention, and Transfer in Experiments 1 and 2.	147
Figure 1	Mean accuracy (percent correct) for letter identification across six acquisition trials and two retention trials for all ulnar nerve	

	paresthesia perturbation, and no paresthesia group combinations from experiment 1. Error bars represent standard errors of the means.	150
Figure 2	Mean accuracy (percent correct) for letter generation across two transfer trials for all ulnar nerve paresthesia perturbation, and no paresthesia group combinations from experiment 1. Error bars represent standard errors of the means.	151
Figure 3	Mean accuracy (percent correct) for letter identification across six acquisition trials and two retention trials for all median nerve paresthesia perturbation, and no paresthesia group combinations from experiment 2. Error bars represent standard errors of the means.	152
Figure 4	Mean accuracy (percent correct) for letter generation across two transfer trials for all median nerve paresthesia perturbation, and no paresthesia group combinations from experiment 2. Error bars represent standard errors of the means.	153
DOCUMENT	$\Gamma 2$	
Table 1	Mean Accuracy (percent correct) by Condition During Acquisition Experiments 1 and 2.	187
Table 2	Mean Total Response Times (TRT in Milliseconds) by Condition During Acquisition in Experiments 1 and 2.	188
Table 3	Mean Early SEP Component Amplitudes (in microvolts) by Condition in Experiments 1 and 2.	189
Figure 1	An example of the significant SEP amplitude increases (N20, N24) from the averaged waveform of a single participant from experiment 1 between baseline and post tactile learning (a). An example of the significant SEP amplitude attenuation (N24) from the averaged waveform of a single participant from experiment 2 between paresthesia, and no paresthesia conditions (b).	192

LIST OF ALL ABBREVIATIONS AND SYMBOLS

Ag- silver

AgCl- silver chloride

AIR – anatomically innervated region

ALS-amyotrophic lateral sclerosis

ANOVA-analysis of variance

C-6-sixth cervical nerve root level

ECG – electrocardiography

EEG – electroencephalography

EMG – electromyography

ERP(s)- event-related potential(s)

FAI- fast adapting, small receptive field

FAII- fast adapting, large receptive field

FCER-foundation for chiropractic education and research

fMRI-functional magnetic resonance imaging

IFCN-international federation of clinical neurophysiology

MEG-mangnetoencephalography

N13- negative polarity SEP waveform, 13 milliseconds latency

N14- negative polarity SEP waveform, 14 milliseconds latency

N18- negative polarity SEP waveform, 18 milliseconds latency

N20- negative polarity SEP waveform, 20 milliseconds latency

N24- negative polarity SEP waveform, 24 milliseconds latency

N25- negative polarity SEP waveform, 25 milliseconds latency

N30- negative polarity SEP waveform, 30 milliseconds latency

NMDA- N-methyl-D-aspartate

NPI- non Pacinian channel I

NPII- non Pacinian channel II

NPIII- non Pacinian channel III

OGS-Ontario graduate scholarship

P13- positive polarity SEP waveform, 13 milliseconds latency

P14- positive polarity SEP waveform, 14 milliseconds latency

P22- positive polarity SEP waveform, 22 milliseconds latency

P27- positive polarity SEP waveform, 27 milliseconds latency

P40- positive polarity SEP waveform, 40 milliseconds latency

PC- Pacinian corpuscle

PCC-percutaneous cervical cordotomy

PD-Parkinson's disease

PDA-persoanl digital assistant

SAI- slow adapting, small receptive field

SAII- slow adapting, large receptive field

S1- primary somatosensory cortex

S2- secondary somatosensory cortex

SEP(s) – somatosensory evoked potential(s)

SMA-supplementary motor area

SOA-stimulus onset asynchrony

swLORETA-standardized weighted low resolution brain electromagnetic tomography

TBI- traumatic brain injury

TRT-total response time

TVSS – tactile visual substitution system

UOIT-University of Ontario, Institute of Technology

DECLARATION OF ACADEMIC ACHIEVEMENT

I Steven Passmore, was the primary investigator and major contributor for each aspect of the research projects that comprised this thesis, including experimental design, testing, analyses, manuscript and dissertation preparation.

Dr. Bernadette Murphy provided lab space for data collection. In addition Dr. Murphy provided the equipment and research background to design and conduct the neurophysiological aspects of the experiments. She also provided feedback in the editing process of the written articles associated with this dissertation.

Jessica Bosse worked as a graduate student research assistant in Dr. Murphy's lab.

Jessica assisted in participant recruitment, and testing during all four experiments.

Dr. Timothy D. Lee was my supervisor during my thesis. Dr. Lee mentored the behavioural research design, and supplied research equipment. He also provided guidance and feedback in the generation of all written materials associated with this dissertation.

PREAMBLE

The research in this dissertation examined the effects of perturbation during the transmission of complex tactile information. A total of four experiments are organized into two documents (for the purpose of manuscript submission). The first document addressed three specific purposes: to determine if induced radiating paresthesia interferes with, (a) the acquisition and/or (b) the application of complex tactile information, and (c) to identify whether any potential interference reflects a tactile masking or response competition (selective attention) effect. The perceptual and cognitive demands of the tactile task were quantified. The impact of perturbation at different innervation regions was tested to determine if the phenomenon of masking complex tactile stimuli was driven by an attentional mechanism, or is physiological. The proposed tactile "response competition effect" (Craig & Evans, 1995) suggests that the mechanism for masking is attentional in nature. There is a competing theory that "masking" is a physiological phenomenon, which may have peripheral (at the cutaneous sensory receptor), or central origins in that there is a "cortical magnification based on innervation density" (Kekoni et al., 1990).

The second document expands on the exploration of potential peripheral or precognitive cortical changes associated with the anatomical location of a masking stimulus relative to a target stimulus for a complex tactile learning task. There were two distinct purposes to the second document. First, to determine if the masking paradigm induced by radiating paresthesia is explained as, (a) a peripheral mask (b) a central mask,

or (c) a combination. The second purpose was to determine if a response competition paradigm reveals changes in somatosensory integration similar to the masking paradigm.

A general introduction precedes both documents. The general introduction is divided into two distinct sections, the first relating to the tactile sense, the second describes the utilization of somatosensory evoked potentials as an investigative technique (for the purpose of manuscript submission). The purpose of the first section is to orient the reader to the utilization and limitations of the tactile system through exploration of tactile reception, perception, communication and perturbation. The purpose of the second section is to document the origin, and application of somatosensory evoked potentials. The general introduction closes with a brief description of the purpose and design of the present research, which is intended to place the work in context for the reader.

A general conclusion section follows the two documents to in order to complete the dissertation. The purpose of the general conclusion is to highlight the contributions of the present research to the field of tactile learning based on using a combination of behavioural and neurophysiological measures to explore the concept of information masking.

GENERAL INTRODUCTION

1.1 The tactile sense - reception, perception, communication and perturbation

The stage of encoding or detection of sensory information represents the gateway to information processing (Donders, 1868; Sternberg, 1969). According to Donders' (1868), once detected, information has an opportunity to pass through a series of processing stages prior to response generation. The response is predicted to be impeded if the quality of the stimuli in the environment is somehow degraded during that essential detection stage (Sternberg, 1969).

Stimuli presented to the human system may impact any of the five senses, but historically, touch was considered to be the most fundamental (Montgomery, 1880). Touch is the first sense to develop, as a fetus will respond to tactile stimuli at the 6th to 7th week of gestation (Berhardt, 1987). The largest sensory organ of the body, the skin, functions as an external barrier that allows for the detection of meaningful information from the environment and contains the cutaneous system. Classically the cutaneous system is comprised of receptors that detect thermal, nociceptive, or pressure stimuli. Receptors transduce environmental stimuli to electrical signals initiating the afferent pathway.

The purpose of this paper is to explore the way mechanical tactile information is detected, and review theories related to attention and memory of tactile stimuli. This is followed by descriptions of the various approaches utilized in the exploration of tactile communication, and language. The final section examines how the acquisition of tactile

information is impacted by other information presented in close temporal proximity.

Touch has capacity for both exteroceptive (from outside the body) and interoceptive (from within the body) experiences. Stimulation being presented passively to the skin surface by mechanical means is considered exteroceptive (Serino & Haggard, 2010). Exteroceptive sensation allows for discriminative judgements regarding the features or identity of a stimulus (McGlone & Spence, 2010). The interoceptive system is thought to reflect the affective feeling of touch such as pain or itch (McGlone & Spence, 2010).

Similar to its visual analog, the cutaneous system has areas of particularly high receptive sensitivity. The hand is considered the "fovea" or peak receptive region of the touch sense (Pallasmaa, 1996; McGlone & Spence, 2010). More specifically, finger tips, in particular have more sensitivity to tactile stimuli compared to other body parts (Weinstein, 1968). Perhaps consequently, the majority of tactile scientific investigation is directed toward capabilities/limitations of the hand and fingertips.

The communication of complex information to the touch system beyond simple detection is limited primarily based on two factors: tactile attention (Lloyd, Bolanowski, Howard, & McGlone, 1999) and tactile memory (Gallace, Tan, Haggard, & Spence, 2008). Many studies have examined the application of the tactile sense to conveying complex information including language (Geldard, 1957; Kirman, 1973; Sherrick, 1985). This was done historically in an attempt to improve quality of life and communication for those who were devoid of other senses (Kirman, 1973; Sherrick 1985). Language and

communication examples include but are not limited to the tactile language Braille for the blind to read, and Tadoma for the deaf to interpret mouth movements and vocal vibrations as speech.

More recently, the purpose of touch research has been to maximize the human operator interface in the workforce for fully, sensory-enabled persons (Gallace, Tan, & Spence, 2007). For example, highway rumble strips create full body vibration to alert drivers of that their current location is deviating from the center of the roadway. Rumble strip placement is selected strategically in areas of risk where driver alertness is crucial (Persaud, Retting, & Lyon, 2004). Tactile stimulation is considered a less disruptive (compared to other modalities) means to identify incoming signals from personal communication devices. In certain instances touch has capabilities that supersede those of the other senses. For example temporal discrimination in touch is superior to vision (Spence, Shore, & Klein, 2001).

Mechanical Tactile Detection & Processing

Tactile information may be revealed upon mechanical deformation of the surface of the skin. This can be achieved through active or passive touch. Active touch is the conscious effort to move an effector across the surface of the to-be detected stimuli (Gibson, 1962). An example of this would be dragging the finger tip across a series of embossed dots on a sheet of paper, as in the Braille language. Passive touch is the receipt of stimuli with no movement initiated by the recipient of the stimuli. An example of this is setting a mobile communication device such as a cellular telephone to its vibration alert

setting, then placing it in a pocket, while waiting for it to receive potential incoming communication. The majority of this review will focus on passive touch, as the study of active touch is thought to be multimodal as a result of the perceptual and proprioceptive processing involved with effector movements (Gallace, & Spence, 2009).

Passive touch is typically explored through vibrotaction, which requires use of a "tactor", a device which vibrates and delivers sensation to the body (Gallace, Tan, & Spence, 2007). The mechanical deformations created by the tactor are detected based on stimulus characteristics by four different mechanoreceptors, each with related channels in glabrous (non-hairy) skin (refer to table 1).

(INSERT TABLE 1 ABOUT HERE)

Once detected the mechanoreceptor transduces the information to an action potential that ascends the afferent nerve pathway and synapses in the dorsal column nuclei in the medulla oblongata in the brainstem. Second-order neurons carry information on to synapse in the ventrobasal nucleus, which is a relay centre in the thalamus. Third-order neurons then carry signals on to the somatosensory cortex where perception is believed to occur (Brodal, 1998).

Information processing of passive touch is believed to undergo more steps of unconscious processing than vision and olfaction prior to conscious perception (Gallace, & Spence, 2008). In their effort to explore tactile consciousness Gallace and Spence (2008) suggested that tactile signals are first unconsciously processed by the primary somatosensory cortex (S1) prior to progressing linearly to the secondary somatosensory

cortex (S2). Once information arrives at S2 it may remain unconsciously perceived until it is compared with information also present in S2 as a result of a feedback loop triggered from S2 with the posterior parietal cortex and the temporo-parietal region that provides amodal and multisensory frames of reference relative to the tactile stimuli detected. This feedback loop takes tactile-encoded information and facilitates consciousness of tactile stimuli perception. Additionally, they note there are factors that may serve to decrease or increase the success of this processing and feedback loop. When tactile information is congruent with information from other sensory modalities, conscious awareness of tactile stimuli is accelerated. In contrast, when other sensory modalities provide information incongruent with tactile information there is a delay, or even prevention of information reaching conscious processing.

Tactile Attention

Tactile attention can be cued endogenously or exogenously (Lloyd, Bolanowski, Howard, & McGlone, 1999). Endogenous attention is considered a "top-down" phenomenon, where an individual voluntarily deploys their attention to a specific sensory modality. Directed by cognition, endogenous attention can be used to capture specific tactile features or attributes of stimuli, or their location. Making the choice to focus attention to heat from the sun on one's arm is an example of a shift in endogenous attention. Exogenous attention is a "bottom-up" phenomenon, where a shift in attention to a region or modality is provoked by an external stimulus onset, sometimes in an abrupt fashion, such as a fly landing on one's hand. Spence and McGlone (2001) found that

responses were more rapid and more accurate even when a vibrotactile stimulus was not predictive of the precise location of the to-be attended stimuli, as long as the precue was ipsilateral to the target stimulus. Turrato (2004) also determined that when a non-informative tactile stimulus serves as a cue, the response to subsequent stimuli in that same modality (ipsimodal) is facilitated. He attributes any limitations in attention as likely centrally located. Based on the work of Spence, McGlone (2001), and Turrato (2004) there is an advantageous capture of attention by an exogenous precue, which provides evidence for Geldard's (1960) hypothesis that touch automatically captures attention.

Once attention is focused to the tactile sense there is difficulty shifting attention away from that modality (Spence, Nicholls, & Driver, 2001). Through multimodal reaction time study (Spence, Nicholls, & Driver, 2001) this has been observed behaviourally. They compared reaction times in the visual, auditory, and tactile domains by having participants be precued to expect an ipsimodal (same modality), or crossmodal (different modality) "go" stimuli. Regardless of modality when participants expected and received an ipsimodal stimulus, their reaction time was significantly decreased. When shifting from the tactile modality expectation to the receipt of a crossmodal stimuli, reaction time was delayed the most, compared to visual and auditory conditions.

Neurophysiological evidence has also yielded differences that may account for this through the study of event-related potentials (ERPs). The ERP studies reflect specific temporal instances where central processing is related to tactile attention.

Other than the difference noted above, many attentional phenomena related to other sensory modalities are also demonstrable in the touch domain (Hollins, 2010). These include attentional blink where for example when multiple tactile stimuli are presented simultaneously, or sequentially they are difficult to process (Hillstrom, Shapiro, & Spence, 2002, Soto-Faraco et al., 2002). In addition, replicable effects across domains have been found for temporal factors including masking (Gallace, Tan, & Spence, 2006), prior entry (Spence, Shore, & Klein 2001), pre cuing (Turatto, 2004) and stimulus onset asynchrony (Spence, & McGlone, 2001). These similarities indicate the central and possibly amodal role of information processing. However, the touch sense demonstrates some unique properties, specifically that when touch is task irrelevant it can be decoupled from attentional orienting (Eimer & Driver, 2000).

In the presence of multiple stimuli, tactile cues compete for the capacity limited resource attention. Of the most drastic factors that impact tactile attention is tactile mask presentation. A tactile mask is the interference of detection of a tactile stimulus by the presentation of an additional tactile stimulus (Craig, 1985). Gallace et al., (2006) investigated tactile change blindness, which is the decreased ability to detect a change in a stimulus on a subsequent presentation. Seven tactors were spread out over the body's surface, on all extremities and the trunk. Each tactor could be triggered independently while a pattern was created over a 200 millisecond trial. Three conditions were compared, no interval between initial and follow-up pattern presentation, a 110 millisecond delay interval between initial presentation and follow-up, and the addition of

a 50 millisecond tactile mask where all 7 tactors were fired simultaneously for 50 milliseconds between the initial presentation sequence and follow-up. The tactile mask condition yielded significantly poorer results and a 70% decrease in change detection ability was found. The question remains was this task performance impeded by the attentional shift from the mask, or the overload of the detection mechanisms of the tactile system?

Dual stimulation of the touch modality has been studied to accommodate for the discrepancy between over stimulated receptors (peripheral mask) and attentional overload. Tactile sensitivity was suppressed by heat delivered to the point of creating pain in a study by Apkarian, Stea and Bolonowski (1994). In their study both stimuli were presented to the thenar eminence (base of the thumb) of the right hand. Participants detected the presence of vibrotactile stimuli with and without concurrent heat-induced pain. The authors interpreted tactile sensitivity suppression with concurrent pain to be a "gating" of the tactile system, and based on the afferent tactile pathway entering the dorsal column tracts and synapsing in the dorsal column nuclei in the brainstem, this disruption of tactile perception is likely to occur centrally. The same findings for heatinduced pain have been demonstrated for patients with persistent musculoskeletal pain in terms of impaired ability to discriminate vibrotactile stimulus frequency (Hollins, Sigurdsson, Fillingim, & Goble, 1996; Hollins, & Sigurdsson, 1998). The opposite effect for detection was found when heat was delivered at a non-noxious intensity. Zhang, Francisco, Holden, Dennis, and Tommerdahl (2009) found that tactile detection was

enhanced by non-noxious heat.

The aforementioned dual touch stimulation studies only considered the detection of simple vibrotactile stimuli, and not complex stimuli. The dual touch stimulation studies therefore only consider the detection, and not the retention, and transfer of information acquired through vibrotactile stimulation. Participants often endogenously orient to the sense of touch, then await an exogenously driven tactile stimuli as the to-beattended stimuli for many complex, vibrotactile-driven tasks. This lack of exploration into the study of higher level cognitive attention studies of complex tactile information has been identified as a priority for future research (Spence, & Gallace, 2007). Spence and Gallace (2007) acknowledge the importance of looking for intramodal attention, and the impact of concurrent distracting stimuli that a participant may need to ignore, with the suggestions of looking for more ecologically-valid testing conditions.

Tactile attention is adversely impacted by loading working memory with information from a non tactile task. Dalton, Lavie, and Spence (2009) found that presentation of a high working memory load task impeded the perception of change in vibrotactile elevations with a pulse distractor on the ipsilateral, or contralateral hand. The high working memory load task was a sequence of random numbers that was briefly presented, and required to be recalled at a later time. While Dalton, Lavie and Spence (2009) hypothesized that this impediment occurred because executive control functions responsible for the maintenance of task priorities in working memory should not be modality specific, they did not test the tactile aspect of working memory. New insight is

needed on how to present more complex tactile stimuli without exceeding the tactile attentional limitations to process it (Spence, & Gallace, 2007).

In summary tactile attention can be cued exogenously or endogenously. Once tactile attention is consciously focused upon it is difficult to shift away from. Tactile attention bares resemblance to attentional phenomena in other modalities. Competing tactile stimuli may mask, or enhance the to be detected stimulus when considering simple detection. In general, complex tactile attention tasks are largely understudied.

Tactile Memory

Cognitive limits associated with tactile information processing are more pronounced compared to visual and auditory stimuli (Gallace, Tan, Haggard, & Spence, 2008; Spence, & Gallace, 2007; Gallace, Tan, & Spence, 2007; Gallace, Tan, & Spence, 2008). Gallace and Spence (2009) questioned whether information becomes represented intrinsically as tactile, visual, verbal (semantic), or amodal information? Fetal studies in humans (pre-language development) would suggest that "yes", there is a non-verbal (non-semantic), and likely non-visual memory representation of tactile information (Bernhardt, 1987). Spelt (1948), utilized a classical conditioning paradigm to illustrate this point. A motor response (kick) to a tactile stimulus can be conditioned prenatally (Spelt, 1948). Spelt (1948) found that a learned conditioned response could be maintained using only the vibrotactile conditioning stimulus, for up to 4 trials, following only 16 acquisition trials of the paired presentation of the conditioning and unconditioned stimulus (known to make a fetus kick). A fetus would not likely have access to a verbal, or visual memory

system in order to develop a multi-modal representation, which suggests tactile memory is represented in a unimodal fashion.

Short term/working memory

Short term memory for tactile information has been found to range from 3.5 to 7.5 stimuli, but within 45 seconds of stimulus presentation there can be almost complete decay of novel information retention (Bliss et al., 1966; Gilson, & Baddeley, 1969; Rabinowitz, Houtsma, Durlach, & Delhorne, 1987, Hillstrom, Shapiro, & Spence, 2002). Bliss et al., (1966) tested short memory by directing 100 millisecond bursts of air to 24 possible locations on the fingers of each hand (1 airjet at the each of the 3 joints on every finger but not thumbs). Each joint or sensory region was given a letter from the alphabet so the participants could quickly report which regions were stimulated. A computer could control how many airjets were active, and the spatial distribution of the jets. Tactile reception of simple information was measured, the participant simply determined whether the stimulus was present or not on a given trial. Participants were tested with stimulation levels of up to 12 of the airjets at a time. When simple detection information is distributed spatially the short term memory performance is only about 30% accurate (Bliss et al., 1966). In comparison, visual short term memory for single numerical digits has been established as roughly 8 items (Brener, 1940) which lended support for Miller (1956) to establish that the short term memory has a capacity of 7 plus or minus 2 chunks of information. Spatially-distributed tactile memory tasks are also subject to rapid decay, particularly with a distribution of up to six different sites (Gallace, & Spence, 2008).

There is also an inaccuracy in the tactile memory for time perception. In the timing domain, vibrotactile memory representation overestimation of stimulus duration increases linearly with stimulus frequency (Khoshnoodi, Motiei-Langroudi, Omrani, Diamond, & Abbassian, 2008). In comparison, visual memory for timing is more precise than tactile memory (Heller, 1987), but the accuracy of visual timing perception can be distorted. Factors that distort visual memory for temporal events include the size of the stimulus, and whether there is a working memory representation for the stimulus. A larger visual stimulus will result in a longer perceived temporal duration (Ono, & Kawahara, 2007). Working memory familiarity with the visual stimulus also yields a longer perceived temporal duration (Pan, & Luo, 2012). Whether tactile memory is also impacted by either the size of the stimulus, or previous working memory experience remains to be seen.

Memory for complex information.

Tactile languages can be considered in the examination of memory for more complex information. Braille is the most successful example of a tactile language (Foulke, 1991). It has both spatial (Loomis, 1990) and temporal components to it (Craig, 1995), can be presented actively or passively (Lederman, 1981). For those with an absence of vision, the tactile language devised of raised bumps embossed on paper developed by Louis Braille in 1821 allows for meaningful independent interpretation of the written word (Moon, 1873). Morse code is another language that can be mechanically pressed into paper generating indentations for the purpose of representing language (Vail, 1845). As a result from its inception, the interpretation of Morse code

was also possible using the tactile system. While Braille consists of spatial arrays of clustered "dots" that make up individual letters, Morse code letters consist of a horizontal sequence of "dot" and "dash" elements (refer to Figure 1). Indentations whether they are "dots" (Braille, Morse code) or "dashes" (Morse code) on paper yield the possibility of being seen or touched (Vail, 1845). Like Braille, studies have utilized the Morse code language as a means of testing tactile memory (Tang, Staines, Black, & McIlroy, 2009; Tan, Durlach Rabinowitz, Reed, Santos, 1997).

(INSERT FIGURE 1 ABOUT HERE)

Memory for tactile Morse code has been partitioned into the learning of "hard", and "easy" letters. Presented vibrotactily, a short vibration is represented as a "dot", and a longer vibration represented as a "dash", with brief cessations or spaces in stimulation to separate multiple elements presented in a serial order. Easy letters are those with all of the same elements repeated such as four dots, each separated by spaces (e.g., H = or I = ---), while hard letters are made up of combined elements such as a dot, a dash, a dash, then a dot each separated by spaces (e.g., P = .--. or Q = --.-). Letters that are deemed hard are those where the learner consistently demonstrates more errors in interpretation, or later in production (Keller, & Taubman, 1943; Keller, & Schoenfeld, 1944; Sidman, Keller, Kennedy & Wilson, 1955). Barrett (1875) first proposed pneumonic devices as a way of remembering the dot and dash components of specific letters to overcome the difficulty in memorization of Morse code. Barrett suggested that the learner think of using words made of the letters "s" and "h" and all the vowels "a", "e", "i", "o", "u" as

representing "dot" elements within the pneumonic word used for any given letter. So if the pneumonic word for the letter "A" is "at", then Morse code for "A" consists of a "dot" ("a" from "at" is a vowel) followed by a "dash" ("t" is a consonant). Likewise, if the word for "B" is "base", the letter "B" in Morse code consists of a "dash" ("b" from "base" is a consonant) followed by three "dots" (2 vowels "a", "e", and an "s"). Bryan and Harter (1897, 1899) also noted in their learning studies that specific letters were more challenging than others. In a series of studies (Keller, & Taubman, 1943; Keller, & Schoenfeld, 1944; Sidman, Keller, Kennedy & Wilson, 1955) specific lists of letters were ranked based on the failure of reception performance, and difficulty to learn for code delivery. Memory for tactile Morse code is also impacted by the rate at which it is delivered for perception. After 75 hours of training vibrotactile novice Morse code operators are not capable of operating accurately at a rate greater than 18 words per minute (Tan, Durlach Rabinowitz, Reed, & Santos, 1997). It would appear that memory for tactile Morse code becomes impeded by presentation rate, which is a finding that contrasts Morse code learning when visual representations are used. In other modalities particularily vision, practiced learners recognize not just letters but begin to identify entire words, or sentences in time (Bryan, &Harter, 1897,1899). The tactile system is constrained in that presentation of Morse code letters cannot be overviewed, but only delivered not just one letter at a time, but one element at a time.

Tactile Learning and Communication

While conditioning, detection, and spatial/temporal/numerosity associations can

be learned in response to simple tactile stimuli, this section will address the learning of complex tactile information. Tactile communication is particularly useful when other systems are overloaded, or unavailable (Gallace, Tan, & Spence, 2007; Maclean, 2008). Tactile language acquisition has been the focus of the majority of studies on learning complex tactile stimuli, with very few studies considering immediate, or delayed, retention and transfer. Morse code and Braille are established letter systems that can be presented passively via vibrotactile stimulation for interpretation of individual letters. Braille has been described as the most useful, and longest-lived example of a synthetic tactile dominant code (Sherrick, 1975). Still, Braille has been criticized as being a slow, and difficult form of communication (Foulke, 1982). Braille could be considered the more temporally efficient language in that a character can be presented at one time, whereas Morse code is dependent on waiting for all the dots, dashes, and spaces in between, before identification of a letter is possible. Spatially, a single vibrating tactor exposed to a single small skin surface could be used to deliver the Morse code signals. Braille requires enough spatial area for the perception of two vertical columns, and three horizontal rows to be perceived as separate, and distinct (Heller, & Mitchell, 1985). The standard Braille icon consists of dots that are oriented 2.5 millimetres horizontally and vertically from each other as measured to the centre of the dot. Letters are typically 6.25 millimetres apart, while different horizontal lines are separated by a 10 millimetre distance. Each dot has a diameter of 1.5 millimetres. A single letter (with a maximum of 6 dots) occupies a space of 4 millimetres (horizontally) by 6.5 millimetres (vertically).

Foulke and Broadbeck (1968) attempted to use electrocutaneous stimuli to deliver Morse code at an isolated location. Using an electrode on the distal pad of the index finger, participants received non-noxious electrical stimulation with temporal patterns identical to those used in traditional aural Morse code delivery. Augmented feedback correctness was provided following each trial. The mean error rate was 40.4% when Morse code letters consisted of a combination of four "dot" and "dash" elements, which Foulke and Broadbeck considered to be too high, rendering the communication rate unacceptably low.

Vibrotactile delivery was compared to auditory reception of Morse Code for novices and experts by Tan et al., (1997). They exposed the participants to four progressive levels of difficulty, which were single-letter identification, three-letter identification, common-word identification, and sentence identification. In a random order, each participant experienced vibration patterns representing each letter of the English alphabet. Five presentations of each letter (130 presentations) were delivered during a session. Participants responded to the letter they believed was presented on a computer keyboard, and augmented feedback was provided on response accuracy. They were allowed to practice until they had attained a run with a 100% accuracy, or 3 runs with 95% accuracy, or 10 runs with highly similar accuracy (indicating a plateau in learning). On single-letter acquisition performance novices required significantly more practice runs than experts to attain a 95% accuracy score. Novices were unable to

auditory Morse code reception were nearly twice as accurate as the vibrotactile delivery scores for both those experienced and inexperienced with Morse code use. The effect that individuals in both experienced and inexperienced Morse code groups were more accurate using auditory reception indicates a generalized reduced reception for tactile information regardless of previous familiarity the information to be delivered. Tan et al., (1997) interpreted the modality accuracy result based on the temporal resolution of sensory reception found by Gescheider (1966). Gescheider suggested that tactile items presented sequentially require a 10 millisecond delay to be perceived as separate events, whereas auditory information only requires a difference of 1.8 milliseconds. A limitation of the Tan et al., (1997) study is that only 4 participants (2 experienced, 2 inexperienced with Morse code), were recruited. Traditional statistical analyses were substituted with percent accuracy scores, and post-hoc Scheffe's tests. Their statistical approach allowed for between group comparisons of individual participants only, but not the interaction of variables or changes in group means.

Tang, Staines, Black, and McIlroy (2009) studied subsets of vibrotactile Morse code letters. They recognized that based on the combinations of "dots", and "dashes" used to create letters, that some patterns were significantly more difficult than others to learn. Participants needed only to respond to whether the vibrotactile letter presented matched, or did not match a letter that appeared on a visual display. A design with only two stimulus response alternatives can be expected to yield a constant response time value. In addition a two response alternative design statistically presents the context for

participants to perform correctly on 50% of trials, even if they only were guessing in the Tang, Staines, Black, and McIlroy (2009) experiment. In the Tan et al., (1997) work the experimental design response accuracy bias was prevented as 26 stimulus response alternatives were used. However, for a study on novice acquisition learning the full alphabet may still be too demanding. Heller (1985) found that novices attempting to learn tactile Morse code when given 5 trials of letters A-Y (25 letters) their performance was too poor for meaningful interpretation, so for their further experiments utilized a truncated letterset of A-J (10 letters). In summary should a tactile learning experiment employ too few response alternatives, the outcome accuracy score could be artificially inflated by participant's guessing at their responses. In addition tactile letter learning is sufficiently difficult that study design should allow either a sufficient number of presentation exposures to ensure learning, or truncate a letter list so as not to overwhelm a novice learner.

Heller and Mitchell (1985) considered the learning of Braille in sighted individuals when vision of the embossed patterns was occluded. Participants with no previous Braille experience were taught 2- and 3-letter Braille words, then in a second study simply individual letters. They were given no feedback between trials, and the study investigated the impact of several factors on learning. These factors included the size, or spacing of characters, sensing at the distal finger pad compared to the fingertip, and the wearing of a vinyl glove on the hand used for detection. They concluded that larger characters and spaces were advantageous in early learning. They also found that

novice Braille learners performed better when allowed to use their finger tip, and the presence of a glove had no effect on learning. However, a limitation to this study is that learners were exposed to 24 different letters, and they were only exposed to those letters twice each. The Heller and Mitchell (1985) study again highlights how a low number of trials for a high number of letters may not have afforded enough presentations to determine if a glove negatively impeded perception, as there were a high number of response alternatives making the task extremely difficult for both groups.

Orientation is a factor that has been found to impede Braille reading, in terms of both the accuracy and speed of letter recognition (Heller, 1987). The impediment was present when the target Braille stimulus was rotated to the left from upright.

Performance was also adversely impacted when the fingertip was rotated to the left, while the letter was kept upright. Heller (1987) indicates the necessary congruency between the orientations of the letter, and the effector used to detect that letter when learning, then reading Braille. It was determined that traditional vertical letter presentation, paired with a finger perpendicular to the horizontal line of Braille characters is optimal. Heller (1987) conducted the orientation experiments to solve whether Braille characters can be identified globally as "shapes"/"outlines" which would theoretically not be impacted by subtle changes in orientation. Heller (1987) concluded that the tactile sense and tactile processing is not based on the recognition of the outline of individual characters, but rather the orientation, and spacing of all components within the tactile character.

While Morse code and Braille have been the most studied, and most applied

tactile languages, other systems and techniques to study tactile learning have been explored. Rothenberg et al., (1977) studied vibrations induced with similar characteristics to speech patterns on the skin, as a means for communication. For example, speech consists of sound waves with specific vibration characteristics including elements that are sustained or separated by pauses each with varying durations. Imagine for a moment if you had no auditory or visual feedback but you could feel the vibrations of someone talking to your hand. Rothenberg et al., (1977) considered the vibratory parameters of pulse width, amplitude, and frequency. They determined that although the skin can allow the perception of different spatial and temporal vibratory parameters, that natural speech while sufficient for the auditory system, when directed to the skin surface is not a salient enough vibratory stimulus for accurate tactile perception. To increase the salience of natural speech vibrations a "vocoder", or device capable of translating/amplifying speech into perceptible tactile vibration parameters would be useful. Other limitations to speech detection at the skin surface also include that male, female, and children's voices have different relative speech parameters, making discrimination more difficult. There have been many vocoder devices studied including the "Queen's vocoder" (Brooks, & Frost, 1983), and the "Tacticon" (Lynch, Eilers, Oller, & Lavoie, 1988; Lynch, Eilers, Oller, Urbano, & Pero, 1989). Training with the Queen's vocoder revealed that 110 words were learned after 48 hours of practice, while using the Tacticon for 44 hours yielded only 50 words. Galvin et al., (1999) studied a vocoder called "The Tickle Talker". They provided participants with an average of 12 hours of exposure to 150 words, and a mean

of only 31 words were learned. The aforementioned devices all allow for speech at the entire word level to be directed toward the tactile sensory system. While the cognitive burden of trying to interpret each individual letter of a word (as in Morse code or Braille), is reduced, in general performance accuracy even with substantial practice is poor.

Teaching reception of tactile language using vocoders is challenging to a point where mainstream usage does not seem practical.

Tactile Visual Substitution Systems (TVSS) were designed to transcode visual information to the tactile domain. The TVSS consisted of a camera that turned visual objects into 2-D tactile sensations (Bach-y-Rita, Collins, Saunders, White, & Scadden, 1969). This was done by converting the image into a series of pins over a fixed spatial area on the skin that could be raised or lowered to reflect the shape of an image. The Optacon (a TVSS) used images of individual English letters to convey language. Experts could interpret this information at speeds of up to 90 WPM after training (Bliss, Katcher, Rogers, & Shepard, 1970). In summary there have been multiple devices designed to isolate complex information traditionally targeted to other modalities and transduce it to something perceivable by the tactile sensory system.

Geldard (1957) proposed a tactile language delivery system "vibratese". Geldard's "vibratese" differed from other tactile information delivery systems, in that his device sent signals to numerous markers, spread out over the recipient's body, which meant multiple tactors could be stimulated concurrently. Participants could recieve the average English word in 0.79 seconds, upon training in vibratese, which Geldard

determined was 2-3 times faster than Morse code. He also suggested that while some operators had received high levels of training in "vibratese", they were not necessarily at their physiological limit for peak performance. Geldard's "vibratese" was a complex system, involving 5 tactile markers spread out over the chest. Three different durations, and three different intensities of vibration could be generated at any of the five sites, resulting in 45 possible, meaningful stimuli to be communicated, that included all 26 English letters, numbers 0-9, and commonly used words including "the", "and", "of" and "in".

More recently, haptic icons, or "hapticons" have been studied. A haptic icon is a vibrotactile pattern that represents a specific concept as opposed to an individual letter. For example, a worker in a mine may wear a vibrotactile alarm system, that vibrates three times to indicate the worker is no longer safe in a safe area, they must cease their work and rapidly evacuate. Enriquez and MacLean (2008) suggest that when a "limited set" (less than 10) of haptic icons are learned they can be used to convey information while the visual, and auditory systems are predisposed. After a 20-minute, self-guided learning session, then a 20-minute computer-guided learning session, participants were able to accurately associate the tactile presentation with the icon it represented with an 80.1% success rate. Following a two-week retention period participants were still capable of correctly identifying at least 70.1%. They conclude that these results are promising in terms of using haptic icons in future display technology.

In summary, tactile learning and communication has been explored used

historically significant languages developed for the auditory or visually impaired including Braille, and Morse code. Accuracy for detection and perception of tactile language is considered unacceptably low. Substantial training is needed to attain expertise in tactile language reception, and previous experience with the target language in another modality is beneficial. Specific regions on the body facilitate the acquisition of tactile communication, predominantly the finger tips for novice performers. Changes in the orientation of a presented stimulus are found to impede accurate perception. Devices that go beyond presenting a code, and attempt to mimic vibration patterns of natural speech have been developed but applied with limited success. In an attempt to replace vision in modality challenged populations, TVSS units that could scan an environment, and turn information into a 2-D representation have been applied with some success. The most successful application of tactile communication for complex information, is the hapticon where complex information is chunked into a relatively simple vibratory stimulus. In essence the greatest success occurs when vibration does not communicate a letter, but rather an entire concept. When less then 10 hapticons are created each associated with a specific concept (such as turn to the left, or leave the room), learning is able to take place in a short period of time with relatively high accuracy. While acquisition of tactile communication is difficult, it is not impossible, and participants demonstrate learning performance that exceeds chance based on guessing responses. Tactile languages therefore facilitate the study of learning complex tactile information, as with enough trials a floor effect could be overcome (demonstrating that some learning is

taking place), but it would be highly unlikely that early learners would reach a ceiling effect (task difficulty is too low and the learner performs beyond the maximum capacity for measurement). As a result a functional bandwidth exists for the study of the tactile learning, and the exploration of factors that may facilitate or impede it.

Tactile Masking

The operator's information processing capacity for touch must not be surpassed in order for the design of technology to be useful (Gallace, Tan, & Spence, 2007). Information processing capacity limitations exist for both the detection of simple information as well as the identification of more complex patterns (Craig, 1982). The more complex the delivery of tactile information, results in the necessity of directing more cognitive resources for analysis and interpretation of that information, which can adversely alter the rate or success of information processing (Gallace et al., 2007). When the ability to detect a stimulus, or interpret a stimuli pattern is reduced, or interfered with by presentation of other information, the target is said to be "masked", or "positively masked" (Craig, 1985; Verrillo, 1985).

History of Tactile Masking

Tactile masking was the term originally used to explain an electrically-induced alteration, first described as "fluttering", followed by reversible sensory obliteration within specific cutaneous nerve distributions (Thompson, & Inman, 1933). Masking was discovered by accident while Thompson and Inman (1933) were attempting to map the sensory course of nerves using electrical stimulation, and cutaneous pressure sensation

assessment devices. Their attempt to identify the optimal electrical stimulus intensity to map the nerve distributions resulted in their discovery of the phenomena. While the stimulation was present over the course of a particular nerve they used von Frey hairs, which are monofilaments of different thicknesses for applying pressure on the skin to determine perception of sensation. The von Frey hairs were applied to trace out sensory nerve distributions on the skin (refer to Figure 2). When the electrical stimulation intensity was increased, a transition from the fluttering sensation along the course of a nerve to the disappearance of tactile sensibility occurred. They observed that the altered/absent sensation along the path of a nerve ceased immediately upon removal of the electrical stimulus. Thompson and Inman (1933), and Thompson (1933) applied the term "masking" to this electrically induced phenomenon as they felt it was a more appropriate, less confusing, and more accurate description than anesthesia for when the tactile system was stimulated beyond normal sensory conditions inhibiting the detection of light touch.

(INSERT FIGURE 2 ABOUT HERE)

Thompson (1933) found that electrically-induced masking inhibited perception of "pressure", and "light touch" most consistently, compared to sensations of "pain" and "temperature". Participants undergoing a masking stimulus had higher thresholds for "pain", but "cold", and "heat" sensation was inconsistently and likely insignificantly impacted along the course of the nerve stimulated. Peterson (1933) agreed and remarked that a high electrical frequency presentation (over 2000 Hz) that diminished sensation of

touch, and pain could be induced to an extent that minor surgery could be performed. Post-surgical pain was immediately experienced when the current was interrupted following an operative procedure (Peterson, 1933).

Target Stimulus Properties versus Mask Stimulus Properties

Masking is thought to occur when the receptors for detecting a tactile stimuli at a particular frequency have their thresholds exceeded by both the to-be attended stimuli and an additional competing stimuli (Gescheider et al., 1982). A target stimulus may have characteristics in common with the masking stimulus. For example, both target and mask stimuli may be vibrotactile, presented at the same frequency, delivered to the same locations. However, the target stimulus may not share prominent characteristics with the masking stimulus. For example, the mask may be presented to an anatomically remote region from the target, or presented at a different frequency. A mask stimuli may be an entirely different method of stimulating the tactile system than the target stimuli. For instance a general vibrating tactor, as opposed to a TVSS pin representation of a letter from the English alphabet. If tactile masking is thought of as a mask stimuli having an impact on a target stimuli, an independent variable in masking studies can be the respective properties of the "target" stimulus, and the "mask" stimulus.

Craig (1982) examined the role of masking stimulus properties directly by comparing outcomes when an energy masker was presented, to when a pattern masker was used (refer to Figure 3). Craig used an Optacon TVSS to deliver both types of masks (in separate conditions) and the meaningful target stimuli, which was a letter. In the

experiment the order of masking stimuli presentation was manipulated relative to the target stimuli presentation, typically known as: "forward" and "backward" masking, respectively. The masking stimulus was presented for 18-52 milliseconds either 4 milliseconds before (forward masking) or 4 milliseconds after (backward masking) the tobe attended letter stimulus, which was presented for 26 milliseconds. He accomplished energy masking by having all pins in the TVSS fire simultaneously creating a nonmeaningful general mask over a defined area (1.1 x 2.7 cm) on the left index finger. In another condition he used a pattern mask. In order to create a pattern mask specific clusters of pins were activated, creating patterns of rows or columns across the same spatial area (1.1 x 2.7 cm) on the left index finger. Essentially for the pattern mask only a specific subset of the total number of pins are activated while for an energy mask all pins are activated. He determined that the presence of an energy mask created less interference than a pattern mask, using a primary outcome measure of percentage correct for letter identification which was the to-be attended stimuli (Craig, 1982). Backward masking and forward masking yielded increased incorrect responses compared to a non masked condition, with backward masking being more detrimental than forward masking. A logical extension to this methodology would be to design an experiment that allows for the concurrent presentation of an energy or pattern mask and the to be attended letter.

(INSERT FIGURE 3 ABOUT HERE)

Manipulating the stimulus onset asynchrony (SOA) of masking and meaningful stimuli has also been attempted (Gescheider, Bolanowski, & Verrillo, 1989) (refer to

Figure 3). They determined that for both forward and backward masking a shorter SOA duration yielded a stronger masking effect. Temporal masking occurs if the to-be attended stimulus consists of a pattern, and there is not sufficient time duration between components for perception (Gescheider, 1966). For example, if there are not sufficient pauses between the elements of Morse code letters, the receiver of information may perceive only one long stimuli (instead of three separate dashes or dots), which prevents accurate information detection.

Differing tactile sensations can be used to present masking stimulation concurrent with target stimulation (positive masking). Heller and Mitchell (1985), and subsequently Thompson and Lambert (1995), employed the used of vinyl, and latex gloves respectively as a physical barrier mask to the finger pads in the study of Braille interpretation, and two point discrimination. Verrillo and Bolanowski (1996) used submersion in water as an attempt to mask vibrotactile stimulation. Zhang and colleagues (2009) used temperature change in the form of "non noxious" heat to elicit a possible masking stimulus concurrent with vibrotactile stimulation. Thermal induced heat as "pain", with vibrotactile stimuli was found to raise vibrotactile threshold, which reflected a successful mask (Apkarian, Stea, & Bolanowski, 1994). These methods can be criticized for being too general in terms of their spatial application. This challenge was overcome in a study by Kekoni, Pertovaara, and Hamalainen (1987), who used a continuous vibrotactile mask stimuli during a task requiring the detection of the presence of a burst of air against the skin. The intensity of the airpuff and the mask stimulus could be independently manipulated.

They found that an increased masking effect was found as mask stimulus intensity was increased or when the airpuff stimuli was decreased.

Spatial masking is determined by the size of the stimulus, and the relevant receptive area (Verrillo, 1963). Masking occurs possibly due to increased interference, or sensory limits of the system, as opposed to the attentional resource limits of the system when task relevant information, and task irrelevant perturbation are in the same location (Lavie, 2005). When the two are in different locations there is reduced distractor processing attributed to the ability to focus spatial attention (Lavie, 2005). Gallace and Spence (2008) suggest there is a close link between the study of the tactile awareness, and the spatial distribution of that information. Gallace and Spence (2009) predicted that the storage and recollection of passive tactile stimulation might be affected by spatial factors between concurrent stimuli. Differences in spatial acuity across body regions are also a concern for spatial distortion when meaningful information is presented (Cholewiack, 1999; Cholewiack, Brill, & Schwab, 2004).

Differential spatial placement of mask, and to-be-attended stimuli may be used to determine whether the mask is impacting the perception at the nerve pathway, or if the mask is simply an attentional distraction (Bolanowksi, Maxfield, Gescheider, & Apkarian, 2000). Kekoni, Tikkala, Pertovaara and Hamalainen (1990) explored this concept in a series of experiments by moving the relative locations of the masking stimuli and the to-be detected stimuli both laterally, and longitudinally. When changing the relative distance between the mask stimulus, and the to-be detected stimulus, across the

palm of the hand they found a decreased masking effect with increased interstimulus distance. In their second experiment, they found that a strong masking effect was present when a vibrotactile masker with a constant intensity was placed at the fingertip, and the to-be-detected air puff was delivered to the base of the finger. This effect was strongest when both occurred on the same finger and weakest when the masking stimulus was presented to a finger that was different than the one receiving the airpuff stimuli. Craig (1983) demonstrated this phenomena years earlier when he studied the same type of spatial effect for both forward, and backward masking of vibrotactile patterns at the fingertip. Craig determined that based on such a finding that perturbation of a finger other than the finger required for a tactile discrimination task does not sufficiently distract attention away from the cognitive demands of the task. Kekoni et al., (1990), in their third experiment, found a decreased masking effect when the spatial location of the masker was switched to the base of the finger, and the to-be attended stimuli was shifted to the fingertip. They determined that a mask is more salient when placed over an area of dense innervation (fingertip). Using their methods they were unable to discern specifically whether this was strictly due to increased density of innervation, or possibly the larger cortical representation of the stimulated area in the brain. Another weakness to Craig's (1983) interpretation of his results is that he failed to consider in his discussions the role of separate, or same peripheral innervation of the regions stimulated by the mask and the to-be-attended stimuli. If these data were reinterpreted with this concept in mind, it would appear in general that a mask is less salient when separately peripheral

innervated regions are presented with masking and meaningful stimuli. Kekoni and colleagues (1990) briefly touched on the concept of crossing innervation regions when discussing their findings (refer to Figure 2). They found on the palm of the hand that spatially when either longitudinal (distance from wrist to the fingers), or transverse (base of the second digit to base of the fifth digit) orientation distance was increased between the mask stimulus and target stimulus, that the masking effect was decreased. Based on this finding they hypothesized that masking may have a central, not a peripheral mechanism, a topic that needs further scientific exploration.

Experience with interpretation of complex tactile stimuli has also been found to reduce tactile masking in the congenitally blind. Bhattacharjee, Ye, Lisak, Vargas, and Goldreich (2010) found that blind individuals who were experienced Braille readers demonstrated a reduced impact of vibrotactile masking on a simple detection task, compared to sighted control participants. This reduced masking effect was present equally when the effector used most often to read Braille was tested compared to its contralateral equivalent finger. This finding might suggest that tactile-receptive neural changes occur in either the congenitally blind or with learning (i.e., Braille expertise).

Tactile Summation/Enhancement/Negative Masking

Under certain circumstances, the presence of additional stimuli increases the ability to detect, or interpret a pattern of target stimuli. This effect has been described in numerous ways over time including summation (Vernon, 1953; Verrillo, 1965), enhancement (Verrillo, 1976; Verrillo, 1983), and negative masking (Hamer, Verrillo, &

Zwislocki, 1983; Gescheider, Verrillo, & Pelli, 1991).

History of Tactile Summation/Enhancement/Negative Masking

Vernon (1953) sought to understand the interaction between mechanical, and electrical stimulation of the skin. He presented an otherwise subliminal electrical stimulation concurrently with a mechanical stimulation, at the known mechanical threshold. The presence of the electrical stimulation in the same temporal patterns as the mechanical stimuli resulted in a decreased mechanical threshold. Vernon described this facilitation, which was a reduction in the mechanical detection threshold, as a summation. Verrillo (1965) independently came to the same conclusion that summation occurred when he approached the tactile system with a modification of the Zwislocki (1960) theory of temporal auditory summation. Zwislocki theorized that as separate auditory stimuli were presented in progressively closer temporal proximity that the threshold to detect them decreased asymptotically. Manipulation of the temporal spacing decreased detection threshold and allowed a summation of one stimuli and a subsequent stimuli making them easier to detect even if they were delivered at the same intensity. Zwislocki (1960) concludes summation is possible due to the exponential decay of the threshold for neural excitation upon repeated stimuli presentation.

Terminology evolved without a clear explanation as to why, when Verrillo (Verrillo, 1976; Verrillo, & Gescheider, 1977; Verrillo, 1985) favoured description of findings as "enhancement" in discussion of previous work described as summation. This vocabulary evolution without apology continued in the Gescheider, Verrillo and Pelli

(1991) article which used the description of negative masking, synonymously with summation, and enhancement. All 3 descriptions of the same phenomena are essentially synonymous and accurate in their own way. When multiple stimuli are presented concurrently, and the summation of their inputs enhances the ability to be detect then perceive the stimuli. Enhancement is the decreased threshold for a stimuli to be perceived. The summation that leads to enhancement of stimuli is the opposite of a "masking" effect, which would be a decreased ability to detect and perceive stimuli, which is why "negative masking" also makes sense as a description. It is possible that "negative masking" was adopted, as it was a term that could describe the entire phenomena of summation leading to enhancement, and be contrasted to the concept of "masking" also known as "positive masking" very clearly in scientific writing.

Target Stimulus Properties versus Negative Mask Stimulus Properties

Gescheider, Verrillo and Pelli (1991) used the analogy of a pedestal in an attempt to explain positive masking, compared to negative masking (enhancement). The pedestal represents the intensity of the to-be attended stimuli, while the additional stimulus signal is described as "noise". When the pedestal was "low", the presence of noise allowed the otherwise subthreshold stimulus to be detected (negative masking) (refer to Figure 4). When the pedestal was "high" the additional presence of noise caused a resultant compound stimulus in excess of the bandwidth of perception (masking). Hamer et al., (1983) proposed that negative masking in the tactile system could have both a peripheral and a central component. The peripheral component has an energy threshold that is either

raised or lowered by the presence of a negative masking stimulus, and the central component has additional neural "noise". The methods of Hamer and et al., (1983) were insufficient to make conclusive judgment regarding the central component of their hypothesis as they employed indirect peripheral threshold measures, and no direct or targeted measure of central nervous system activity.

(INSERT FIGURE 4 ABOUT HERE)

The properties of the negative mask (enhancement) stimulus, compared to the target stimulus appear to be of significant consequence to yielding a successful enhancement. McAuley, Ewing, and Devasundaran (1993) found that submersion in water increased the sensitivity of the skin. More specifically, vibrotactile stimulation of the hand's thenar eminence (base of the thumb on the palmar side of the hand) increases after being submersed in seawater for 20 minutes (Verrillo, & Bolanowski, 1996). Zhang, Francisco, Holden, Dennis, and Tommerdahl (2009) found that tactile detection was enhanced by non-noxious heat. The question of whether this type of facilitation is due to a peripheral sensory receptor threshold decrease, or an exogenous capture of attention to the site of detection remains to be seen and requires further study.

Conclusion

The tactile system is complicated, diverse, and like other modalities can be challenged in terms of its capabilities, and limitations. Studies of peripheral detection, central processing including attention, memory, learning, and the factors that mask, or enhance such information have been studied. Future directions testing the learning of

complex information, and the concepts of masking, or enhancement can delve into integration associated with perceptual learning. These studies should include investigation beyond acquisition performance, and explore the retention, and transfer performance of tactile acquired information. Additional perceptual integration work, combining behavioural and neurophysiological study of the paradigms associated with the touch sense may further illuminate what remains unclear about the utilization of the tactile sense, from converging perspectives.

SOMATOSENSORY EVOKED POTENTIALS REVIEW

I was the primary investigator and major contributor for each aspect of this research review, including the concept, design, and manuscript preparation. This paper will be submitted to the Journal of the Canadian Chiropractic Association.

Running Head: SOMATOSENSORY EVOKED POTENTIALS

The origin, and application of somatosensory evoked potentials as a neurophysiological

investigative technique

Steven R. Passmore^{1,2,3}, Bernadette Murphy⁴, Timothy D. Lee¹

¹McMaster University

² University of Manitoba

³New York Chiropractic College

⁴ University of Ontario, Institute of Technology

Corresponding Author Address: Steven Passmore, School of Medical Rehabilitation,

University of Manitoba, R106-771 McDermot Avenue, Winnipeg, Manitoba, Canada,

R3E 0T6

e-mail: passmore@cc.umanitoba.ca

telephone: (204) 787-1899

39

1.2 The origin, and application of somatosensory evoked potentials as a neurophysiological investigative technique

Evoking and recording somatosensory evoked potentials (SEPs) is appearing in scientific literature that pertains to spinal manipulation (SM). There is evidence to support that SEPs is a neurophysiological technique capable of elucidating differences in cortical activity associated with an SM intervention (Haavik-Taylor & Murphy, 2007; 2008). Haavik and Murphy (2012) hypothesized that appropriate spinal movement normalizes afferent input and restores sensorimotor function and integration by filtering and processing appropriate somatosensory input. The purpose of this manuscript is to provide an overview of the origin, and application of somatosensory evoked potentials as a neurophysiological investigative technique. Understanding what the technique is, and how it has been applied will allow chiropractors, educators, and other manual therapists with an interest in SM to better understand the context, and importance of research findings from SM studies that involve SEPs as an outcome measure.

The most basic form of electrical communication between cells in the human body is the action potential (Brodal, 1997). A neuron, stimulated by other cells or other external stimuli, will reach a point at which an "all or none" burst of electricity is generated, and propagated. Depending on the type of neuron where this propagation is generated the result will be either inhibitory, or excitatory in nature at the synapse where it terminates. Excitatory post synaptic potentials facilitate action potential generation at the cells upon which they synapse. Such changes in electrical activity occur as a result of

of positive and negative ions crossing the cellular membrane. The ion flow results in changing regional polarity, and the resulting voltage changes in the area can be measured to demonstrate activity in the brain.

The brain is the site of integration, and perception of all external and internal stimuli, it is the keystone of the central nervous system. The somatosensory system is comprised of elements of the peripheral and central nervous system that serve the modalities of touch, vibration, temperature, pain and kinesthesia (Arezzo et al., 1982). Neurologically this pathway consists of a peripheral receptors and afferent neurons that enter the dorsal root ganglion prior to ascending the spinal cord to the medulla where they synapsewith an ipsilateral dorsal column nucleus. Once in the medulla they cross to the contralateral side of the brain (decussate) and the pathway continues to the contralateral ventral posterior lateral nucleus of the thalamus prior arrival at the primary somatosensory cortex for processing (Leeman, 2007). This pathway consists of the dorsal column – medial lemniscal, and thalamo – cortical sensory systems (Walsh, Kane, & Butler, 2005). Knowledge of the anatomical pathway of afferent and subsequently perceptual information can serve as a roadmap to the study of information acquisition and processing.

Origins of Somatosensory Evoked Potentials

An evoked potential is the stimulation of a neuron within a sensory or afferent nerve past its resting threshold resulting in the generation of a compound action potential. While not mutually exclusive the evocative stimulation can consist of tactile, vibrational,

painful or electrical elements (Lew, Lee, Pan, & Chiang, 2007). The compound action potential transmitted can be recorded using electrodes to study the post-stimulus characteristics (Heinbecker, Bishop, & O'Leary, 1934). Potentials evoked by peripheral nerve stimulation can be recorded in the sensorimotor cortex (Bartley, & Heinbecker, 1938).

A somatosensory evoked potential (SEP) is the electrical activity response measured at the skin's surface following controlled peripheral nerve stimulation. Electrical activity from peripheral stimulation measured over the scalp reflects cerebral action potentials and are best recorded contralateral to peripheral nerve stimulation (Dawson, 1947). The recorded electrical potential of this afferent volley bombardment generates a complex waveform (Eccles, 1951).

Waveform reproducibility is confirmed by taking the average of several controlled stimulation to waveform generation time-locked trials. The resulting average waveform can then be analysed in terms of the peaks and troughs present at different time points relative to the stimulation. To understand the significance of the waveforms, their components and their neurological interpretation, Giblin (1964), observed SEPs in both healthy participants and patients with impairments including lesions of the peripheral nerves, spinal cord, and the brain. He described "early potentials" as those of brief duration that occur within the first 35 msec after stimulation. Early potentials were accurately reproducible and Giblin (1964) noted the positive and negative voltage changes at particular times in milliseconds.

Early SEP studies had substantial variability in many facets of technique application. This variability included, but was not limited to: the stimulus intensity and interstimulus interval of the peripheral evoked potentials, the impedance and location of recording electrodes, the number of signals recorded to generate an average waveform, the filtering and amplification of recorded signals, and the measurement and recognition of specific peaks. Acknowledging this heterogeneity of method, but the usefulness of this approach to the study of the nervous system, the International Federation of Clinical Neurophysiology (IFCN) generated a report from a committee of recommended standards for short latency somatosensory evoked potentials (Nuwer et al., 1994). The findings from the report have been used in part to generate suggested SEP stimulating and recording parameters as detailed in the following section of this manuscript.

Parameters for SEP generation & recording of waveforms

Different from electroenchephalography (EEG) which reflects the brain's spontaneous electrical activity over a short period of time, SEPs are not recorded continuously to spontaneous stimuli but are time locked to a stimulus with a pretrigger (Mauguiere, 2005). SEP peak amplitudes are traditionally in the under $10\mu V$ range (smaller then EEG [tens of μV], EMG [mV], ECG [V]) (Mauguiere, 2005). The stimulation most favoured is electrical stimulation as it has parameters that are easily manipulated and controlled (Aminoff, & Eisen, 1998).

According the updated IFCN guidelines (Cruccu et al., 2008) the recommended electrical stimulus should consist of a 0.1-0.2 ms duration square wave pulse. These

pulses can be delivered by constant current stimulators applied transcutaneously over the targeted nerve. When stimulating a mixed (motor and sensory fibre containing) nerve, stimulus intensity should exceed the motor threshold for eliciting a muscle twitch. The pulse delivery should repeat at a frequency between 3 and 5 Hz. Stimulation frequencies up to 8 Hz can be used for pulse delivery if the latency of a target peak to be measured occurs before 30 ms. After 30 ms peaks resulting from this higher (8hz) frequency of stimulation are subject to reduction or attenuation which is why a bandwidth of 3-5Hz is preferred. Yamada, Yeh, & Kimura, 2004). Electrodes for stimulation should be placed over the course of the desired nerve, with the cathode placed 2 cm proximal to the anode (Cruccu et al., 2008).

To most effectively, and efficiently record SEPs signals to measures the changing activity in the brain and central nervous system it is recommended that recording EEG electrodes should be placed as per the 10-20 international EEG system (Mauguiere, 2005). The cortical locations that should be used contralateral to the site of stimulation are the Cc (contralateral frontal) and Pc (contralateral parietal) (Cruccu et al., 2008). Skin at the scalp EEG electrodes should have less than 5 Kohms impedance. The number of waveforms that should be averaged are from between 500 and 2000 stimuli presentations. Yamada, Yeh, and Kimura (2004) recommend a filtering bandwidth with a high pass of 1 Hz and low pass of 3000 Hz to isolate reproducible waves from background noise. Scalp electrodes may utilize an earlobe reference (Cruccu et al., 2008), and a lip placement for the ground electrode (Turker, Miles & Le, 1988). Adherence to these recommendations

will allow the optimal uniform technical recording environment to assess the neurophysiological changes associated with behavioural or perceptual experimental interventions and the resulting information processing.

SEP peak nomenclature, interpretation and generators

Waveform peaks are assigned a letter representing their polarity (positive or negative). By convention an upward wave deflection is a negative polarity (N) and also assigned an integer based on the post stimulus latency (in ms) at which they appear in a healthy population (Cruccu et al., 2008). Both the latency and the amplitude (uV) of these peaks can be used to interpret changes in neural activity. The amplitudes and latencies of the peaks are thought to represent a combination of the peripheral and central nervous system reception of the external stimulus, and how neural structures respond to that stimulus.

The waveform is a post-stimulation cortical-electrical potential with predictable and reproducible peak and trough amplitudes and latencies based on recording site. The signals recorded are reflective of their neural generators (Crucca et al., 2008). The neural generator can be "near field", or anatomically close to the electrode (cortex surface), or "far field" relatively anatomically distant (subcortical) (Leeman, 2007). This means that the near field potentials represent the direct region of polarity change proximal to the electrode. Far-field potential responses reflect structures with a diffuse signal to a larger area of the surface, they are more likely to be detected at multiple electrode sites (Magueire, 2005).

Early SEP peaks also referred to as "short latency" SEPs are considered to be the most useful for the study of neurological activity as they are the least variable among participants with intact nervous systems free from pathology considered to represent the normal population (Magueire, 2005). Short latency refers to the peaks and troughs present within the first 40 msec following a single stimulation to the upper limb, and less than 50 msec for the lower limb (Allison, McCarthy, Wood, & Jones, 1991). Peaks of longer latency than 45 ms may be susceptible to cognitive factors, which may further increase their variability (Cruccu et al., 2008).

Identification and meaning associated with specific temporal peaks have been derived from several different methodologies. One methodological example are the techniques used in laboratory obliteration studies which are traditionally performed with animal populations. Severe attenuation or abolishment of all SEPs occurs in primates when the dorsal columns of the upper thoracic, or mid cervical aspects of the spinal cord are ablated (Cusick, Myklebust, Larson, & Sances, 1979). No SEP anomalies occur when there are lesions to other parts of the spinal cord but the dorsal columns are left intact. This finding suggests the dorsal column tracts are essential in the mediation of SEPs (Aminoff, & Eisen, 1998). Additionally, SEP peaks have been shown to result mainly from stimulation of large myelinated sensory afferents such as 1a muscle afferents and, possibly, cutaneous afferents (Gandevia & Burke, 1988; Gandevia, Burke, & McKeon, 1984). The low intensity of stimulation applied, which is just above motor threshold, means that large myelinated sensory afferents which are also the most rapidly

conducting afferents are preferentially excited, and reach the cortex prior to other afferent fibres.

The presence of a specific pathology is another factor that impacts SEP peak amplitude, latency or total absence. Peaks may be delayed or absent in pathology cases with an etiology that is degenerative, traumatic or congenital (Aminoff & Eisen, 1998). Degenerative pathologies such as multiple sclerosis (MS) (Ganes, 1980; Mastaglia, Black, & Collins, 1976; Trojaborg, & Peterson, 1979; Small, Beauchamp, & Matthews, 1977), spinal cord tumours affecting the posterior columns (Linden, & Berlit, 1996) amyotrophic lateral sclerosis (ALS), Freidrich's ataxia (Mastaglia, Black, Edis, & Collins, 1978; Jones, Baraitser, & Halliday, 1980) and Gullain-Barre Syndrome (Brown, & Feasby, 1984) will alter SEP waveforms. Traumatic or compressive pathologies including focal nerve lesions (Desmedt, 1971; Synek, 1985), brachial plexus lesions/nerve root avulsion (Synek, & Cowan, 1982; Synek, 1983; Jones, Wynn Parry, & Landi, 1981), meralgia paresthetica (Synek, 1985), or nervous system lesions from a traumatic brain injury (TBI) (Sarno, Erasmu, Lipp, & Schlaegel, 2003) or surgery (Aminoff, & Eisen, 1998) are visible in the presence or absence of SEP components. Congenital pathology such as achondroplasia with associated foramen magnum stenosis will yield an abnormal SEP study (Nelson, Goldie, Hecht, Butler, & Scott, 1984). SEPs can even be used to conclusively identify brain death. A peak at N13/N14 with no peaks of further latency indicate that signals are reaching the cervical spine close to the medulla, but with no cerebral activity (Aminoff, & Eisen, 1998).

It is possible to identify many SEP peaks, their origin, and significance. For the purpose of brevity, this review will focus on the origin of the P14-N18 complex for N18, N20-P27 complex for N20, P22-N24 complex for N24, and P22-N30 complex for N30. These peaks have different possible implications for the study of tactile information processing (N18: Jones, 1981; N20: Buchner, Reinartz, Waberski, Gobbele, Noppeney, & Scherg, 1999; N24: Restuccia et al., 2001; N30: Waberski et al., 1999).

The N18 Peak

The far field, widespread, N18 component is distinct in SEP traces. It has the broadest elevation from baseline following the P13-14 potential (Desmedt & Cheron, 1981). Mauguiere (2005) suggested that there are multiple generators of the N18 scalp-recorded potential. Clinical evidence indicates that the N18 component is generated in the brain stem at the level of the midbrain-pontine region (Urasaki et al., 1992). Such brainstem lesions significantly attenuate the N18 amplitude (Urasaki et al., 1992). Noel, Ozaki and Desmedt (1996) suggested that the N18 peak originates in the lower medulla nuclei including the accessory inferior olives and dorsal column nuclei. Noel, Ozaki and Desmedt (1996) presented three patients whose N18 component remained intact although they had lesions at the medial lemniscus levels including the midbrain and upper medulla. The finding that N18 is related to the dorsal column nuclei also supported Manzano, Negrao and Nobrega 1998) who found N18 as the only SEP component resistant to vibratory changes. Sonoo, Sakuta, Shimpo, Genba, and Mannen (1991), and later Sonoo et al. (1992) concluded that the cuneate nucleus was likely responsible for the N18

potential based on several observed cases of patients with deep sensation disturbance and high cervical brain stem, thalamic, and pontine lesions.

The N20 Peak

The primary somatosensory cortex lies in the posterior bank of the rolandic fissure representing Brodmann's area 3b in the parietal lobe. This is the site of N20 peak generation (Desmedt & Cheron, 1980). It is known to respond to contralateral tactile stimuli (Hlushchuk & Hari, 2006). The parietal N20 peak is consistent and occurs contralateral to the site of stimulation (Maugueire, 2005). Brodmann's area 3b (the primary somatosensory cortex) responds to cutaneous inputs, but not joint movement input. Desmedt and Osaki (1991) confirmed this N20 cutaneous response, and not joint movement, in a study on passive finger movement. In healthy normal paricipants the N20 peak is the earliest cortical processing in the primary somatosensory cortex.

The N24 peak

The origin of peak N24 is located close to the location of N20. N24 is a frontal lobe negativity that appears on the ascending slope of peak N30. Garcia Larrea, Bastuji and Mauguiere (1992) found that N24 is best revealed at high stimulus rates that selectively decrease the N30 peak. Due to its mild variability in latency the N24 peak has also been referred to as N23 (Cheron, & Borenstein, 1991), or N25 (Waberski et al., 1999). Waberski et al. (1999) used source localization to identify to the posterior wall of the central sulcus in area 3b of the somatosensory cortex as the site of N24 generation. In order for this pathway to be completed the input sent to the somatosensory cortex travels

through the cerebellar cortex and deep cerebellar nuclei (Molinari, Restuccia, & Leggio, 2009). The N24 amplitude is enhanced if the cerebellar cortex is disrupted. N24 is reduced or absent, but all preceding peaks are left intact if the cerebellar cortex and deep cerebellar nuclei are lesioned (Restuccia et al., 2001). The characteristics of N24 are linked directly to the integrity of the cerebellum through its cortex and its deep nuclei.

The N30 Peak

The N30 frontal lobe peak reflects sensory integration (Rossi et al., 2003). This peak is negatively impacted by imagined or actual voluntary muscle contraction. Cheron and Borenstein (1991) demonstrated that both imagined and actual finger movements attenuated the N30 peak. As a result this peak is believed to reflect complex cortical and subcortical loops that link the basal ganglia, thalamus, pre-motor areas, and primary motor cortex (Kanovský et al., 2003; Mauguiere et al., 1983; Rossini et al., 1989; Rossini et al., 1987; Waberski et al., 1999). Parkinson's disease (PD) is known to degrade components of the basal ganglia. A PD patient population has demonstrated a decreased N30 peak compared to a control population (Pierantozzi et al., 1999; Pierantozzi et al., 2000). Muscle tone rigidity decreases and N30 amplitude increases in PD patients when the neuromuscular junction is blocked (Pierantozzi et al., 2000). Basal ganglia deep brain stimulation also produces increased N30 amplitude, which is attributed to improved supplementary motor area (SMA) activity (Pierantozzi et al., 1999). Basal ganglia efferents are anatomically found to terminate in the ventrolateral thalamus, from where they project to the SMA (Schell, & Strick, 1984; Wiesendanger, & Wiesendanger, 1985).

Waberski et al. (1999) employed a technique known as "source localisation" to suggest that primary motor cortex or more specifically the pre-central motor cortex is the N30 peak generator. Primate (Strick & Preston, 1982; Tanji & Wise, 1981), and subsequently human (Balzamo et al., 2004) intracortical recordings support that N30 is generated at the motor cortex.

The neural generators of the N30 SEP peak have recently been explored using novel technology. Cebolla, Palmero-Soler, and Cheron (2011) used swLORETA (standardized weighted Low Resolution Brain Electromagnetic Tomography) and determined that the N30 is generated by network activity in the motor, premotor and prefrontal cortex. This finding sheds light on the role N30 plays as a marker of neural processing relevant to sensorimotor integration.

Utilization and Application of SEPs

Clinical

SEP recording is an objective and often more sensitive than the traditional neurological component of physical examination (Walsh, Kane, & Butler, 2005). For example, SEPs can be used in comatose, anesthetised patients (Walsh, Kane, & Butler, 2005). Interpretation of the presence and absence of specific waveforms can be utilized to predict comatose patient prognosis. When SEPs are recorded within 72 hours of entering the comatose state prediction of prognosis is >99% accurate (Wang, Young, & Connolly, 2004).

Based on the reliability of SEP peaks, it is increasingly accepted for use in the

operating room. Operating room monitoring of SEP peaks is done to correct spinal cord ischaemia, prior to it becoming a debilitating issue. SEPs are used in perpetual repetition to continuously monitor for detection of neurological impairment during scoliosis surgery. This technique has resulted in a 50-60% decrease in paraplegia post surgery (Nuwer et al., 1995).

Surface recording electrodes, while relatively non invasive, cause the spatial accuracy of SEP recording to be decreased compared to other direct neuromeasurement techniques. SEPs are regarded as having high temporal and low spatial resolution (Legon & Staines, 2006). The meaningfulness of the interpretation of SEP waveforms is established enough that is has been used as a pre-screening tool for inclusion or exclusion of participants in scientific research. SEPs were collected prior to selection for experimental inclusion in a traumatic brain injury (TBI) study by Sarno, Erasmu, Lipp and Schlaegel (2003). This technique allowed the reduction and refinement of a pool of participants for a reaction time study. Understanding limitations and performance of a TBI population can otherwise be problematic to test due to the possible heterogeneity of symptoms. Examination of the quality of the N20 peak allowed the exclusion of participants with severe sensory impairment, thus yielding an objective test to produce a more homogenous experimental group. SEPs may be used as a neurophysiologic outcome measure when behavioural findings are absent (clinically silent) (Aminoff & Eisen, 1998).

SEPs Study Design and Concurrent Cortical Representation

Pascual-Leone and Torres (1993) utilized tactile presentations resembling Braille characters as their SEP-provoking stimuli. They compared the amplitude and latency of SEPs, and via source localization, the area of the region activated in healthy controls and blind participants. They found that blind participants had an increased area in the sensorimotor cortex representation of the reading finger.

Meehan, Legon and Staines, (2009) explored early somatosensory processing of spatiotemporal information. SEPs were recorded while participants tracked the intensity changes in vibrotactile or visual stimulation, via fluctuation of their motoric output. In different conditions participants were asked to attend to or ignore either the visual stimulation or the tactile stimulation while both were presented. Further variants in their series of studies included changes in orientation both spatially, and temporally of the stimuli relative to the participant. They found that changes in SEP peak P27 amplitude indicated an intermodal gating mechanism.

Control/pretest SEPs then SEPs concurrent with an experimental task

SEPs when recorded concurrently to an experimental task reflect online processing associated with task performance, when compared to no intervention or control group performance. Legon and Staines (2006) used a concurrent SEPs design to test target-stimulus predictability and vibrotactile tracking in a within-participants design. Participants were exposed to two different test conditions, and four control conditions. The test conditions presented either a predictable or unpredictable vibrotactile waveform

to the dominant hand while the opposite hand attempted to motorically reproduce the sensation by isometrically squeezing and releasing in relation to perceived vibrotactile intensity. While performing the unpredictable task the amplitudes of two SEPs peaks were differentially modulated, N20 was attenuated while P27 was enhanced. Legon and Staines (2006) concluded that areas in the primary somatosensory cortex are modulated by the attentional constraints of continuous task relevant sensory stimulation.

Buchner et al. (1999) measured cortical plasticity related to attention and anesthesia. They first elicited SEPs at base line, then again concurrent with conditions of directed attention. They found that an immediate cortical reorganization occurs at peak N20 when partial deafferentation (anesthesia) was present. Waberski, Gobbele, and Buchner (2003) found similar results before and during air puff stimulation of the anesthetised thumb. Cortical representation of the thumb decreased in the presence of anesthesia compared to a preanesthetic condition. They interpreted this finding to indicate that anesthesia yields an immediate cortical reorganization of the representation of the affected and adjacent digits.

Psychophysical literature that pertains to tactile stimulation raises concerns regarding the generation and recording of SEPs concurrent with perception or performance related to another task. It is possible that concurrent SEPs stimulation could negatively impact accurate performance when responding to multiple tactile stimuli, or distractors, leading to unintended masking or enhancement, for example Giblin (1964) determined that SEP peaks are attenuated or masked in the presence of additional tactile

stimulation meant to be irrelevant to SEPs technique recording. Morita, Petersen, and Nielsen (1998), cautioned that SEPs gating can occur with concurrent motor activation in the lower extremity. In as few as 60 ms post contraction tibial nerve SEPs would become attenuated when either foot was plantar or dorsi flexed concurrent with SEPs recording.

SEPs Tactile Masking/Pain Studies

Early animal research by Marshall, Woolsey, and Bard (1937) on somatosensory evoked potentials used direct recording of electrical signals from the brain, and warned of the risk of masking. When using a tactile stimulus to elicit a SEP, if a second tactile stimulus was presented within the same sensory region, neural recordings were attenuated or obliterated which they determined were masked. They also concluded that if a second tactile stimulus fell outside the region of cortical representation of the primary tactile stimulus then no masking effect was present. They found this to be especially true in the lower extremity with stimulation along specific dermatomes.

In a subsequent study from the same laboratory Marshall, Woolsey, and Bard (1941) determined that masking had both peripheral and central components. They predicted that peripherally a majority of neurons were occupied during the presence of one stimulus and that there were few neurons available to respond to or discriminate a second stimulus. Then they found that SEP recordings revealed a masking effect when areas in close cortical but distant anatomical regions were delivered a tactile stimulation. For example stimulation of the thumb, and parts of the face could mask each other at the cortical level.

Tinazzi et al. (1997) explored the impact of tactile sensory disruption using a passive tactile stimulus (no other cognitive, perceptual or motor intervention), in a within-participant SEPs study. Spinal (N14) and subcortical (N18) peaks remained unchanged. The parietal lobe N20 and frontal lobe N30 cortical SEP amplitudes were increased during anesthetic block of the ipsilateral ulnar nerve. This anesthesia, which the authors termed "transient deafferentation" was induced via injection of a 2% lidocaine solution. The amplitudes differed significantly during anesthesia compared to baseline, and following when anesthesia was worn off.

Tinazzi, Rosso, Zanette, Fiaschi, and Aglioti (2003) tested whether the cortical activity created by stimulating ulnar innervated muscles would be altered by cutaneous anethesia of a radial nerve innervated region. They used a between-participant design with groups receiving one of the following interventions: saline injection (inert solution), 2% lidocaine injection (anesthesia), or no injection. They considered differences between groups at baseline, following injection (during anesthesia), and following anesthesia fade out. Only under conditions of anesthesia did N20, P27 and N30 display significant amplitude increases, and only if participants received the 2% lidocaine injection to the ulnar nerve. A limitation to their design is that they could not directly control the nerve affected by the anesthesia injection. The fluid would be free to migrate around the area damaged by injection.

Unilateral radicular pain from the C-6 nerve root level demonstrates SEP amplitude differences compared to both the unimpaired side and to healthy controls

(Tinazzi et al., 2000). Ten participants with a cervical disc protrusion compressing the C-6 nerve root, and ten healthy age matched controls were recruited. SEPs were recorded in a between-limb, and between-participants design. Amplitudes of peaks N13, P14, N20, P27, N30 were all significantly amplified in the limb with the presence of pain. This suggests that peak enhancement can reflect a positive correlation between the presence of pain and SEP amplitude. Tinazzi et al. (2000) concluded that SEPs might be a sensitive neurophysiologic tool to investigate physiopathological changes in humans before the appearance of hard neurological (absent reflex, or motor impairment) symptoms. The same experimental design was used earlier to examine a population with EMG evidence of chronic unilateral carpal tunnel syndrome (Tinazzi et al., 1998). Identical to the radiculopathy study, peaks N13, P14, N20, P27 were all increased in amplitude when generated from the pathological limb compared to the healthy limb, and to an asymptomatic healthy age-matched control group. While all pain and function loss in patient participants impacted the median nerve, ulnar nerve stimulation was used to generate and record the SEPs. Based on their finding Tinazzi et al. concluded that changes associated with chronic pain detected by peripheral nerves may cause plastic changes that can be detected in the brainstem prior to reaching the cortex. Limitations to both studies are the inability to completely homogenize the onset, duration, and intensity of the symptoms in the pain-participant population.

The issue of standardizing pain delivered to participants has been overcome using an experimentally-induced pain model (Rossi, Decchi, Groccia, Della Volpe, &

Spidalieri, 1998). Rossi et al. (2003) built on their foundation to understand how their induced perturbation impacted behavioural, specifically motoric and imagined movement findings in a subsequent study. The induced tonic hand pain using a Levo-Ascorbic solution injection in the first dorsal interosseous muscle. They found that the N18 SEP peak was significantly increased when the pain was present. There was a significant decrease in N30 amplitude when asked to imagine finger movement during the pain condition. The attenuation of N30 was even more pronounced during actual motor recruitment. The strength of this study is the consideration of neurophysiological measurement, and behavioural or imagined movement. A weakness is that no behavioural outcome measures were recorded to quantitatively assess motor task performance.

SEPs Design (Pre and Post) and Neural Reorganization/Neuroplasticity

SEPs when recorded at baseline and compared to a SEPs recorded following a separate perceptual, sensory or motor task reflect the neuroplasticity associated with a perceptual (Pellicciari et al., 2009), or motor task (Haavik Taylor & Murphy, 2003) A pre-test and post-test experimental design can be used to avoid inadvertently masking the tactile system while utilizing the SEPs technique. Pellicciari, Miniussi, Rossini and De Gennaro (2009) compared SEP recordings in the elderly and in a young population, pre-and post-exposure to paired-associative stimuli. While neuroplasticity may take place in both populations with learning, the patterns and underlying structures reflecting plastic changes may differ. This suggests possible compensatory changes to accommodate the

abilities of the elderly population. Murphy, Haavik Taylor, Wilson, Oliphant, and Mathers (2003) used pre- and post-task SEPs as a neurophysiologic measure for plasticity related to motor output. In a within-participants design 10 individuals had SEPs recorded at baseline, then immediately after a 20-minute repetitive-typing task. Attenuation of the N13 peak, N14-18 complex, and N30-P40 complex all occurred immediately following the typing task. Had Murphy et al. (2003) attempted to concurrently record SEPs while performing the typing task, the stimulus intended to be used to stimulate the somatosensory system may have served as an attentional, cognitive, or peripheral perturbation to motor performance that could have masked changes in the targeted SEP peaks.

Haavik Taylor and Murphy (2007) used a pre- and post-SEPs design to consider plasticity associated with the clinical intervention of spinal manipulation. Prior to the intervention, in a between-participant design, 24 individuals were pseudorandomized to receive either manipulation, or passive head motion. Only the spinal manipulation group yielded a significant attenuation of peaks N20 and N30, for about 20 minutes post-manipulation. This plasticity effect provides evidence for altered cortical somatosensory processing and sensorimotor integration following spinal manipulation.

Gobbele, Halboni, Buchner, and Waberski (2007) used a sophisticated experimental design to test thalamocortical signal processing. Ten participants completed 5 different SEPs recording sessions: baseline, during light tactile perturbation, post-tactile perturbation, during cold-induced pain, and post-cold induced pain. They concluded that

the somatosensory system responds to tactile perturbation with similar neural plastic changes as it does to cold-induced pain.

In a repeated measures design Rosso et al. (2003) compared the lower extremity provoked SEP amplitudes of peaks pre- and post-unilateral percutaneous cervical cordotomy (PCC). The PCC was done to obliterate the lateral spinothalamic tract of patient participants suffering from drug-resistant malignant pain. Following the surgically-induced lesion, all participants had contralateral hypoalgesia (pain relief) below the level of the PCC, however the pyramidal, and dorsal columns remained intact. Cortical peaks demonstrated increased amplitude following the surgery, no peaks below the brain stem changed from pre to post intervention. This only occurred in the peaks that were on the side affect by the PCC, peaks on the contralateral side remained intact. They concluded that their findings indicated that cross modality neural plasticity occurs since dorsal column medial lemniscal cortical responses increase as a results of spinothalamic obliteration.

The application of SEPs to the exploration of tactile perceptual gain was recently applied in a pre- and post-test design (Hoffken et al., 2007). Participants had SEPs collected and performed a tactile discrimination task at six time points: four prior to tactile coactivation, one immediately post-coactivation and one that was 24 hours post-coactivation. Discrimination ability was compared between hands at each time point. Tactile co-activation was delivered as a 10 ms tactile vibration at the index finger between two probes 6mm apart with a variable interstimulus interval that average out to

be 1 Hz. This was done for 3 hours. Participants were instructed to ignore the stimulus while performing their activities of daily living. They found that an increase of excitability correlated with individual improvement in discrimination performance. They concluded that tactile co-activation modifies cortical activity, and these changes reflect both discrimination learning, and plasticity associated with perceptual learning. The perceptual task was a simple discrimination task. The co-activation task was coupled with non-specific activities of daily living that varied between participants. Studies requiring more stimulus-response alternatives for decisions, and controlled complex learning under perturbation conditions need to be designed to better understand plasticity related to learning, and not just detection.

Dinse, Ragert, Pleger, Schwenkreis, and Tegenthoff (2003) explored the effects of pharmacology on tactile discrimination and SEPs. Participants were randomized to either be administered a placebo control, the N-methyl-D-aspartate (NMDA) receptor blocker, memantine, or amphetamine. Their coactivation methods were similar to the protocol eventually used by Hoffken et al. (2007), which was derived from Pleger et al. (2001). Participants received tactile co-activation for 3 hours and had tactile discrimination and SEPs recorded at different time points pre- and post-pharmacological intervention. Their hypothesis was that NMDA receptors may play a crucial role in neuroplasticity (Bliss & Coolingridge, 1993). When NMDA receptors are blocked they predicted decreased neural activation. They contrasted the NMDA blocker group by having another group use amphetamine, as a drug to possibly enhance cortical activity. Hoffken et al. found that

tactile coactivation significantly improved 2-point discrimination in the placebo group. Amphetamine enhanced the effect of coactivation significantly by almost doubling the 2-point discrimination ability compared to the placebo group. The memantine group was resistant to plastic changes associated with tactile coactivation. The SEPs changes at the N20 peak supported these findings, suggesting that NMDA receptors are associated with neural plasticity. The authors concluded that their findings improved understanding of the mechanisms that facilitate or inhibit perceptual learning at the receptor level.

Conclusion

Somatosensory evoked potential recording has been established as a meaningful neurophysiological measurement technique in both clinical and research contexts.

Specific parameters for eliciting and measuring SEPs have been created as recommendations for uniform testing conditions. Obliteration and pathology studies have allowed understanding of the significance and origin of several peaks. Changes in activity resulting in peak latency and amplitude modulation allow the visualization and quantification of precognitive neural plasticity associated with perceptual, cognitive, and motor tasks or phenomena. Future studies should consider designs that control for or eliminate the possibility of tactile masking, or enhancement, and that can control the neurological perturbation or pain impairment in the participant.

1.3 The perturbation of complex tactile learning

Pathologies are inevitable in humans and several lead to impaired tactile sensory ability. A short list of pathologies impacting tactile sensation includes traumatic brain injury, stroke, spinal cord injury, spinal stenosis, and diabetes (Marks & Zukerberg, 2004). Even in the presence of moderate or severe pathology people are expected to attempt to lead independent and meaningful lives. A clinical feature found in some sensory impaired patients is paresthesia. Paresthesia is the sensation of "pins and needles" that can radiate along the course of a specific nerve. How impaired sensation like upper extremity paresthesia impacts the ability to interact with the tactile environment is not widely known.

Paresthesia can occur as a symptom of pathology, but it can also be artificially created. Radiating paresthesia can be induced using transcutaneous electrical stimulation over the suspected course of a peripheral nerve (Zehr & Chua, 2000). From the site of stimulation an orthodromic response will radiate from proximal to distal along the nerve pathway. Paresthesia may indicate the presence of pathology, but it has no other inherent meaning. It is a persistent stimulus to the tactile system, and has no specific information or message attached to it that a person needs to be concious of -- it simply creates interference. Paresthesia requires nothing but a simple response, it is either present or absent which makes it ideal as a meaning-neutral perturbation tool to investigate interference with complex information delivery. The study of interference as is pertains to the reception of meaningful tactile information is either attributed to masking,

enhancement or response competition (selective attention) effects (Craig, 1995).

When simple information is presented to the tactile system, a discrimination of whether it was perceived or not is all that is required to respond. Complex information requires a more sophisticated model of information processing, as information is not only detected, but must be interpreted before an appropriate response can be made.

Considerable study has been devoted to the study of the detection of simple tactile stimuli and the factors that can lead to tactile information masking, or enhancement.

Considerably less effort has been applied to factors that mask or enhance the learning of complex tactile stimuli.

A masking stimulus is thought to interfere with information acquisition in three possible ways. The first is a distortion of temporal integration of the target by the non-target stimulus (Evans, 1987; Evans & Craig, 1986). The second is a distortion of target features by the non-target stimulus (Evans & Craig, 1986). The third is a deletion of target features by the presence of a non-target stimulus (Evans & Craig, 1986). To maximize the extent of masking and to minimize the response competition that occurs, the non-target (masking stimulus) should be neutral and require no response generation (Craig, 2000). Failure to use a neutral masker may have lead to an underrepresentation of masking effects in previous studies (Craig, 2000). Craig (1995) proposed that future masking or response competition studies could incorporate more complex tactile tasks, could measure changes in the time to respond to stimuli, and that as stimulation techniques grow, more sophisticated patterns can be presented to the same spatial area of

skin.

The present dissertation examined paresthesia as a potential masking perturbation during complex tactile information transmission. The four experiments provide evidence regarding sensory and information processing demands in the early stages of complex tactile learning under perturbation. The purpose of document one was to address the suggestions made by Craig (1995) in order to further explore whether tactile interference during complex tactile learning occurs due to masking, or response competition. The design used in the first two experiments presented in this dissertation identifies if the presence of a masking stimulus serves to exceed the capacity of peripheral sensory receptors, or if the masking stimulus is merely an attentional distraction (response competition). The general focus of the two experiments was to extend knowledge of interference effects related to the simple detection findings of Craig (1983) and Kekoni et al. (1990) to a more complex tactile learning task. Specifically the purpose of these experiments is: to determine if induced radiating paresthesia interferes with (a) the acquisition and/or (b) the application of complex tactile information, and (c) to identify whether any potential interference reflects a tactile masking or response competition (selective attention) paradigm. In both experiments the implications of interference are explored in how they impact the acquisition, and recollection of complex meaningful tactile information.

Several of the issues raised by Craig (1995) regarding previous studies on masking were accounted for in experiment 1. The first issue resolved was the spatial

overlap of both a neutral and a complex meaningful stimulus. The target (vibrotactile Morse code) and masking (ulnar paresthesia) stimuli were both presented to the same anatomical innervation region. The second issue resolved was the application of a complex tactile task as the target stimuli rather than a simple detection task. The vibrotactile Morse code design used was based on the methodological paper by Tang et al. (2009)

The purpose of experiment 2 was to resolve whether the findings of experiment one were due to a masking effect or a response competition effect. The experimental design of the first study specifically examined a masking paradigm by having a concurrent neutral secondary stimulus and overlapping the spatial presentation of target and non-target stimuli. However, if masking is the phenomenon of overwhelming peripheral sensory receptors at the site of target information uptake, then the spatial separation of concurrent target and non-target stimulation will represent a response competition effect (Craig & Evans, 1995; Evans & Craig, 1991; Evans, Craig, & Rinker, 1992; Rinker & Craig, 1994). Response competition is the balance of two competing stimuli. It involves the ability to process the correct information being presented and also the ability to selectively ignore, or inhibit processing of irrelevant stimuli (Frings et al., 2008). Experiment 2 applied the same complex target (vibrotactile Morse code) and nontarget neutral stimulation (paresthesia) as in experiment 1, but shifted the non target to impact an adjacent peripheral nerve. By stimulating the median nerve pathway with paresthesia, while the reception of the complex tactile task was delivered to the ulnar

nerve pathway, the cutaneous peripheral sensory receptors of the ulnar-innervated regions were spared from additional perturbation. This procedure allowed for a response competition paradigm to be tested for the complex vibrotactile target stimulus.

The goal of the second document was twofold. First to replicate the behavioural acquisition findings from document 1, and second to determine whether masking, and response competition paradigms are reflected by measurable electrical changes at the cortical level. A somatosensory evoked potential (SEP) is the electrical activity response measured at the skin's surface following controlled peripheral nerve stimulation.

Electrical activity from peripheral stimulation measured over the scalp reflects cerebral action potentials and are best recorded contralateral to peripheral nerve stimulation (Dawson, 1947). Evoked potentials are a window into the reception and processing of somatosensory information. To understand the significance of the waveforms, their components and their neurological interpretation, comparison of SEPs in both healthy participants and patients with impairments including lesions of the peripheral nerves, spinal cord, and the brain have been observed (Giblin, 1964). Utilization of SEPs in the present study allowed the interpretation of both behavioural results and the impact of the presence of a temporarily induced pathology (paresthesia) at the cortical level.

In experiment 3 (first experiment of document #2), the acquisition aspect of the vibrotactile Morse code paradigm from experiment 1 (document #1) was examined. The use of SEPs allowed for the interpretation of whether masking: 1) is strictly the overwhelming of peripheral subcortical receptors, 2) is a central component to discerning

a mask from target stimuli, or 3) if masking is a combination of the two. If changes in SEPs were equivalent in participants under Morse code learning conditions whether paresthesia was received or not, then changes could be interpreted as general changes as a result of tactile learning. If no SEPs changes occurred, then tactile learning was not reflected cortically. If SEP changes were differentially impacted by the presence or absence of paresthesia then a central component to masking could be inferred.

Experiment 4 (second experiment of document #2), examined the acquisition aspect of the vibrotactile Morse code paradigm from experiment 3. The use of SEPs allowed for the interpretation of whether response competition is a subcortical phenomena, or if there was a central component to discerning competing stimuli, or if there was a combination of the two. If changes in SEPs were equivalent in participants under Morse code learning conditions whether paresthesia was received or not, then changes could be interpreted as general changes as a result of tactile learning. If no SEPs changes occurred, then tactile learning was not reflected cortically. If SEP changes were differentially impacted by the presence or absence of paresthesia then a central component to response competition could be inferred.

In summary, the four experiments were conducted to address the shortcomings of previous studies on tactile studies as observed by Craig (1995) – specifically, the spatial separation of masking and target stimuli and the complexity of the tactile stimulation. The present studies examined the manipulation of spatial locations of temporally overlapped presentations of complex target, and neutral non-target tactile stimuli. The studies also

utilized the learning of complex tactile stimuli as opposed to the detection of simple stimuli. The result of this research was a unique contribution to the understanding of both masking, and response competition paradigms, achieved by the identification of subcortical and cortical changes associated with the perturbation of complex tactile learning. The findings serve as a steppingstone to further exploration of complex tactile learning in patients with tactile sensory impairment.

References

- Allison, T., McCarthy, G., Wood, C.C., & Jones, S.J. (1991). Potentials evoked in human and monkey cerebral cortex by stimulations of the median nerve: a review of scalp and intracranial recordings. *Brain*, *114*, 2465-2503.
- Aminoff, M.J., & Eisen, A.A. (1998). AAEM minimonograph 19: somatosensory evoked potentials. *Muscle Nerve*, 21, 277-290.
- Apkarian, A.V., Stea, R.A., & Bolanowski, S.J. (1994). Heat-induced pain diminishes vibrotactile perception: a touch gate. *Somatosensory & Motor Research*, 11, 259-267.
- Arezzo, J.C., Schaumburg, H.H., & Spencer, P.S. (1982). Structure and function of the somatosensory system: a neurotoxicological perspective. Environmental Health *Perspectives*, 44, 23-30.
- Bach-y-Rita, P., Collins, C.C., Saunders, F.A., White, B., & Scadden, L. (1969). Vision substitution by tactile image projection. *Transactions of the Pacific Coast Oto-Opthalmological Society Annual Meeting*, 50, 83-91.
- Balzamo, E., Marquis, P., Chauvel, P., & Regis, J. (2004). Short-latency components of evoked potentials to median nerve stimulation recorded by intracerebral electrodes in the human pre- and postcentral areas. *Clinical Neurophysiology*, 115, 1616-1623.
- Barrett, W.F. (1875). The Morse code. *Nature*, 11, 328.
- Bartley, S.H., & Heinbecker, P. (1937). The response of the somatosensory cortex to

- stimulation of a peripheral nerve. American Journal of Physiology, 121, 21-31.
- Bernhardt, J. (1987). Sensory capabilities of the fetus. MCN, American Journal of Maternal Child Nursing, 12, 44-46.
- Bhattacharjee, A., Ye, A.J., Lisak, J.A., Vargas, M.G., & Goldreich, D. (2010).

 Vibrotactile masking experiments reveal accelerated somatosensory processing in congenitally blind Braille readers. *The Journal of Neuroscience*, 30, 14288-14298.
- Bliss, J.C., Crane, H.D., Mansfield, P.K., & Townsend, J.T. (1966). Information available in brief tactile presentations. *Attention, Perception & Psychophysics*, 1, 273-283.
- Bliss, J.C., Katcher, M.H., Rogers, C.H., & Shepard, R.P. (1970). Optical-to-tactile image conversion for the blind. *IEEE Transactions on Man-Machine Systems*, 11, 58-65.
- Bliss, T.V., & Collingridge, G.L. (1993). A synaptic model of memory: long term potentiation in the hippocampus. *Nature*, *361*, 31-39.
- Bolanowski, S.J., Maxfield, L.M., Gescheider, G.A, & Apkarian, A.V. (2000). The effects of stimulus location on the gating of touch by heat- and cold-induced pain. Somatosensory & Motor Research, 17, 195-204.
- Bolanowski, S.J., Gescheider, G.A., Verrillo, R.T., & Checkosky, C.M. (1988). Four channels mediate the mechanical aspects of touch. *Journal of the Acoustical Society of America*, 84, 1680-1694.
- Brammer, A.J., Piercy, J.E., Pyykko, I., Toppila, E., & Starck, J. (2007). Method for detecting small changes in vibrotactile perception threshold related to tactile acuity. *Journal of the Acoustical Society of America*, *121*, 1238-1247.

- Brener, R. (1940). An experimental investigation of memory span. *Journal of Experimental Psychology*, 26, 467-482.
- Brodal, P. (1998). The central nervous system: Structure and function. New York, NY:
 Oxford University Press.
- Brooks, P.L. & Frost, B.J. (1983). Evaluation of a tactile vocoder for word recognition. *Journal of the Acoustical Society of America*, 74, 34-39.
- Brown, W.F., & Feasby, T.E. (1984). Sensory evoked potentials in Guillain-Barre polyneuropathy. *Journal of Neurology Neurosurgery and Psychiatry*, 47, 288-291.
- Bryan, W.L. & Harter, N. (1897). Studies in the physiology and psychology of the telegraphic language. *Psychological Review*, *4*, 27-53.
- Bryan, W.L. & Harter, N. (1899). Studies on the telegraphic language: the acquisition of a hierarchy of habits. *Pscyhological Review*, *6*, 345-375.
- Buchner, H., Reinartz, U., Waberski, T.D., Gobbele, R., Noppeney, U., & Scherg, M. (1999). Sustained attention modulates the immediate effect of de-afferentation on the cortical representation of the digits: source localization of somatosensory evoked pontentials in humans. *Neuroscience Letters*, 260, 57-60.
- Cebolla, A.M., Palmero-Soler, E., & Cheron, D.B. (2011). Frontal phasic and oscillatory generators of the N30 somatosensory evoked potential. *NeuroImage*, *54*, 1297-1306.
- Cheron, G., & Borenstein, S. (1991). Gating of the early components of the frontal and parietal somatosensory evoked potentials in different sensory-motor interference

- modalities. Electroencephalography & Clinical Neurophysiology. 80, 522-530.
- Cholewiak, R. (1999). The perception of tactile distance: influences of body site, space, and time. *Perception*, 28, 851-875.
- Cholewiak R.W., Brill, J.C., & Schwab, A. (2004). Vibrotactile localization on the abdomen: effects of place and space. *Perception & Psychophysics*, 66, 970-987.
- Craig, J.C. (1982). Vibrotactile masking: a comparison of energy and pattern maskers.

 *Perception & Psychophysics, 31, 523-529.
- Craig, J.C. (1983). The role of onset in the perception of sequentially presented vibrotactile patterns. *Perception & Psychophysics*, *34*, 421-432.
- Craig, J.C. (1985). Tactile pattern perception and its perturbations. *Journal of the Acoustical Society of America*, 77, 238-246.
- Craig, J.C. (1995). Vibrotactile masking: the role of response competition. *Perception & Psychophysics*, *57*, 1190-1200.
- Craig, J.C. (2000). Vibratory temporal integration as a function of pattern discriminability. *Perception & Psychophysics*, 62, 596-606.
- Craig, J.C. & Evans, P.M. (1995). Tactile selective attention and temporal masking.

 *Perception & Psychophyics, 57, 511-518.
- Cruccu, G., Aminoff, M.J., Curio, G., Guerit, J.M., Kakigi, R., Mauguiere, F., Rossini, P.M., Treede, R.D., & Garcia-Larrea, L. (2008). Recommendations for the clinical use of somatosensory-evoked potentials. *Clinical Neurophysiology*, 119, 1705-1719.

- Cusick, J.F., Myklebust, J.B., Larson, S.J., & Sances, A. (1979). Spinal cord evaluation by cortical evoked potentials. *Archives of Neurology*, *36*, 140-143.
- Dalton, P., Lavie, N., & Spence, C. (2009). The role of working memory in tactile selective attention. *The Quarterly Journal of Experimental Psychology*, 62, 635-644.
- Dawson, G.D. (1947). Cerebral responses to electrical stimulation of peripheral nerve in man. *Journal of Neurology Neurosurgery and Psychiatry*, *10*, 134-140.
- Desmedt, J.E. (1971). Somatosensory cerebral evoked potentials in man. In W.A. Cobb (Ed.), Handbook of Electroencephalography and Clinical Neurophysiology (p 55).

 Amsterdam: Elsevier.
- Desmedt, J.E., & Cheron, G. (1980). Central somatosensory conduction in man: neural generators and interpeak latencies of the far-field components recorded from neck and right or left scalp and earlobes. *Electroencephalography & Clinical Neurophysiology*, 50, 382-403.
- Desmedt, J.E., Cheron, G. (1981). Non-cephalic reference recording of early somatosensory potentials to finger stimulation in adult or aging normal man: differentiation of widespread N18 and contralateral N20 from the prerolandic P22 and N30 components. *Electroencephalography & Clinical Neurophysiology*, *52*, 553-570.
- Desmedt, J.E., and Osaki, I. (1991). SEPs to finger joint input lack the N20-P20 response that is evoked by tactile inputs: contrast between cortical generators in areas 3b

- and 2 in humans. *Electroencephalography & Clinical Neurophysiology*, 80, 513-521.
- Dinse, H.R., Ragert, P., Pleger, B., Schwenkreis, P., and Tegenthoff, M. (2003).

 Pharmacological modulation of perceptual learning and associated cortical reorganization. *Science*, *301*, 91–94.
- Donders, F.C. (1868). Over de snelheid van psychische processen. *Onderzoekingen*gedaan in het Physiologisch Laboratorium der Utreschtsche Hoogeschool, 2, 92
 120.
- Drew, F. (1896). Attention: experimental and critical. *The American Journal of Psychology*, 7, 533-573.
- Eccles, J.C. (1951). Interpretation of action potentials evoked in the cerebral cortex. *Electroencephalography & Clinical Neurophysiology, 3,* 449-464.
- Eimer, M., & Driver, J. (2000). An event-related brain potential study of cross-modal links in spatial attention between vision and touch. *Psychophysiology*, *37*, 697-705.
- Enriquez, M., & MacLean, K. (2008). The role of choice in longitudinal recall of meaningful tactile signals. Proceedings 16th Symposium Haptic Interfaces for Virtual Environments and Teleoperator Systems (HAPTICS '08), pp 49-56.
- Evans, P.M. (1987). Vibrotactile masking: Temporal integration, persistence, and strengths of representations. *Perception & Psychophysics*, 42, 515-525.
- Evans, P.M., & Craig, J.C. (1986). Temporal integration and vibrotactile backward

- masking. *Journal of Experimental Psychology: Human Perception & Performance*, 12, 160-168.
- Evans, P.M., & Craig, J.C. (1991). Tactile attention and the perception of moving tactile stimuli. *Perception & Psychophysics*, 49, 355-364.
- Evans, P.M., Craig, J.C., & Rinker, M.A. (1992). Perceptual processing of adjacent and nonadjacent tactile targets. *Perception & Psychophysics*, 52, 571-581.
- Foulke, E. (1982). Reading Braille. In W. Schiff & E. Foulke (Eds.), Tactual perception (168-208). New York, NY: Cambridge University Press.
- Foulke, E. (1991). Braille. In M.A. Heller & W. Schiff (Eds.), The psychology of touch (219-233). Hillsdale, NJ: Lawrence Erlbaum Associates Incorporated.
- Foulke, E., & Broadbeck, A.A. (1968). Transmission of Morse code by electrocutaneous stimulation. *The Psychological Record*, *18*, 617-622.
- Frings, C., Bader, R., & Spence, C. (2008). Selection in touch: negative priming with tactile stimuli. *Perception & Psychophysics*, 70, 516-523.
- Gallace, A., Tan, H.Z., & Spence C. (2006). The failure to detect tactile change: a tactile analogue of visual change blindness. *Psychonomic Bulletin & Review, 13*, 300-303.
- Gallace, A., & Spence, C. (2009). The cognitive and neural correlates of tactile memory. *Psychological Bulletin*, 135, 380-406.
- Gallace, A., & Spence, C. (2008). The cognitive and neural correlates of "tactile consciousness": a multisensory perspective. *Consciousness and Cognition*, 17,

370-407.

- Gallace, A., Tan, H.Z., Haggard, P., & Spence, C. (2008). Short term memory for tactile stimuli. Brain Research, 1190, 132-142.
- Gallace, A., Tan, H.Z., & Spence C. (2007). The body surface as a communication system: the state of the art after 50 years. *Presence*, *16*, 655-676.
- Gallace, A., Tan, H.Z., & Spence C. (2008). Can tactile stimuli be subitised? An unresolved controversy within the literature on numerosity judgments. *Perception*, *37*, 782-800.
- Galvin, K., Blamey, P.J., Oerlemans, M., Cowan, R.S.C., & Clark, G.M. (1999).

 Acquisition of a tickle-alone vocabulary by normally hearing users of the Tickle

 Talker TM. Journal of the Acoustical Society of America, 106, 1084-1089.
- Gandevia, S.C., Burke, D. (1988). Projection to the cerebral cortex from proximal and distal muscles in the human limb. *Brain*, *111*, 389-403.
- Gandevia, S.C., Burke, D., & McKeon, B. (1984). The projection of muscle afferents from the hand to cerebral cortex in man. *Brain*, *107*, 1-13.
- Ganes, T. (1980). Somatosensory evoked responses and central afferent conduction times in patients with multiple sclerosis. *Journal of Neurology Neurosurgery and Psychiatry*, 43, 948-953.
- Garcia Larrea, L., Bastuji, H., Mauguiere, F. (1992). Unmasking of cortical SEP components by changes in stimulus rate: a topographic study.

 Electroencephalography & Clinical Neurophysiology, 84, 71-83.

- Geldard, F.A. (1957). Adventures in tactile literacy. American Psychologist, 12, 115-124.
- Geldard, F.A. (1960). Some neglected possibilities of communication. *Science*, *131*, 1583-1588.
- Gescheider, G.A. (1966). Resolving of successive clicks by the ears and skin. *Journal of Experimental Psychology*, 71, 378-381.
- Gescheider, G.A., Verrillo, R.T., & Van Doren, C.L. (1982). Prediction of vibrotactile masking functions. *Journal of the Acoustical Society of America*, 72, 1421-1426.
- Gescheider, G.A., Bolanowski, S.J., & Verrillo, R.T. (1989). Vibrotactile masking: effects of stimulus onset asynchrony and stimulus frequency. *Journal of the Acoustical Society of America*, 85, 2059-2064.
- Gescheider, G.A., Verrillo, R.T., & Pelli, D.G. (1991). Effects of noise on detection of amplitude increments of sinusoidal vibration of the skin. *Journal of the Acoustical Society of America*, *91*, 348-353.
- Giblin, D.R. (1964). Somatosensory evoked potentials in healthy subjects and in patients with lesions of the nervous system. *Annals New York Academy of Sciences*, 112, 93-142.
- Gibson, J.J. (1962). Observations on active touch. *Psychological Review*, 69, 477-491.
- Gilson, E.Q., & Baddeley, A.D. (1969). Tactile short-term memory. *The Quarterly Journal of Experimental Psychology*, 21, 180-184.
- Gobbele, R., Halboni, P., Buchner, H., Waberski, T.D. (2007). Interference of tactile and pain stimuli on thalamocortical signal processing in humans revealed by median

- nerve SEPs. Clinical Neurophysiology, 118, 2497-2505.
- Haavik-Taylor, H., Murphy, B. (2007). Cervical spine manipulation alters sensorimotor integration: a somatosensory evoked potential study. *Clinical Neurophysiology*, 118, 391-402.
- Haavik-Taylor H, & Murphy B. (2008) Altered sensorimotor integration with cervical spine manipulation. *Journal of Manipulative & Physiological Therapeutics*, *31*, 115–126.•
- Haavik, H., & Murphy, B. (2012). The role of spinal manipulation in addressing disordered sensorimotor integration and altered motor control. *Journal of Electromyography and Kinesiology*, 22, 768-776.
- Hamer, R.D., Verrillo, R.T., & Zwislocki, J.J. (1982). Vibrotactile masking of Pacinian and non-Pacinian channels. *Journal of the Acoustical Society of America*, 73, 1293-1303.
- Heinbecker, P., Bishop, G.H., & O'Leary, J. (1934). Analysis of sensation in terms of the nerve impulse. *Archives of Neurology and Psychiatry*, 31, 34-53.
- Heller, M.A. (1985). Tactual perception of embossed Morse code and braille: the alliance of vision and touch. *Perception*, *14*, 563-570.
- Heller, M.A. (1987). The effect of orientation on visual and tactual braille recognition. *Perception*, *16*, 291-298.
- Heller, M.A., & Mitchell, B.Y. (1985). Helping new braille readers: effects of spacing, finger locus, and gloves. *Perceptual and Motor Skills*, 61, 363-369.

- Hick, W. E. (1952) On the rate of gain of information. *Quarterly Journal of Experimental Psychology*, 4, 11-26.
- Hillstrom, A.P., Shapiro, K.L., & Spence, C. (2002). Attentional limitations in processing sequentially presented vibrotactile targets. *Attention, Perception & Psychophysics*, 64, 1068-1082.
- Hlushchuk, Y., & Hari, R. (2006). Transient suppression of ipsilateral primary somatosensory cortex during tactile finger stimulation. *The Journal of Neuroscience*, 26, 5819-5824.
- Hoffken, O., Veit, M., Knossalla, F., Lissek, S., Bliem, B., Ragert, P., Dinse, H.R. & Tegenthoff, M. (2007). Sustained increase of somatosensory cortex excitability by tactile coactivation studied by paired median nerve stimulation in humans correlates with perceptual gain. *Journal of Physiology*, 584, 463-471.
- Hollins, M., & Sigurdsson, A. (1998). Vibrotactile amplitude and frequency discrimination in temporomandibular disorders. *Pain*, 75, 59-67.
- Hollins, M., Sigurdsson, A., Fillingim, L., & Goble, A.K. (1996). Vibrotactile threshold is elevated in temporomandibular disorders. *Pain*, *67*, 89-96.
- Hollins, M. (2010). Somesthetic senses. Annual Review of Psychology, 61, 243-271.
- Jones, S.J., Baraitser, M., & Halliday, A.M. (1980). Peripheral and central somatosensory nerve conduction defects in Friedreich's ataxia. *Journal of Neurology*Neurosurgery and Psychiatry, 43, 495-503.
- Jones, S.J., Wynn Parry, C.B., & Landi, A. (1981). Diagnosis of brachial plexus traction

- lesions by sensory nerve action potentials and somatosensory evoked potentials. *Injury, 12,* 376-382.
- Jones, S.J. (1981). An "interference" approach to the study of somatosensory evoked potentials in man. *Electroencephalography & Clinical Neurophysiology*, *52*, 517-530.
- Kanovský, P., Bare, M., Rektor, I. (2003). The selective gating of the N30 cortical component of the somatosensory evoked potentials of median nerve is different in the mesial and dorsolateral frontal cortex: evidence from intracerebral recordings. *Clinical Neurophysiology*, 114, 981-991.
- Kekoni, J., Pertovarra A., & Hamalainen, H. (1987). Vibrotactile masking effects on airpuff-elicited sensations vary with skin region in the human hand.

 *Somatosensory & Motor Research, 5, 93-105.
- Kekoni, J., Tikkala, I., Pertovarra A., & Hamalainen, H. (1990). Spatial features of vibrotactile masking effects on airpuff-elicited sensations in the human hand. Somatosensory & Motor Research, 7, 353-363.
- Keller, F.S., & Schoenfeld, W.N. (1944). Studies in international Morse code III: the efficiency of the code as related to errors made during learning. *Journal of Applied Psychology*, 28, 254-266.
- Keller, F.S., & Taubman, R.E. (1943). Studies in international Morse code II: errors made in code reception. *Journal of Applied Psychology*, *27*, 504-509.
- Khoshnoodi, M.A., Motiei-Langroudi, R., Omrani, M., Diamond M.E., & Abbassian

- A.H. (2008). Effect of tactile stimulus frequency on time perception: the role of working memory. *Experimental Brain Research*, 185, 623-633.
- Kirman, J.H. (1973). Tactile communication of speech: a review and an analysis. *Psychological Bulletin*, 80, 54-74.
- Klein, R.M., & Shore, D.I. (2000). Relations among modes of visual orienting. In S.
 Monsell & J. Driver (Eds.), Attention and performance XVIII: control of cognitive processes (195-208). Cambridge, MA: MIT Press.
- Lavie, N. (2005). Distracted and confused?: selective attention under load. *Trends in cognitive sciences*, *9*, 75-82.
- Lederman, S.J. (1981). The perception of surface roughness by active and passive touch.

 *Bulletin of the Psychonomic Society, 18, 253-255.
- Leeman, S.A. (2007). SSEPs: from limb to cortex. *American Journal of Electroneurodiagnostic Technology*, 47, 165-177.
- Legon, W. & Staines, W.R. (2006). Predictability of the target stimulus for sensory-guided movement modulates early somatosensory cortical potentials. *Clinical Neurophysiology*, 117, 1345-1353.
- Lew, H.L., Lee, E.H., Pan, S.S.L., & Chiang J.Y.P. (2007). Electrophysiologic assessment techniques: evoked potentials and electroencephalography. In N.D. Zasler, D.I. Katz, & R.D. Zafonte (Eds.), Brain injury medicine: principles and practice (157-166). New York, NY: Demos Publishing.
- Linden, D., Berlit, P. (1996). Spinal arteriovenous malformations: clinical and

- neurophysiological findings. *Journal of Neurology*, 243, 9-12.
- Lloyd, D.M., Bolanowski, S.J., Howard, L., & McGlone, F. (1999). Mechanisms of attention in touch. *Somatosensory & Motor Research*, *16*, 3-10.
- Loomis, J.M. (1990). A model of character recognition and legibility. *Journal of Experimental Psychology: Human Perception and Performance, 16*, 106-120.
- Lynch, M.P., Eilers, R.E., Oller, D.K., & Lavoie, L. (1988). Speech perception by congenitally deaf subjects using an electrocutaneous vocoder. *Journal of Rehabilitation Research and Development*, 25, 41-50.
- Lynch, M.P., Eilers, R.E., Oller, D.K., Urbano, R.C., & Pero, P.J. (1989). Multisensory narrative tracking by a profoundly deaf subject using an electrocutaneous vocoder and a vibrotactile aid. *Journal of Speech and Hearing Research*, 32, 331-338.
- MacLean, K. (2008). Foundations of transparency in tactile information design. *IEEE Transactions on Haptics*, 1, 84-95.
- Manzano, G.M., Negrao, N., Nobrega, J.A.M. (1998). The N18 component of the median nerve SEP is not reduced by vibration. *Electroencephalography & Clinical Neurophysiology*, 108, 440-445.
- Marks, P.W., & Zukerberg, L.R. (2004). Case records of the Massachusetts General Hospital. Weekly clinicopathological exercises. Case 30-2004. A 37-year-old women with paresthesias of the arms and legs. *New England Journal of Medicine*, 351, 1333-1341.
- Marshall, W.H., Woolsey, C.N., & Bard, P. (1941). Observations on cortical somatic

- sensory mechanisms of cat and monkey. Journal of Neurophysiology, 4, 1-24.
- Marshall, W.H., Woolsey, C.N., & Bard, P. (1937). Cortical representation of tactile sensibility as indicated by cortical potentials. *Science*, 85, 388-390.
- Mastaglia, F.L., Black, J.L., & Collins, D.W.K. (1976). Visual and spinal evoked potentials in diagnosis of multiple sclerosis. *British Medical Journal*, 2, 732.
- Mastaglia, F.L., Black, J.L., Edis, R., & Collins, D.W.K. (1978). The contribution of evoked potentials in the functional assessment of the somatosensory pathway. In J.H. Tyrer, & M.J. Eadie (Eds.), Clinical and Experimental Neurology:

 Proceedings of the Australasian Association of Neurologists (p 279). Sydney:

 Adis Press.
- Mauguiere, F., Desmedt, J.E., Courjon, J. (1983). Astereognosis and dissociated loss of frontal or parietal components of somatosensory evoked potentials in hemispheric lesions: detailed correlations with clinical signs and computerized tomographic scanning. *Brain*, 106, 271-311.
- Mauguiere, F. (2005). Somatosensory evoked potentials: normal responses, abnormal waveforms, and clinical applications in neurological diseases. In E. Niedermeyer, & F.H. Lopes da Silva (Eds.), Electroencephalography: basis principles, clinical applications, and related fields (p 1067). Philidelphia: Lippincott, Williams & Walkin.
- McAuley, D.M., Ewing, P.A., & Devasundaram, J.K. (1993). Effect of hand soaking on sensory testing. *International Journal of Leprosy and Other Mycobacterial*

- Diseases, 61, 16-19.
- McGlone, F., & Spence, C. (2010). The cutaneous senses: touch, temperature, pain/itch, and pleasure. *Neuroscience and Biobehavioral Reviews*, *34*, 145-147.
- Meehan, S.K., Legon, W., & Staines, R. (2009). Spatiotemporal properties modulate intermodal influences on early somatosensory processing during sensory-guided movement. *Clinical Neurophysiology*, *120*, 1371-1380.
- Miller, G.A. (1956). The magical number seven, plus or minus two: some limits on our capacity for processing information. *Psychological Review*, *63*, 81-97.
- Molinari, M., Restuccia, D., & Leggio, M.G. (2009). State estimation, response prediction, and cerebellar sensory processing for behavioural control. *Cerebellum*, 8, 399-402.
- Montgomery, E. (1880). The dependence of quality on specific energies. *Mind*, *5*, 1-29. Montgomery, E. (1885). Space and touch, I. *Mind*, *10*, 227-244.
- Moon, W. (1873). Light for the blind. London, UK: Longmans & Company.
- Moss, F., Ward, L.M., & Sannita, W.G. (2004). Stochastic resonance and sensory information processing: a tutorial and review of application. *Clinical Neurophysiology*, 115, 267-281.
- Morita, H., Petersen, N., & Nielsen, J. (1998). Gating of somatosensory evoked potentials during voluntary movement of the lower limb in man. *Experimental Brain**Research, 120, 143-152.
- Murphy, B.A., Haavik Taylor, H., Wilson, S.A., Oliphant, G. & Mathers, K.M. (2003).

- Rapid reversible changes to multiple levels of the human somatosensory system following the cessation of repetitive contractions: a somatosensory evoked potential study. *Clinical Neurophysiology*, *114*, 1531-1537.
- Neal, S.L., & Fields, K.B. (2010). Peripheral nerve entrapment and injury in the upper extremity. *American Family Physician*, 81, 147-155.
- Nelson, F.W., Goldie, W.D., Hecht, J.T., Butler, I.J., & Scott, C.I. (1984). Short latency somatosensory evoked potentials in the management of patients with achondroplasia. *Neurology*, *34*, 1053-1058.
- Noel, P., Ozaki, I., Desmedt, J.E. (1996). Origin of N18 and P14 far-fields of median nerve somatosensory evoked potentials studied in patients with a brain-stem lesion. *Electroencephalography & Clinical Neurophysiology*, 98, 167-170.
- Nuwer, M.R., Aminoff, M., Desmedt, J., Eisen, A.A., Goodin, D., Matsuoka, S., Mauguiere, F., Shibasaki, H., Sutherling, W., Vibert, J.F. (1994). IFCN recommended standards for short latency somatosensory evoked potentials: report of an IFCN committee International Federation of Clinical Neurophysiology. *Electroencephalography & Clinical Neurophysiology*, 91, 6-11.
- Nuwer, M.R., Dawson, E.G., Carlson, L.G., Kanim, L. & Sherman, J.E. (1995).

 Somatosensory evoked potential spinal cord monitoring reduces neurologic deficits after scoliosis surgery: results of a large multicenter survey.

 Electroencephalography and Clinical Neurophysiology, 96, 6–11.
- Ono, F., & Kawahara, J.I. (2007). The subjective size of visual stimuli affects the

- perceived duration of their presentation. *Perception and Psychophysics*, 69, 952-957.
- Pallasmaa, J. (1996). The eyes of the skin: Architecture and the senses. Landam, MD: Academy Editions.
- Pan, Y., & Luo, Q.Y. (2012). Working memory modulates the perception of time.

 *Psychonomics Bulletin and Review, 19, 46-51.
- Pascual-Leone A, Torres F. 1993. Plasticity of the sensorimotor cortex representation of the reading finger in Braille readers. *Brain*, *116*, 39-52.
- Pellicciari, M.C., Miniussi, C., Rossini, P.M., & De Gennaro, L. (2009). Increased cortical plasticity in the elderly: changes in the somatosensory cortex after paired associative stimulation. *Neuroscience*, *163*, 266-276.
- Persaud, B.N., Retting, R.A., & Lyon, C.A. (2004). Crash reduction following installation of centerline rumble strips on rural two-lane roads. *Accident Analysis & Prevention*, *36*, 1073-1079.
- Peterson, F. (1933). Local electric anesthesia. Science, 77, 326.
- Pierantozzi, M., Mazzone, P., Bassi, A., Rossini, P.M., Peppe, A., Altibrandi, M.G., Stefani, A., Bernardi, G., & Stanzione, P. (1999). The effect of deep brain stimulation on the frontal N30 component of somatosensory evoked potentials in advanced Parkinson's disease patients. *Clinical Neurophysiology*, 110, 1700-1707.
- Pierantozzi, M., Sabato, A.F., Leonardis, F., Marciani, M.G., Cicardi, C., Giacomini, P., Bernardi, G., & Stanzione, P. (2000). Curariform peripheral block of muscular

- tone selectively increases precentral N30 somatosensory evoked potentials component. A pharmacological study carried out on healthy subjects and parkinsonian syndromes. *Experimental Brain Research*, *133*, 368-376.
- Pleger, B., Dinse, H.R., Ragert, P., Schwenkreis, P. Malin, J.P., & Tegenthoff, M. (2001).

 Shifts in cortical representations predict human discrimination improvement.

 Proceedings of the National Academy of Science, 98, 12255-12260.
- Rabinowitz, W.M., Houtsma, A.J., Durlach, N.I., & Delhorne, L.A. (1987).

 Multidimensional tactile displays: identification of vibratory intensity, frequency, and contactor area. *The Journal of the Acoustical Society of America*, 82, 1243-1252.
- Restuccia, D., Valeriani, M., Barba, C., Le Pera, D., Capecci, M., Filippini, V., & Molinari, M. (2001). Functional changes of the primary cerebral cortex in humans. *Brain*, *124*, 757-768.
- Rinker, M.A., & Craig, J.C. (1994). The effect of spatial orientation on the perception of moving tactile stimuli. *Perception & Psychophysics*, 56, 356-362.
- Rossi, A., Decchi, B., Groccia, V., Della Volpe, R., & Spidalieri, R. (1998) Interactions between nociceptive and non-nociceptive afferent projections to somatosensory cortex in patients with unilateral cerebellar lesions. *Neuroscience Letters*, 248, 155-158.
- Rossi, S., della Volpe, R., Ginanneschi, F., Ulivelli, M., Bartalini, S., Spidalieri, R., Rossi, A. (2003). Early somatosensory processing during tonic muscle pain in

- humans: relation to loss of proprioception and motor 'defensive' strategies. *Clinical Neurophysiology, 114,* 1351-1358.
- Rossini, P.M., Babiloni, F., Bernardi, G., Cecchi, L., Johnson, P.B., Malentacca, A., Stanzione, P., Urbano, A. (1989). Abnormalities of short-latency somatosensory evoked potentials in parkinsonian patients. *Electroencephalography & Clinical Neurophysiology*, 74, 277-289.
- Rossini, P.M., Gigli, G.L., Marciani, M.G., Zarola, F., Caramia, M. (1987). Non-invasive evaluation of input-output characteristics of sensorimotor cerebral areas in healthy humans. *Electroencephalography & Clinical Neurophysiology*, 68, 88-100.
- Rosso, T., Aglioti, S.M., Zanette, G., Ischia, S., Finco, G., Farina, S., Fiaschi, A. & Tinazzi, M. (2003). Functional plasticity in the human primary somatosensory cortex following acute lesion of the anterior lateral spinal cord: neurophysiological evidence of short-term cross-modality plasticity. *Pain, 101,* 117-127.
- Rothenberg, M., Verrillo, R.T., Zahorian, S.A., Brachman, M.L., & Bolanowski, S.J.

 (1977) Vibrotactile frequency for encoding a speech parameter. *The Journal of the Acoustical Society of America*, 62, 1003-1012.
- Sarno, S., Erasmu, L.P., Lipp, B., & Schlaegel, W. (2003). Multisensory integration after traumatic brain injury: a reaction time study between pairings of vision, touch and audition. *Brain Injury*, 17, 413-426.
- Schell, G.R., Strick, P.L. (1984). The origin of thalamic inputs to the arcuate premotor

- and supplementary motor areas. The Journal of Neuroscience, 4, 539-560.
- Serino, A., & Haggard, P. (2010). Touch and the body. *Neuroscience and Biobehavioral Reviews*, 34, 224-236.
- Sherrick, C.E. (1975). The art of tactile communication. *American Psychologist*, *30*, 353-360.
- Sherrick, C.E. (1985). Touch as a communicative sense: introduction. *Journal of the Acoustical Society of America*, 77, 218-219.
- Sidman, M., Keller, F.S., Kennedy, E.J., & Wilson, M.P. (1955). Teaching Morse-code reception with signals weighted in frequency according to their difficulty. *Journal of Applied Psychology*, 39, 1-4.
- Small, D.G., Beauchamp, M., Matthews, W.B. (1977). Spinal evoked potentials in multiple sclerosis. *Electroencephalography & Clinical Neurophysiology*, 42, 141.
- Sonoo, M., Sakuta, M., Shimpo, T., Genba, K., & Mannen, T. (1991). Widespread N18 in median nerve SEP is preserved in a pontine lesion. *Electroencephalography & Clinical Neurophysiology*, 80, 238–240.
- Sonoo, M., Genba, K., Zai, W., Iwata, M., Mannen, T., & Kanazawa, I. (1992). Origin of the widespread N18 in median nerve SEP. *Electroencephalography & Clinical Neurophysiology*, 84, 418–425.
- Soto-Faraco, S., Spence, C., Fairbank, K., Kingstone, A., Hillstrom, A.P., & Shapiro, K. (2002). A crossmodal attentional blink between vision and touch. *Psychonomic Bulletin and Review*, *9*, 731-738.

- Spelt, D.K. (1948). The conditioning of the human fetus in utero. *Journal of Experimental Psychology*, *38*, 338-346.
- Spence, C., & McGlone, F.P. (2001). Reflexive spatial orienting of tactile attention. *Experimental Brain Research*, 141, 324-330.
- Spence, C., & Gallace, A. (2007). Recent developments in the study of tactile attention.

 Canadian Journal of Experimental Psychology, 61, 196-207.
- Spence, C., Nicholls, M.E., & Driver, J. (2001). The cost of expecting events in the wrong sensory modality. *Perception & Psychophysics*, *63*, 330-336.
- Spence, C., Shore, D.I., & Klein, R.M. (2001). Multisensory prior entry. *Journal of Experimental Psychology: General*, 130, 799-832.
- Sternberg, S. (1969). The discovery of processing stages: extensions of Donders' method.

 Acta Psychologica, 30, 276-315.
- Strick, P.L., & Preston, J.B. (1982). Two representations of the hand in area 4 of a primate II: somatosensory input organization. *Journal of Neurophysiology*, 48, 150-159.
- Synek, V. (1983). Somatosensory evoked potentials from musculocutaneous nerve in the diagnosis of brachial plexus injuries. *Journal of Neurological Science*, 61, 443-452.
- Synek, V.M., & Cowan, J.C. (1982). Somatosensory evoked potentials in patients with supraclavicular brachial plexus injuries. *Neurology*, *32*, 1347-1352.
- Synek, V.M. (1985). Assessing sensory involvement in lower limb nerve lesions using

- somatosensory evoked potential techniques. Muscle Nerve, 8, 511-515.
- Tan, H.Z., Durlach, N.I., Rabinowitz, W.M., Reed, C.M., & Santos, J.R. (1997).Reception of Morse code through motional, vibrotactile, and auditory stimulation.Perception & Psychophysics, 59, 1004-1017.
- Tang, K., Staines, W.R., Black, S.E., & McIlroy, W.E. (2009). Novel vibrotactile discrimination task for investigating the neural correlates of short-term learning with fMRI. *Journal of Neuroscience Methods*, 178, 65-74.
- Tanji, J., & Wise, S.P. (1981). Submodality distribution in sensorimotor cortex of the unanesthetized monkey. *Journal of Neurophysiology*, 45, 467-481.
- Thompson, I.M. (1933). The effects of alternating currents upon cutaneous sensory thresholds. *Science*, 78, 268-269.
- Thompson, I.M., & Inman, V.T. (1933). A method of outlining cutaneous nerve areas. *Science*, 77, 216-217.
- Thompson, P.B., & Lambert, J.V. (1995). Touch sensitivity through latex examination gloves. *Journal of General Psychology*, 122, 47-58.
- Tinazzi, M., Fiaschi, A., Rosso, T., Faccioli, F., Grosslercher, J., & Aglioti, S.M. (2000).

 Neuroplastic changes related to pain occur at multiple levels of the human somatosensory system: a somatosensory-evoked potentials study in patients with cervical radicular pain. *Journal of Neuroscience*, 20, 9277-9283.
- Tinazzi, M., Rosso, T., Zanette, G., Fiaschi, A., & Aglioti, S.M. (2003). Rapid modulation of cortical proprioceptive activity induced by transient cutaneous

- deafferentation: neurophysiological evidence of short-term plasticity across different somatosensory modalities in humans. *European Journal of Neuroscience*, 18, 3053-3060.
- Tinazzi, M., Zanette, G., Polo, A., Volpato, D., Manganotti, P., Bonato, C., Testoni, R., & Fiaschi, A. (1997). Transient deafferentation in humans induces rapid modulation of primary sensory cortex not associated with subcortical changes: a somatosensory evoked potential study. *Neuroscience Letters*, 223, 21-24.
- Trojaborg, W., & Petersen, E. (1979). Visual and somatosensory evoked cortical potentials in multiple sclerosis. *Journal of Neurology Neurosurgery and Psychiatry*, 42, 323-330.
- Turker, K.S., Miles, T.S., & Le, H.T. (1988). The lip-clip: a simple, low-impedance ground electrode for use in human electrophysiology. *Brain Research Bulletin*, *21*, 139-141.
- Turrato, M., Galfano, G., Bridgeman, B., & Umilta, C. (2004). Space-independent modality-driven attentional capture. *Experimental Brain Research*, 155, 301-310.
- Urasaki, E., Wada, S., Kadoya, C., Tokimura, T., Yokota, A., Yamamoto, S., Fukumura, A., & Hamada, S. (1992). Amplitude abnormalities in the scalp far-field N18 of SSEPs to median nerve stimulation in patients with midbrain-pontine lesions.

 Electroencephalography and Clinical Neurophysiology, 84, 232-242.
- Vail, A. (1845). Electro Magnetic Telegraph: with the reports of congressk and a description of all telegraphs known employing electricity or galvanism.

- Washington, DC: J. and G.S. Gideon Printing.
- Verrillo, R.T. (1985). Psychophysics of vibrotactile stimulation. *Journal of the Acoustical Society of America*, 77, 225-232.
- Vernon, J. (1953). Cutaneous interaction resulting from simultaneous electrical and mechanical vibratory stimulation. *Journal of Experimental Psychology*, 45, 283-287.
- Verrillo, R.T., & Gescheider, G.A. (1976). Effect of double ipsilateral stimulation on vibrotactile sensation magnitude. *Sensory Processes*, *1*, 127-137.
- Verrillo, R.T. (1963). Effect of contactor area on the vibrotactile threshold. *The Journal of the Acoustical Society of America*, 35, 1962-1966.
- Verrillo, R.T. (1965). Temporal summation in vibrotactile sensitivity. *The Journal of the Acoustical Society of America*, *37*, 843-846.
- Verrillo, R.T. (1983). Vibrotactile subjective magnitude as a function of hand preference. *Neuropsychologica*, 21, 383-395.
- Verrillo, R.T., Bolanowski, S.J., Baran, F., & Smith, P.F. (1996). Effects of underwater environmental conditions on vibrotactile thresholds. *Journal of the Acoustical Society of America*, 100, 651-658.
- Verrillo, R.T., & Gescheider, G.A. (1977). Effect of prior stimulation on vibrotactile thresholds. *Sensory Processes*, 1, 292-300.
- Waberski, T.D., Buchner, H., Perkuhn, M., Gobbele, R., Wagner, M., Kucker, W., & Silny, J. (1999). N30 and the effect of explorative finger movements: a model of

- the contribution of the motor cortex to early somatosensory potentials. *Clinical Neurophysiology*, 110, 1589-1600.
- Waberski, T.D., Gobbele, R., Kawohl, W., Cordes, C. & Buchner, H. (2003). Immediate cortical reorganization after local anesthetic block of the thumb: source localization of somatosensory evoked potentials in human subjects. *Neuroscience Letters*, 347, 151-154.
- Walsh, P., Kane, N., & Butler, S. (2005). The clinical role of evoked potentials. *Journal of Neurology Neurosurgery and Psychiatry*, 76(Supplementary II), ii16-ii22.
- Wang, J.T., Young, G.B., & Connolly, J.F. (2004). Prognostic value of evoked responses and event-related brain potentials in coma. *Canadian Journal of Neurological Sciences*, 31, 438-450.
- Weinstein, S. (1968). Intensive and extensive aspects of tactile sensitivity as a function of body part, sex and laterality. In D.R. Kenshalo (Ed.), The skin senses (193-218). Springfield, IL: C.C. Thomas.
- Wiesendanger, R., & Wiesendanger, M. (1985). The thalamic connections with medial area 6 (supplementary motor cortex) in the monkey (macaca fascicularis). *Experimental Brain Research*, 59, 91-104.
- Yamada, T., Yeh, M., Kimura, J. (2004). Fundamental principles of somatosensory evoked potentials. *Physical Medicine and Rehabilitation Clinics of North America*, 15, 19-42.
- Zehr, E.P., & Chua, R. (2000). Modulation of human cutaneous reflexes during rhythmic

- cyclical arm movement. Experimental Brain Research, 135, 241-250.
- Zhang, Z., Francisco, E.M., Holden, J.K., Dennis, R.G., & Tommerdahl, M. (2009). The impact of non-noxious heat on tactile information processing. *Brain Research*, 1302, 97-105.
- Zwislocki, J. (1960). Theory of temporal auditory summation. *Journal of the Acoustical Society of America*, 32, 1046-1060.

TABLES

Table 1

Mechanoreceptors*/Tactile Reception Channels**

Receptor Type	Receptor Characteristics	Anatomic Structure	Receptor Channel
I	Slow adapting, small	Merkel disks	Non Pacinian
	receptive field (SAI)		channel III (NP III)
II	Slow adapting, large	Ruffini endings	Non Pacinian
	receptive field (SAII)		channel II (NP II)
III	Fast adapting, small	Meissner corpuscles	Non Pacinian
	receptive field (FAI)		channel I (NP I)
IV	Fast adapting, large	Pacinian corpuscles	Pacinian channel
	receptive field (FAII)		(PC)

Note. *Mechanoreceptors (Brammer et al., 2007)

^{**}Tactile Reception Channels (Bolanowski et al., 1988)

Figure Captions

Figure 1. Item "1" is the Morse code representation of the letter "P", while item "2" is the Braille representation of the letter "P".

Figure 2. Adapted from Neal and Fields (2010). Peripheral nerve innervation regions on the anterior and posterior skin surface of the hand.

Figure 3. White dots represent active pins, and black dots represent inactive pins.

Sequence "1" presents: a forward "energy" mask (1A), a period of tactile silence (1B), the letter "T" (1C), a period of tactile silence (1D), a backward "energy" mask (1E).

Sequence "2" presents a forward "pattern" mask (2A), a period of tactile silence (2B), the

letter "T" (2C), a period of tactile silence (2D), a backward "pattern" mask (2E). The

amount of time that cells 1B, and 2B are presented for determine the duration of stimulus

onset asynchrony (SOA) for forward masking. The SOA for backward masking is the

duration of time that cells 1D and 2D are presented.

Figure 4. Adapted from Gescheider, Verrillo and Pelli (1991). The right half of the illustration demonstrates a 730ms "pedestal" where a 300Hz vibrotactile stimulus was presented, this results in a high pedestal. The left half of the illustration has an additional 300ms 300Hz signal embedded within the 730ms 300Hz "pedestal" stimulus, this lowers the pedestal. Participants were challenged to identify when a signal was embedded within

the "pedestal" stimuli. When the pedestal and signal were presented together the detection threshold (pedestal to overcome) was lowered (negative masking).

Figure 1.

Figure 2.

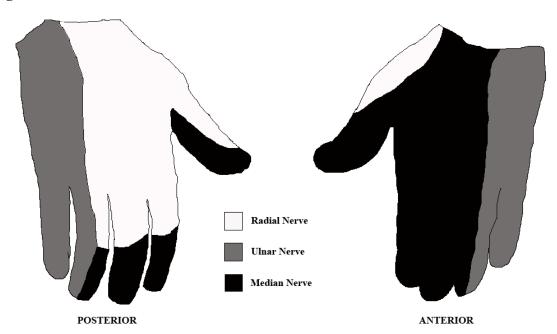


Figure 3.

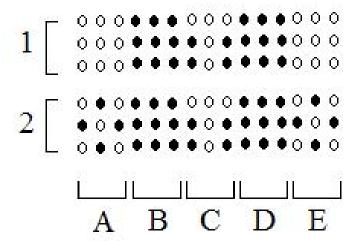
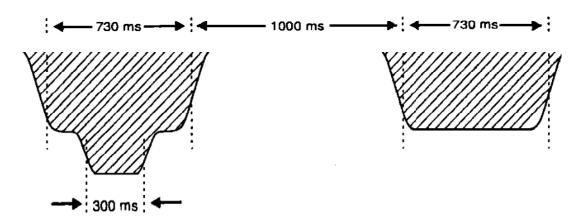


Figure 4.



DOCUMENT ONE

I was the primary investigator and major contributor for each aspect of this research project, including experimental design, testing, analyses and manuscript preparation. This paper will be submitted to the journal Attention, Perception & Psychophysics.

Running Head: NERVE PERTURBATION AND VIBROTACTILE LEARNING

The impact and specificity of nerve perturbation on novel vibrotactile

sensory letter learning.

Steven R. Passmore^{1,2,3}, Jessica Bosse⁴, Bernadette Murphy⁴, Timothy D. Lee¹

¹McMaster University

² University of Manitoba

³New York Chiropractic College

⁴ University of Ontario, Institute of Technology

Corresponding Author Address: Steven Passmore, School of Medical Rehabilitation,

University of Manitoba, R106-771 McDermot Avenue, Winnipeg, Manitoba, Canada,

R3E 0T6

e-mail: passmore@cc.umanitoba.ca

telephone: (204) 787-1899

105

Abstract

Three purposes were the driving factors of this study: to determine if induced radiating paresthesia interferes with the (a) acquisition and/or (b) the application of complex tactile information, and (c) to identify whether any potential interference reflects a tactile masking or response competition (selective attention) effect. In experiment 1 the impact of induced radiating ulnar nerve paresthesia (a concurrent non target stimulus) was quantified on both vibrotactile Morse Code letter acquisition and knowledge recollection tasks. In experiment 2 the letter acquisition and knowledge recollection tasks remained constant while the radiating paresthesia was shifted to the median nerve in an attempt to alter the concurrent non target stimulus to a location spatially removed from the target vibrotactile letter stimuli. The impact of induced paresthesia differentially impacted letter acquisition and recollection, but only when presented to the same anatomical spatial location. These findings are discussed as they relate to masking, and enhancement (summation/negative masking).

The impact and specificity of nerve perturbation on novel vibrotactile sensory letter learning

Tactile communication is particularly useful when other sensory systems are overloaded, or unavailable (Gallace, Tan, & Spence, 2007; Maclean, 2008). Tactile language acquisition has been the focus of the majority of studies on learning complex tactile stimuli. Few studies have considered immediate, or delayed, retention and transfer of tactile knowledge or perturbations that may cause interference with tactile learning performance. This paucity of information regarding complex tactile learning is troubling since several common pathologies create symptoms that perturb the tactile system such as diabetes, and spinal injuries (Marks & Zukerberg, 2004). If tactile interfaces are designed for widespread societal use, it would seem important to investigate how interfering factors may impact not simply the reception of complex tactile information, but also the effects of interference on recollection and application of tactile-driven information. Interference during tactile reception is either attributed to masking, or response competition (selective attention) (Craig, 1995).

Information masking is a perturbation to the identification of a target stimulus at an early stage of processing (Craig, 1995). Masking occurs when the ability to detect a stimulus, or interpret a stimuli pattern is reduced, or interfered with by presentation of other information (Craig, 1985; Verrillo, 1985). A physiological explanation of the paradigm is that masking occurs when the receptor thresholds for detecting tactile stimuli at a particular frequency are exceeded by both the target stimuli and additional competing

stimuli (Gescheider et al., 1982). However, there is a broader, perhaps more generalizable explanation for the concept of masking. A masking stimulus is thought to interfere with information acquisition in three possible ways. The first is a distortion of temporal integration of the target by the non-target stimulus (Evans, 1987; Evans & Craig, 1986). The second is a distortion of target features by the non-target stimulus (Craig, 1986). The third is a deletion of target features by the presence of a non-target stimulus (Evans & Craig, 1986). A target stimulus may have characteristics in common with the masking stimulus. For example, both target and mask stimuli may be vibrotactile, presented at the same frequency, delivered to the same location(s). In contrast the target stimulus may not share characteristics with the masking stimulus. For example, the mask may be presented to an anatomically remote region from the target, or be presented at a different frequency, or stimulate the tactile modality in an alternate way.

Non-target letters, non-objective patterns, dynamic arrays, and energy maskers are all examples of previously-used masking stimuli delivered on tactile visual substitution systems (TVSS) that used different combinations of active and passive pins to the skin surface within a fixed space (Cholewiak & Collins, 1997; Craig, 1982). A limitation of a TVSS is that target, and non-target stimuli cannot be presented concurrently to the same anatomical space. Additionally, even though no response may be assigned to them, it is possible that some maskers may contain features that compete with response selection rather than being completely neutral. To maximize the extent of masking and to minimize the response competition that occurs, the non-target (masking stimulus) should be neutral

and require no response generation (Craig, 2000). Failure to use a neutral masker may have lead to an underrepresentation of masking effects in previous studies (Craig, 2000). For example, a pattern mask (a pattern of TVSS pins fired) degrades performance accuracy compared to an energy mask (all TVSS pins fired) which is predicted to occur because the pattern of pins may closely resemble a target stimulus, which is a response competition effect (Craig, 1982). An energy mask is less likely to elicit a response competition effect since its characteristics bear no resemblance to the target stimulus (Craig & Evans, 1995).

Concurrent presentation of the target stimulus and the non-target stimulus at the same site is important. Spatial separation of non-target and target stimuli is criticized due to the changes in density of innervation across the anatomical region being stimulated. Studies of changes in the spatial location of tactile stimuli have not always accounted for the peripheral anatomical innervation region (AIR) changes associated with different stimulation sites (Craig, 1984; Gilson, 1969). Heller (1986) identified innervation density as an explanation of his results when presenting two alphabetic letters to the same area in succession compared to two anatomically separated sites. Horner (2000) noted innervation density differences in his explanation of why stimuli presented to the distal index finger pad were detected more accurately than at the medial index finger pad. Innervation density was cited as a limitation for a simple tactile discrimination task comparing vibrotactile, and air puff detection (Kekkoni, et al., 1987). Kekkoni et al., (1990) further demonstrated the importance of innervation density when they utilized the

two aforementioned stimuli separately in space but concurrently in time at the fingertip and the base of the fingers. Regardless of the type of stimulation (vibration or airpuff), when the target stimuli was presented to the base of the finger, it was masked by stimulation of the non-target stimuli at the finger tip. Kekkoni et al., (1990) proposed that masking at the fingertip is due to a larger cortical representation of the more heavily innervated fingertip.

Differential spatial placement of mask and target stimuli may be used to determine whether the mask is impacting perception at the nerve pathway, or if the mask is simply an attentional distraction, reflecting response competition (Bolanowski et al., 2000). Kekoni et al., (1990) found that a strong masking effect was present when a vibrotactile masker with a constant intensity was placed at the fingertip, and the to-be-detected air puff was delivered to the base of the finger. The masking effect was strongest when both occurred on the same finger and weakest when the masking stimulus was presented to a finger that was different than the one receiving the air-puff stimuli. Craig (1983) demonstrated the same type of spatial effect for both forward (mask before target), and backward (mask after target) masking of vibrotactile patterns at the fingertip. Craig determined that perturbation of a finger other than the finger required for a tactile discrimination task does not sufficiently distract attention away from the cognitive demands of the task. However, Craig (1983) did not consider the spatial effect during concurrent masking, and both Craig (1983) and Kekoni et al. (1990) only considered the role of masking in the detection of simple stimuli. New insight is needed on how to

present more complex tactile stimuli without exceeding the tactile attentional limitations to process it (Spence & Gallace, 2007).

Selective attention is not simply the ability to process the correct information being presented, but also the ability to selectively ignore, or inhibit the processing of irrelevant stimuli (Frings et al., 2008). The balance between ignoring one stimuli and attending to the other is an example of response competition. Ignoring the irrelevant stimuli is an active process demonstrated in studies that utilized a stimulus as a target on some trials, but presented that same stimulus with a "do not respond" instruction on other trials (Frings et al., 2008). Changes in the role of a stimulus can significantly increase response time. In order to correctly ignore a stimulus it must be processed at a neurological level where a decision to ignore it is made.

Location priming is the presentation of a non-target stimuli either before or concurrent with a target stimuli in order to draw attention to an anatomical location.

Location priming is largely ignored as an explanation for the response competition effect, as priming would predict that greater interference would occur when the non-target precedes the target. In experimental findings, more interference is noted when the non-target stimulus follows the target stimulus, a phenomenon described as backward masking (Craig & Evans, 1995). When there is a stimulus onset asynchrony of zero seconds between the target and non-target stimuli, both are presented simultaneously, which is defined as common onset masking. Enriquez and Maclean (2008) found that common onset masking produced a greater masking effect than backward masking [in which the

non-target (masking) stimulus was delivered thirty milliseconds post-target stimulation delivery]. Since a masking stimulus concurrent with a target stimulus yields a stronger masking effect than a backward masking paradigm (Enriquez & Maclean, 2008), stimulus onset asynchrony is not as important a measure to evaluate masking as previously thought unless the specific research question pertains to the time difference between a target and non-target stimuli. A continuous masker, while awaiting the presentation of target stimuli, eliminates the need for manipulation of stimulus onset asynchrony and is predicted to generate a masking effect (Kekkoni et al., 1987; Kekkoni et al., 1990).

To test masking, target and non-target stimuli are presented to the same site (Bliss et al., 1966; Craig, 1982, 1983, 1985; Craig & Evans, 1987,1995; Evans & Craig 1986; Schindler & Knapp, 1976). To test response competition (selective attention), the target and non-target stimuli are presented to different sites (Craig & Evans, 1995; Evans & Craig, 1991; Evans, Craig, & Rinker, 1992; Rinker & Craig, 1994). Craig (1995) proposed that future masking or response competition studies could incorporate more complex tactile tasks, could measure changes in the time to respond to stimuli, and that as stimulation techniques grow more sophisticated patterns can be presented to the same spatial area of skin.

In the design of the present study, we have attempted to address the suggestions made by Craig (1995) in order to further explore whether tactile interference during a complex tactile learning task occurs due to masking, or response competition. The present studies used a non-target stimulus that created a perturbation along the entire

course of a stimulated nerve orthodromically from the site of stimulation. The disruption creates impairment but not complete obliteration of sensation (Zehr & Chua, 2000), and is experienced as a "pins and needles" sensation similar to the common pathological phenomena known as radiating paresthesia (Marks & Zukerberg, 2004). Three goals can be accomplished by creating radiating paresthesia along the course of a specific upper extremity nerve pathway: 1) a non-target perturbation stimulus, that can be quantitatively assessed and controlled, can be presented to the AIR where the target stimuli is presented, which eliminates stimulus onset asynchrony, 2) the non-target stimuli can be moved to a separate AIR to explore response selection (attention) interference, and 3) a masking effect can be maximized as the neutral non-target stimulus has different physical properties then the vibrotactile target stimulus, even though both impact the tactile system.. The paresthesia serves a neutral, non-target stimulus as it has no properties aside from location in common with the target stimuli. As a neutral stimulus paresthesia should reduce additional response competition, and facilitate the investigation of a masking paradigm.

The design used in the experiments presented identifies if the presence of a masking stimulus serves to exceed the capacity of peripheral sensory receptors, or if the masking stimulus is merely an attentional distraction (response competition). The general focus of the two experiments was to extend knowledge of interference effects related to the simple detection findings of Craig (1983) and Kekoni et al., (1990) to a more complex tactile learning task. Specifically the purpose of these experiments is: to determine if

induced radiating paresthesia interferes with the (a) acquisition and/or (b) the application of complex tactile information, and (c) to identify whether any potential interference reflects a tactile masking or response competition (selective attention) paradigm. In both experiments the implications of interference are explored in how they impact the acquisition, and recollection of complex meaningful tactile information.

Experiment 1

The general purpose of Experiment 1, as suggested by Craig (1995), is to move beyond testing simple stimuli detection ability and to consider how well a complex tactile target stimulus is detected, retained, and subsequently integrated to allow for information transfer under conditions of interference at the same anatomically sensory innervated region. We used a non-target neutral stimulus presented concurrently with a target stimulus to maximize the presence of a masking effect, should one exist (Enriquez & Maclean, 2008). Specifically the purpose of this experiment was to determine if induced radiating paresthesia interfered with the (a) acquisition and/or (b) the application of complex tactile information. The goal of Experiment 2 was to address interference effects.

Method

Participants.

Twenty-four volunteer participants (15 women, age range 19-31 years, M = 22.0 years, SD = 3.1 years) took part in this study. All were naïve regarding the purpose of the experiment, 22 were right-handed by self-report. All had normal or corrected to normal

vision, and none reported any history gross neurological sensory deficits. Participants were asked to rate their knowledge of Morse code on a 5-point Likert scale (Likert, 1932). Where 5 represented no knowledge, and 1 represented Morse code fluency. None of the participants reported any level of competency in Morse code, which lead to inclusion of all screened participants. Approval by the University of Ontario Institute of Technology (UOIT) and McMaster University ethics boards was granted and informed consent was obtained from all participants.

Apparatus and materials.

Participants were seated in a comfortable chair approximately 150 cm away from a computer monitor. They were sensory tested for two-point discrimination (Touch-Test® Two-Point Discriminator by Northcoast Medical, Gilroy, CA), and monofilament pressure sensitivity (Touch-Test® Sensory Evaluators by Northcoast Medical, Gilroy, CA), over the palmar surface of the distal aspect of their fifth digit of their right hand. Participants were blindfolded during sensory testing.

Half of the participants were pseudorandomly assigned to receive stimulation from a DS7A Constant Current Stimulator (Digitimer Ltd., Welwyn Garden City, Hertfordshire) for the duration of the acquisition phase of the experiment, and in some instances during retention and transfer phases. Stimulation was delivered transcutaneously through 7 mm Ag/AgCl disposable, adhesive electrodes (Hydrospot from Physiometrix, Inc., Billerica, MA). Two electrodes were placed on the surface of dorsal medial aspect of the arm 2 cm proximal to the ulnar notch, over the predicted

course of the ulnar nerve. Custom LabVIEW (National Instruments, Austin, TX) software triggered a current stimulator generating a stimuli duration of 0.2 ms, with an interstimulus interval of 10 ms, and a voltage edge of 0.2 V. The measurement of discrimination thresholds (sensory, radiating, premotor), served as the indicator levels to establish settings for the constant current stimulator. The lowest stimulation level the participant detects is the sensory threshold. Radiating threshold is the lowest stimulation level to elicit an orthodromic response from the point of stimulation along the course of the entire nerve stimulated (Zehr & Chua, 2000). Premotor threshold is the most intense signal that can be delivered before motor contraction. These participants had their sensory testing repeated while being stimulated at their premotor threshold, which was the intensity used for the duration of the experiment.

Upon initiation of the experiment all participants placed their right hand in a prone position with their elbow bent to 90° while supported by an armrest, and while the distal aspect of their left index finger rested atop the "V" key (used as the home position) on an QWERTY keyboard on their lap. The distal aspect of their right hand's 5th digit, rested atop a 12mm diameter x 3.4mm thick, 200Hz vibrating disc motor (Solarbotics Ltd, Calgary, AB). Custom E-Prime (Psychology Software Tools, Inc., Pittsburgh, PA) software was utilized to guide participants through the experiment, record dependent variables, and to trigger the vibrotactile motor to create patterns representing Morse code letters. Morse code letter presentation was delivered through patterns of vibrations (long and short pulses with spaces in between) using only letters with no more than 4

components, and no less than 3 components (e.g., Z = "--."; R = ".-."). Pulses of 750 ms duration represented "dash" (-) signals, and 250 ms duration represented "dot" (.) signals. Spaces between letters were set to 125 ms (Tang, Staines, Black, & McIlroy, 2009). The experimental apparatus remained consistent for the acquisition, retention, and transfer components of the experiment.

Design.

The study was a between-participants design, comparing two separate groups during six acquisition trials, and then four distinct groups during immediate and delayed retention and transfer trials. Combinations of the presence or absence of paresthesia stimulation distinguished groups across the different phases of the experiment (acquisition, retention/transfer). At baseline sensory data was collected for all participants to ensure they had intact pressure sensation and 2 point discrimination. After collection of sensory data, participants were pseudo randomly assigned to either receive paresthesia, or not, during the acquisition phase of the experiment. Participants were then again pseudo randomly assigned to receive paresthesia, or not, for the retention/transfer phases of the experiment. The four final groups for comparison (n=6) were: 1) acquisition with stimulation, retention/transfer with stimulation; 2) acquisition with stimulation, retention/transfer with no stimulation, retention/transfer with no stimulation.

Procedure.

Participants were sensory tested (Pascual-Leone & Torres, 1993) then they were

then pseudorandomly assigned to groups that either received stimulation, or no stimulation. The experiment was divided into five phases, over two days. Day one consisted of acquisition, immediate retention, and immediate transfer phases, while day two consisted of only delayed retention, and delayed transfer phases.

During the acquisition component participants were exposed to 8 different Morse code letters in a random presentation until each letter was presented 6 times (48 total letter presentations). Immediately following a pattern of stimuli, participants were asked to indicate on an alphanumeric keyboard with their left index finger which letter had been presented. They had to choose the letter from a list of 8 possible options presented on the computer screen. Augmented feedback was provided regarding the accuracy of their response, and the actual letter presented visually appeared in its roman alphabetic form on the screen. Augmented information was provided retroactively because it facilitates learning compared to providing the correct information before a response is made (Patterson & Lee, 2005). Once the participant felt comfortable reviewing the letter and their performance, they depressed the space bar, and returned their left index finger to the home "V" key to move on to the next stimulus presentation. Total response time (TRT) was defined as the duration from which the screen requesting a letter selection appeared (immediately following vibrotactile presentation) until the response key was selected and depressed. The correctness of the response was defined as the selection accuracy.

Participants were tested to determine their retention of the vibrotactile information following a ten-minute rest period (the immediate retention phase). Participants were

presented, via vibrotactile stimulation, with 4 letters learned during acquisition, one letter at a time. They were given the choice of one of the 8 letters from the initial letters learned to identify which letter was presented. However no feedback was provided in the retention test. The participant self-selected their readiness to move on to the next letter presentation. Their TRT and selection accuracy scores were recorded.

Immediately after retention testing, participants were given the opportunity to apply the Morse Code knowledge they gained during acquisition in a different fashion. This was defined as the immediate transfer phase. Participants were visually presented with a single letter on the screen. The letters presented in random sequence were the remaining 4 of the 8 letters acquired that were not tested during retention. They were then asked to produce the pattern of Morse Code that represented each letter as accurately as possible (dots, dashes, and spaces between). This was initiated when the left index finger moved from the home "V" key to the number "1" key. The duration of time, the participant held down a key was considered a "dot" if it were less the 350 ms, and a "dash" if it were held down for longer than 350 ms. The time duration from when they released the "1" key, until the time they depressed it again was considered the space of time between the "dots" and "dashes". To signal the completion of their Morse code pattern replication of the letter displayed, the "0" key was selected. TRT, accuracy, and time durations of what they perceived to be time intervals of the "dots, dashes, and spaces in between" were recorded. All sets of retention and transfer letters were counterbalanced within each group so that the 4 letters of retention differed from the 4 transfer letters

presented without repetition (each of the 8 different letters were employed). Within each letter set presentation the order of letters was presented at random.

Delayed retention and transfer testing occurred on day 2, which was approximately 24 hours after the initial acquisition/retention/transfer session. The procedures utilized and dependent measures collected for delayed testing were identical to those used for immediate testing. All sets of retention and transfer letters presented were counterbalanced from the previous day. For example, the 4 letters tested in delayed retention were different from the 4 letters tested in immediate retention. This allowed one presentation of each of the 8 letters to be recorded for both retention and transfer respectively.

Analysis.

For acquisition, separate 2 (Group: Stimulation, No Stimulation) x 6 (Trial: Acquisition 1-6) mixed factorial ANOVA models with repeated measures on the last factor were employed to interpret both acquisition accuracy and TRT data.

For retention, separate 2 (Acquisition context: with or without stimulation) x 2 (Retention context: with or without stimulation) x 3 (Trial: Acquisition 6, Retention 1, Retention 2) mixed factorial ANOVA models with repeated measures on the last factor were employed to interpret both accuracy and TRT data.

For transfer separate 2 (Acquisition context: with or without stimulation) x 2 (Transfer context: with or without stimulation) x 3 (Trial: Retention 1, Retention 2) mixed factorial ANOVA models with repeated measures on the last factor were employed to

interpret both accuracy and TRT data.

Results

Sensory testing.

Paired Student's T-tests were used to compare the sensory data when stimulated for participants who received stimulation at some point in the experiment to their own sensory ability when stimulation was not present. Significant differences were found for both 2 point discrimination (all values in mm) between non stimulation (M = 2.8, SD = 0.5) and stimulation groups (M = 3.6, SD = 1.5), t(17) = -2.95; p = 0.009; and pressure monofilament testing (all values in millinewtons) between non stimulation (M = 2.9, SD = 0.3) and stimulation groups (M = 3.7, SD = 0.2), t(17) = -12.841; p < 0.001. The presence of stimulation reduced the participant's ability to discriminate between two points spatially, and their ability to detect pressure. The non-target stimulation had a negative impact on tactile perception ability.

Unpaired t-tests were used to compare the sensory data for participants from the stimulation group to the no stimulation group at baseline before any stimulation was applied. Analysis of the data collected for both 2 point discrimination, non stimulation (M = 3.0, SD = 0.7) and stimulation groups (M = 2.8, SD = 0.6), t (22) = 0.616; p = 0.544, and pressure monofilament testing, non stimulation (M = 3.0, SD = 0.3) and stimulation groups (M = 2.9, SD = 0.23), t (22) = 0.596; p = 0.557 revealed no significant difference. Participants in both groups had intact and normal tactile sensory ability for 2 point discrimination, and pressure detection.

Acquisition.

For accuracy significant main effects were found for trial, F(5,110) = 8.00; p < .001, $\eta^2 = .19$, and for group F(1, 22) = 8.41; p = .008, $\eta^2 = .38$ (Figure 1). Participants mean accuracy increased following the first trial. Participants exposed to stimulation performed less accurately (M = 25.7%) than participants who learned the Morse code letters in the absence of stimulation (M = 37.8%). There was a 12.5% chance of guessing the correct response on each trial. Participants selected one of 8 response alternatives for consideration based on which one of the 8 possible letters they believed was presented.

INSERT FIGURE 1 ABOUT HERE

Analysis of all TRT data yielded a significant main effect for trial, F(5,110) = 7.68; p < .001, $\eta^2 = .096$ (Table 1). No other significant differences we found. Following the first trial mean TRT decreased.

INSERT TABLE 1 ABOUT HERE

Retention.

For accuracy a main effect for trial was present, F(2,40) = 3.18; p < .05, $\eta^2 = .090$. Mean accuracy decreased when comparing acquisition trial 6 (M = 40.1%) to the delayed retention trial (M = 24.2%) (Figure 1). Additionally, a between group main effect was found for retention test stimulation context, F(1,20) = 5.58; p < .05, $\eta^2 = .279$. Participants were more accurate (M = 38.0%) in the presence of stimulation during retention testing when compared to no stimulations (M = 24.3%). Again, there was a 12.5% chance of guessing the correct response on each trial. Participants selected one of

8 response alternatives for consideration based on which one of the 8 possible letters they believed was presented.

Analysis of all TRT data yielded a significant main effect for the trial, F(2,40) = 8.84; p < .001, $\eta^2 = .125$ (Table 2). Mean TRT increased in the progression from acquisition trial 6 (M = 3101 ms) to both immediate (M = 4250 ms) and delayed (M = 4351 ms) retention trials. Additionally, a between group main effect was found for retention test stimulation context, F(1,20) = 6.10; p < .05, $\eta^2 = .305$. Participants were slower to respond when receiving stimulation (M = 4585 ms) on retention trials compared to when they received no stimulation (M = 3217 ms).

Transfer.

For accuracy a between group main effect for sensory group was present, F(1,20) = 8.46; p < .05, $\eta^2 = .423$ (Figure 2). Participants were more accurate in the presence of stimulation during transfer testing. A 3-way interaction was also noted F(1,20) = 5.81; p < .05, $\eta^2 = .087$ Post-hoc analysis of the 3-way interaction revealed three significant findings. The first finding occurred upon immediate transfer when paresthesia had been present for both acquisition and transfer performance. Under such conditions performance was significantly more accurate (M = 33.3%) then when no paresthesia was experienced (M = 8.3%). The second finding occurred when paresthesia was experienced for the first time during transfer. In that case immediate transfer was less accurate (M = 15.0%) than delayed transfer (M = 40.0%). The third finding was for the group that experienced paresthesia for the first time during retention and transfer. They

demonstrated significantly better delayed accuracy (M = 40.0%) than both of the groups that had no paresthesia during retention and transfer trials (M = 4.7%; M = 12.5%). These results indicate that in the presence of paresthesia stimulation during transfer to a novel task is superior to transfer when no stimulation is present.

INSERT FIGURE 2 ABOUT HERE

Analysis of TRT data yielded a significant main effect for the within group factor trial, F(1,20) = 7.95; p = .011, $\eta^2 = .108$ (Table 2). As transfer trial number increased, mean TRT decreased, meaning participants took significantly less time to respond at trial two (M = 3241 ms) compared to trial one (M = 3972 ms). Additionally, a between group main effect was found for transfer test stimulation context, F(1,20) = 5.77; p < .05, $\eta^2 = .288$. Participants were slower to respond when receiving stimulation (M = 4076 ms) on transfer trials compared to no stimulation (M = 3137 ms).

INSERT TABLE 2 ABOUT HERE

Discussion

A perturbation is created while concurrent task-irrelevant stimulation is presented to the area of innervation specific to meaningful vibrotactile stimulation. That perturbation negatively impacts the accuracy of the acquisition of vibrotactile information, yet it serves to enhance the accuracy of performance when transferring abstract conceptual information acquired in a novel task. The results attained could represent a masking/enhancement effect or indicate that a secondary stimulus draws increased attentional resources toward discerning the meaningful stimulus.

The sensory data collected at baseline confirms that participants in both groups were equivalent in terms of having intact sensory systems prior to stimulation. The presence of paresthesia stimulation was sufficient to perturb the tactile sensory system by having a negative impact on both pressure detection and two-point discrimination.

Acquisition performance demonstrated that tactile information was detected and processed by all participants. Evidence for successful acquisition is demonstrated through improved accuracy and decreased TRT recorded as trial number increased. The decreased accuracy demonstrated by the paresthesia stimulation group indicates that acquisition of tactile information in the presence of task irrelevant cutaneous stimulation is diminished or impeded.

Like other letter learning paradigms, information is subject to decay when tested following retention delays (Patterson & Lee, 2005; Richardson & Lee, 1999). Evidence for decay of learning was demonstrated in decreased accuracy for delayed retention testing and increased TRT upon both immediate and delayed retention testing.

Transfer to a novel task tests the abstract concept learning of the stimuli presented (Thorndike & Woodworth, 1901). Transfer was tested by having participants attempt to recreate the temporal components of Morse code patterns that examined the cognitive integration of information perceived and processed via vibrotactile stimulation. Of particular interest was the finding that when paresthesia stimulation was present under transfer conditions accuracy performance was significantly better than for the no stimulation group.

As predicted by previous studies, the accuracy of performance for both groups on the complex vibrotactile task was poor. The delivery of tactile information for abstract concepts has been found to be difficult. Craig (2000) found an accuracy rate of 30-60% for vibrotactile letter learning, while likewise Foulke and Broadbeck (1968) found a 40.4% error rate in teaching Morse code letter using electrocutaneous stimulation. Tactile task difficulty is one reason why tactile interfaces that require complex information processing are sparse.

The first experiment has limitations in its design. While the experiment allowed for measurement of the impact of perturbation on complex tactile information reception, and application performance it did not allow for the delineation of whether that effect was as a result of a masking or response competition effect. A typical masking effect would explain poor acquisition performance during stimulation, while negative masking or enhancement could explain the improvement seen in both retention and transfer performance. Negative masking occurs when mild background stimulation lowers the threshold for simple tactile detection, thus facilitating tactile performance (Gescheider, Verrillo, & Pelli, 1991). A contrasting view is that the results from experiment one could also be interpreted using a response competition paradigm, particularly during the retention and transfer testing. For example, in providing a concurrent non-target stimulus to the same region as the target stimulus, more attentional resources may have been directed to the area priming the receptive awareness of the region and positively impacting target task performance. Response competition (selective attention) effects

have been identified by Craig and Evans (1995) who found that when spatially separating tactile stimulation by applying the stimulation to an adjacent finger tip, participants are able to use spatial cues to aid their response accuracy. Craig and Evans (1995) found that target and non-target stimulus properties (direction of motion) were processed at a cognitive level and that independent responses could be made to either stimuli, as opposed to a masking paradigm where performance is degraded overall. In order to improve on the limitations of the study design in experiment one, a follow up study that replicates the presentation and usage of complex tactile information in the presence of a non target perturbation was performed, where the non target was presented to a region of different anatomical innervation than the target stimuli. By presenting the non target stimulation to an anatomical region with separate peripheral nerve innervation,, the cognitive attentional distraction of a secondary stimulus would be kept consistent, and it would not directly draw spatial attention to the region used to receive target stimulation.

Experiment 2

The purpose of study two is to build upon the results of experiment one, and attempt to understand if the results were dependent on masking, or if a response competition effect can be used to explain interference with complex tactile learning. Experiment one revealed that the presence of a secondary non-target stimulus negatively impacted acquisition performance, but served to improve the accuracy of the application of complex tactile learned information. The reason why non-target stimulation impacts performance accuracy is not clear based on the limitations of the study design of

experiment one. In order to test whether the outcome is explained by a masking – negative masking/enhancement paradigm or a response competition effect, an alteration of the experimental method was devised. The alteration was accomplished by presenting interference to a region with separate anatomical sensory innervation from the target stimuli.

Selection of a separate AIR for the site of non-target stimulation presentation accomplished two objectives. First, it allowed for the same temporal presentation of target and non target stimulation, which allows for the same temporal attentional constraints to be placed on the participant during target task performance. Second, it allowed for the separation of spatial attentional factors. For example, the target and non target stimuli are delivered to two different spatial regions, the context allows for a response competition effect to be teased apart from a masking – negative masking paradigm. If the results of experiment two are identical to those of experiment one, then the outcome can be attributed to response competition. If the results of experiment two demonstrated equal tactile accuracy performance between conditions where a non-target stimulus is present or absent, than a masking – negative masking effect is plausible for the interpretation of the results of experiment one.

Method

Participants.

Twenty-four new volunteer participants (9 women, age range 19-29 years, M = 22.8 years, SD = 3.1) took part in this study. All were naïve regarding the purpose of the

experiment. All had normal or corrected to normal vision, and none reported any history of gross neurological sensory deficits.

Apparatus, materials, design, procedure and analysis.

These sections were similar to those used in Experiment 1 with the exception of the change in location of the transcutaneous electrode placement used to create radiating paresthesia. These electrodes were moved to the anterior aspect of the forearm along the midline, over the predicted course of the median nerve, 5 cm proximal to the carpal line. The DS7A Constant Current Stimulator (Digitimer Limited, Hertfordshire, England) was set to deliver stimulation as in experiment one, with the exception that radiating paresthesia was now directed to the median nerve. Radiating paresthesia was reported by participants as perceived along the first through third digits, and the lateral aspect of the fourth digit on the right hand. The tactor was still placed under the palmer surface of the fifth digit.

Analysis.

For acquisition, retention and transfer the ANOVA model designs were identical to experiment 1.

Results

Sensory testing.

Paired Student's t-tests were used to compare the sensory data during stimulation for participants who received stimulation at some point in the experiment to their own sensory ability when stimulation was not present. Significant differences were found for

both 2 point discrimination (M = 3.4, SD = 0.8; M = 4.6, SD = 2.1), t(17) = -2.56; p < 0.05 and pressure monofilament testing (M = 3.1, SD = 0.4; M = 3.3, SD = 0.4), t(17) = -2.20; p < 0.05. The presence of stimulation again reduced the participant's ability to discriminate between two points spatially and their ability to detect pressure. Replicating the finding from experiment 1, the non-target stimulation again had a negative impact on tactile perception ability.

Unpaired Student's t-tests were used to compare the sensory data for participants from the stimulation group to the no stimulation group at baseline before any stimulation was applied. Analysis of the data collected for both 2 point discrimination, and pressure monofilament testing revealed no significant difference. Again, participants in both groups had intact and normal tactile sensory ability for 2 point discrimination, and pressure detection.

Acquisition

For accuracy significant main effects were found for trial, F(5,110) = 6.11; p < .001, $\eta^2 = .140$ but not for group or the interaction of trial and group (p > .05) (Figure 3). Mean accuracy increased following the first three trials.

INSERT FIGURE 3 ABOUT HERE

Analysis of all TRT data yielded a significant main effect for trial, F(5,110) = 15.87; p < .001, $\eta^2 = .225$ (Table 1). No other significant differences we found. Following the first trial mean TRT decreased.

Retention

When considering mean accuracy no significant main effects, or interactions were found (Figure 3).

Analysis of TRT data yielded a significant main effect for the trial, F(2,40) = 6.67; p < .05, $\eta^2 = .089$ (Table 2). TRT increased in the progression from acquisition trial 6 (M = 2674 ms) to immediate retention (M = 3522 ms).

Transfer

When considering mean accuracy no significant main effects, or interactions were found. (Figures 4).

Analysis of TRT data yielded a significant main effect for the trial, F(1,20) = 8.43; p < .05, $\eta^2 = .059$ (Table 2). As transfer trial number increased, mean TRT decreased from immediate (M = 4143 ms) to delayed (M = 3292 ms) meaning participants took significantly less time to respond.

INSERT FIGURE 4 ABOUT HERE

Discussion

Observing no between group differences for retention and transfer trials, suggests that task irrelevant cutaneous stimulation served to neither enhance, nor inhibit the retention and transfer of vibrotactile delivered information at an AIR separate from non-meaningful tactile stimulation. From the lack of differences found between separate AIRs we conclude that attention was not a factor between the target and non-target stimulation.

The sensory data collected at baseline again confirms that participants in both groups were equivalent in terms of having intact sensory systems, replicating the results of experiment 1. Even though not directly impacting the distal aspect of the palmar surface of the fifth finger, the presence of paresthesia stimulation had a negative impact on both pressure detection, and two-point discrimination that suggests it created a perturbation in tactile detection.

Acquisition results demonstrated that tactile information was being detected and processed by all participants. This is evidenced through improved accuracy and decreased TRT recorded as trial number increased. In experiment 2 there were no differences in accuracy between the group receiving tactile information in the presence of task irrelevant cutaneous stimulation over the course of the median nerve and the no stimulation group. The lack of difference between sensory condition groups may be because the median nerve does not directly innervate the palmar surface of the fifth digit, which is where the tactor delivered the stimuli.

General Discussion

The results of the two experiments reported in this study provide empirical evidence that when a tactile perturbation is delivered to the same AIR as target stimuli consisting of complex vibrotactile information that a concurrent masking paradigm is replicated. When perturbation is delivered to a separate AIR from target stimuli there is no significant effect of the perturbation which rules out a response competition (selective attention) effect.

Performance during complex tactile learning is generally poor. High errors rates have been demonstrated by studies using an array of devices that deliver tactile stimulation meant to represent letters to the hands of participants where multiple response alternatives are presented to assess accuracy (Heller, 1985; Tan et al., 1997). High error rates are likely why present technology allows for a mobile communication device to use vibrotactile stimuli to alert you to an incoming message rather than conveying the entire message via the tactile modality. Participants have difficulty in the cognitive interpretation associated with novel patterns of vibrotactile information. The accuracy results from the present study are in agreement with previously established accuracy data regarding tactile letter acquisition. For example Craig (2000) found accuracy performance in the range of 30-60% correct when vibrotactile letters were presented. Foulke and Broadbeck (1968) conducted a study that that also found poor performance accuracy when they attempted to use electrocutaneous stimuli to deliver Morse code to participants at an isolated location. Using an electrode on the distal pad of the index finger, participants received non-noxious electrical stimulation with temporal patterns identical to those used in traditional aural Morse code delivery. Augmented feedback correctness was provided following each trial. The mean error rate was 40.4% when Morse code letters consisted of a combination of four "dot" and "dash" elements, which Foulke and Broadbeck (1968) considered too high, rendering the communication rate unacceptably low.

While acquisition of tactile communication is difficult, it is not impossible, and

participants demonstrated learning performance that exceeds chance based on guessing responses. In the present studies accuracy performance was consistently above chance (12.5% correct;1 in 8). Tactile language presentation therefore facilitates the study of learning complex tactile information, as with enough trials a floor effect could be overcome (demonstrating that some learning is taking place), but it would be highly unlikely that early learners would reach a ceiling effect (task difficulty is too low and the learner performs beyond the maximum capacity for measurement). As a result a functional bandwidth exists for the study of the tactile learning, and the exploration of factors that may facilitate or impede it.

Why tactile learning is so difficult is not entirely clear. The novel nature of passive tactile reception has been blamed for difficulty in tactile learning. Poor performance on complex tactile tasks has been attributed to a lack of familiarity with passive tactile stimulation (Sherrick, 1975). Passively delivered tactile information, which was used in the present experiments, is considered consistently worse in learning performance compared to active touch (Heller, 1985). Information processing capacity limitations exist for both the detection of simple information as well as the identification of more complex patterns (Craig, 1982). The more complex the delivery of tactile information is, it necessitates directing more cognitive resources for analysis and interpretation of that information, which can adversely alter the rate or success of information processing (Gallace et al., 2007).

In addition to poor accuracy scores, participants demonstrated slow TRT

performance. These findings are consistent with previous research on both tactile letter learning, and letter learning in a challenging context. For example, Frings et al. (2008) found probe reaction times in the range of 1760-2285 ms when evaluating participants' ability to learn vibrotactile letters in the presence of a vibrotactile distractor. Beyond the tactile domain, retroactive letter learning, which was used in the present experiments, creates an even greater challenging context for information acquisition. Patterson and Lee (2005) used retroactive learning for the acquisition of written letters from a language used on personal digital assistant (PDA) devices. During six acquisition trials their reaction time scores ranged from 2000 ms – 8000 ms.

Masking not Response Competition

Several studies have been performed that manipulated the spatial distance between the target and non-target stimuli. Few of those studies have considered their findings relative to the anatomically known density of innervation, or pathway of innervation relative to the different spatial locations (Gilson, 1969). For simple stimuli detection, innervation density has been used to describe the results of concurrent tactile masking studies (Horner, 2000; Kekkoni, et al., 1987; Kekkoni et al., 1990). Innervation density of target location has also been used to describe letter acquisition study results (Craig, 1984; Heller, 1986). Masking occurs when the ability to identify a pattern is reduced or interfered with by presentation of other patterns (Craig, 1985). Based on the results of the present study when nerve perturbation is specific to the AIR of the finger used to detect a target stimuli, there is an initial masking effect observed during acquisition.

The presence of a response competition effect (attention/priming) (Craig & Evans, 1995) was not supported for complex tactile information in this context. This is evidenced in the present study when target and non-target stimuli were separated anatomically differences were not found compared to their control condition, although participants demonstrated successful acquisition. When no anatomical separation occurred acquisition demonstrated masking, retention demonstrated no difference, but transfer demonstrated enhancement. It is noteworthy that the most challenging acquisition context lead to improved transfer.

Summation/Enhancement.

Under certain circumstances, the presence of additional stimuli increases the ability to detect, or interpret a pattern of target stimuli. This effect has been described in numerous ways over time including summation (Vernon, 1953; Verrillo, 1965), enhancement (Verrillo, 1976; Verrillo, 1983), and negative masking (Gescheider, Verrillo, & Pelli, 1991; Hamer, Verrillo, & Zwislocki, 1983) which are essentially synonymous.

Verrillo (1965) came to the conclusion that summation occurred when he approached the tactile system with a modification of the Zwislocki (1960) theory of temporal auditory summation. Zwislocki theorized that as separate auditory stimuli were presented in progressively closer temporal proximity that the threshold to detect them decreased asymptotically. Manipulation of the temporal spacing decreased detection threshold and allowed a summation of one stimuli and a subsequent stimuli making them

easier to detect even if they were delivered at the same intensity. Zwislocki (1960) concludes summation is possible due to the exponential decay of the threshold for neural excitation upon repeated stimuli presentation.

Enhancement is the decreased threshold for stimuli to be perceived (Verrillo, 1985). The summation that leads to enhancement of stimuli is the opposite of a "masking" effect. In the tactile context numerous studies have compared the presence of a concurrent target and secondary stimulus which lead to enhancement of the target stimuli. For example, submersion in water has been found to increase the sensitivity of the skin (McAuley, Ewing, & Devasundaran, 1993). More specifically, after being submersed in seawater for 20 minutes vibrotactile stimulation of the hand's thenar eminence sensitivity increases (Verrillo & Bolanowski, 1996). A second example is when heat is delivered at a non-noxious intensity concurrent with target stimulus. Zhang et al., (2009) found that tactile detection was enhanced by non-noxious heat. The results of the present study provide support for the enhancement of knowledge transfer with the presence of a non-target stimuli in the same AIR as a complex tactile target stimuli. We conclude that masking in the context of learning may need to be re evaluated. Initially what is perceived as a "masking" stimulus during the acquisition of tactile information, may actually be a stimulus that provides "enhancement" when tested in the context of knowledge transfer.

Future directions

Craig (1995) discussed his prediction that to resolve the way in which tactile

patterns are reflected in the nervous system and at what level they are processed, neurophysiological studies are needed. Investigation utilizing a tool capable of investigating central nervous system neural plasticity in response to novel stimuli presentation with and without perturbation would be a means to achieve such future exploration.

The application of tactile learning under induced radiating paresthesia creates a context of potentially high ecological validity. For example a patient with advanced uncontrolled diabetes may experience peripheral neuropathy, or degradation in peripheral sensation, but also experience failure of vision through diabetic retinopathy. The understanding of the limitations and learning strategies for an uncontrolled diabetic patient's ability to learn to communicate using an already partially impaired tactile sense could be useful. Future studies on clinical populations would be required to determine the parallels between the results of the present work and a pathological context.

Conclusion

In summary, the results of the two experiments reported here provide evidence that induced radiating paresthesia interferes with acquisition, while it enhances the application of complex tactile driven information. In addition when interference is spatially and temporally concurrent with tactile reception, results are congruent with a masking paradigm, and not a selective attention/response competition effect. From our results, we conclude that a perturbation eliciting a concurrent masking effect creates a challenging context initially that facilitates tactile learning.

Acknowledgements

The lead author was initially supported with fellowships from the Foundation for Chiropractic Education and Research (FCER), and New York Chiropractic College. Subsequently, support was provided from the Ontario Graduate Scholarship (OGS) program and the Natural Sciences and Engineering Research Council of Canada.

References

- Bliss, J.C., Crane, H.D., Mansfield, P.K., & Townsend, J.T. (1966). Information available in brief tactile presentations. *Attention, Perception & Psychophysics*, 1, 273-283.
- Bolanowski, S.J., Maxfield, L.M., Gescheider, G.A, & Apkarian, A.V. (2000). The effects of stimulus location on the gating of touch by heat- and cold-induced pain. *Somatosensory & Motor Research*, 17, 195-204.
- Cholewiak, R.W., & Collins, A.A. (1997). Individual differences in the vibrotactile perception of a "simple" pattern set. *Perception & Psychophysics*, *59*, 850-866.
- Craig, J.C. (1982). Vibrotactile masking: a comparison of energy and pattern maskers.

 *Perception & Psychophysics, 31, 523-529.
- Craig, J.C. (1983). The role of onset in the perception of sequentially presented vibrotactile patterns. *Perception & Psychophysics*, *34*, 421-432.
- Craig, J.C. (1984). Vibratory temporal integration as a function of pattern discriminability. *Perception & Psychophysics*, *35*, 579-582.
- Craig, J.C. (1985). Tactile pattern perception and its perturbations. *Journal of the Acoustical Society of America*, 77, 238-246.
- Craig, J.C. (1995). Vibrotactile masking: the role of response competition. *Perception & Psychophysics*, *57*, 1190-1200.
- Craig, J.C. (2000). Vibratory temporal integration as a function of pattern discriminability. *Perception & Psychophysics*, 62, 596-606.
- Craig, J.C. & Evans, P.M. (1987). Vibrotactile masking and the persistence of tactual

- features. Perception & Psychophysics, 42, 309-317.
- Craig, J.C. & Evans, P.M. (1995). Tactile selective attention and temporal masking.

 *Perception & Psychophyics, 57, 511-518.
- Enriquez, M., & MacLean, K. (2008). The role of choice in longitudinal recall of meaningful tactile signals. *Proceedings 16th Symposium Haptic Interfaces for Virtual Environments and Teleoperator Systems* (HAPTICS '08), pp 49-56.
- Evans, P.M. (1987). Vibrotactile masking: Temporal integration, persistence, and strengths of representations. *Perception & Psychophysics*, 42, 515-525.
- Evans, P.M., & Craig, J.C. (1986). Temporal integration and vibrotactile backward masking. *Journal of Experimental Psychology: Human Perception & Performance*, 12, 160-168.
- Evans, P.M., & Craig, J.C. (1991). Tactile attention and the perception of moving tactile stimuli. *Perception & Psychophysics*, 49, 355-364.
- Evans, P.M., Craig, J.C., & Rinker, M.A. (1992). Perceptual processing of adjacent and nonadjacent tactile targets. *Perception & Psychophysics*, 52, 571-581.
- Foulke, E., & Broadbeck, A.A. (1968). Transmission of Morse code by electrocutaneous stimulation. *The Psychological Record*, *18*, 617-622.
- Frings, C., Bader, R., & Spence, C. (2008). Selection in touch: negative priming with tactile stimuli. *Perception & Psychophysics*, 70, 516-523.
- Gallace, A., Tan, H.Z., & Spence C. (2007). The body surface as a communication system: the state of the art after 50 years. *Presence*, *16*, 655-676

- Gescheider, G.A., Verrillo, R.T., & Van Doren, C.L. (1982). Prediction of vibrotactile masking functions. *Journal of the Acoustical Society of America*, 72, 1421-1426.
- Gescheider, G.A., Verrillo, R.T., & Pelli, D.G. (1991). Effects of noise on detection of amplitude increments of sinusoidal vibration of the skin. *Journal of the Acoustical Society of America*, *91*, 348-353.
- Gilson, R.D. (1969). Vibrotactile masking: some spatial and temporal aspects. *Perception & Psychophysics*, *5*, 176-180.
- Hamer, R.D., Verrillo, R.T., & Zwislocki, J.J. (1982). Vibrotactile masking of Pacinian and non-Pacinian channels. *Journal of the Acoustical Society of America*, 73, 1293-1303.
- Heller, M.A. (1985). Tactual perception of embossed Morse code and braille: the alliance of vision and touch. *Perception*, *14*, 563-570.
- Heller, M.A. (1986). Central and peripheral influences on tactual reading. *Perception & Psychophysics*, *39*, 197-204.
- Horner, D.T. (2000). Perceptual processing at adjacent locations on a single finger: masking and response competition. *Perception & Psychophysics*, 62, 1545-1555.
- Kekoni, J., Pertovarra A., & Hamalainen, H. (1987). Vibrotactile masking effects on airpuff-elicited sensations vary with skin region in the human hand.

 *Somatosensory & Motor Research, 5, 93-105.
- Kekoni, J., Tikkala, I., Pertovarra A., & Hamalainen, H. (1990). Spatial features of vibrotactile masking effects on airpuff-elicited sensations in the human hand.

- Somatosensory & Motor Research, 7, 353-363.
- Likert, R. (1932). A technique for the measurement of attitudes. *Archives of Psychology*, 22, 55.
- MacLean, K. (2008). Foundations of transparency in tactile information design. *IEEE Transactions on Haptics*, 1, 84-95.
- Marks, P.W., & Zukerberg, L.R. (2004). Case records of the Massachusetts General Hospital. Weekly clinicopathological exercises. Case 30-2004. A 37-year-old women with paresthesias of the arms and legs. *New England Journal of Medicine*, 351, 1333-1341.
- McAuley, D.M., Ewing, P.A., & Devasundaram, J.K. (1993). Effect of hand soaking on sensory testing. *International Journal of Leprosy and Other Mycobacterial Diseases*, 61, 16-19.
- Pascual-Leone, A., & Torres, F. (1993). Plasticity of the sensorimotor cortex representation of the reading finger in Braille readers. *Brain*, *116*, 39-52.
- Patterson, J.T., & Lee, T.D. (2005). Learning a new human-computer alphabet: the role of similarity and practice. *Acta Psychologica*, *120*, 267-287.
- Richardson, J.R., & Lee, T.D. (1999). The effects of proactive and retroactive demonstrations on the learning of signed letters. *Acta Psychologica*, 101, 79-90.
- Rinker, M.A., & Craig, J.C. (1994). The effect of spatial orientation on the perception of moving tactile stimuli. *Perception & Psychophysics*, *56*, 356-362.
- Schindler, U., & Knapp, A. (1976). The causes of mutual masking of tactile letters:

- interruption, summation, or delay? Psychological Research, 38, 303-318.
- Shea, J.B., & Morgan, R.L. (1979). Contextual interference effects on the acquisition, retention and transfer of a motor skill. *Journal of Experimental Psychology:*Human Learning and Memory, 5, 179-187.
- Sherrick, C.E. (1975). The art of tactile communication. *American Psychologist*, *30*(3), 353-360.
- Spence, C., & Gallace, A. (2007). Recent developments in the study of tactile attention.

 Canadian Journal of Experimental Psychology, 61, 196-207.
- Tan, H.Z., Durlach, N.I., Rabinowitz, W.M., Reed, C.M., & Santos, J.R. (1997).Reception of Morse code through motional, vibrotactile, and auditory stimulation.Perception & Psychophysics, 59, 1004-1017.
- Tang, K., Staines, W.R., Black, S.E., & McIlroy, W.E. (2009). Novel vibrotactile discrimination task for investigating the neural correlates of short-term learning with fMRI. *Journal of Neuroscience Methods*, 178, 65-74.
- Thorndike, E.L., & Woodworth, R.S. (1901). The influence of improvement in one mental function upon the efficiency of other functions. *Psychological Review*, 8, 247-261.
- Vernon, J. (1953). Cutaneous interaction resulting from simultaneous electrical and mechanical vibratory stimulation. *Journal of Experimental Psychology*, 45, 283-287.
- Verrillo, R.T., Bolanowski, S.J., Baran, F., & Smith, P.F. (1996). Effects of underwater

- environmental conditions on vibrotactile thresholds. *Journal of the Acoustical Society of America*, 100, 651-658.
- Verrillo, R.T. (1965). Temporal summation in vibrotactile sensitivity. *The Journal of the Acoustical Society of America*, *37*, 843-846.
- Verrillo, R.T. (1983). Vibrotactile subjective magnitude as a function of hand preference. *Neuropsychologica*, 21, 383-395.
- Verrillo, R.T. (1985). Psychophysics of vibrotactile stimulation. *Journal of the Acoustical Society of America*, 77, 225-232.
- Verrillo, R.T., & Gescheider, G.A. (1976). Effect of double ipsilateral stimulation on vibrotactile sensation magnitude. *Sensory Processes*, 1, 127-137.
- Zehr, E.P., & Chua, R. (2000). Modulation of human cutaneous reflexes during rhythmic cyclical arm movement. *Experimental Brain Research*, *135*, 241-250.
- Zhang, Z., Francisco, E.M., Holden, J.K., Dennis, R.G., & Tommerdahl, M. (2009). The impact of non-noxious heat on tactile information processing. *Brain Research*, 1302(1), 97-105.
- Zwislocki, J. (1960). Theory of temporal auditory summation. *Journal of the Acoustical Society of America*, 32, 1046-1060.

TABLES

Table 1

Mean Total Response Times (TRT in Milliseconds) by Condition During Acquisition in

Experiments 1 and 2

		Acquisition Trial											
		1		2		3		4		5		6	
Experiment	Condition	M	SD	M	SD	М	SD	М	SD	М	SD	М	SD
1	Paresthesia	4597	1938	3682	1539	4139	2023	3611	1523	3261	1434	3272	1444
	No Paresthesia	4179	1872	3160	861	3068	993	3412	965	2933	825	2798	849
2	Paresthesia	4482	1908	3112	966	3126	896	2550	780	2529	881	2538	739
	No Paresthesia	4053	1519	3111	1205	3243	864	2690	762	2908	1097	2811	962

Table 2

Mean Total Response Times (TRT in Milliseconds) by Condition During Retention, and

Transfer in Experiments 1 and 2

			Retenti	on Trial		Transfer				
	Condition	1		2		1		2		
Experiment		M	SD	M	SD	M	SD	M	SD	
1	Paresthesia	4974	2528	5954	2239	4126	1070	3787	1536	
	acquisition &									
	retention/transfer									
	Paresthesia	2778	1306	3598	1570	3568	809	3296	1680	
	acquisition, no									
	paresthesia									
	retention/transfer									
	No paresthesia	5187	1825	4237	1839	5143	1114	3249	529	
	acquisition,									
	paresthesia									
	retention/transfer									
	No paresthesia	4063	1557	3618	1071	3051	1049	2633	979.9	
	acquisition or									
	retention/transfer									

2	Paresthesia	3255	1747	2906	1137	3368	1532	2307	1441
	acquisition &								
	retention/transfer								
	Paresthesia	3344	2219	2814	1263	3779	2234	2709	2021
	acquisition, no								
	paresthesia								
	retention/transfer								
	No paresthesia	3501	1313	3448	1169	4893	3132	3695	1413
	acquisition,								
	paresthesia								
	retention/transfer								
	No paresthesia	3995	137	3348	857	2215	1682	2020	1285
	acquisition or								
	retention/transfer								

Figure Captions

Figure 1. Mean accuracy (percent correct) for letter identification across six acquisition trials and two retention trials for all ulnar nerve paresthesia perturbation, and no paresthesia group combinations from experiment 1. Error bars represent standard errors of the means.

Figure 2. Mean accuracy (percent correct) for letter generation across two transfer trials for all ulnar nerve paresthesia perturbation, and no paresthesia group combinations from experiment 1. Error bars represent standard errors of the means.

Figure 3. Mean accuracy (percent correct) for letter identification across six acquisition trials and two retention trials for all median nerve paresthesia perturbation, and no paresthesia group combinations from experiment 2. Error bars represent standard errors of the means.

Figure 4. Mean accuracy (percent correct) for letter generation across two transfer trials for all median nerve paresthesia perturbation, and no paresthesia group combinations from experiment 2. Error bars represent standard errors of the means.

Figure 1.

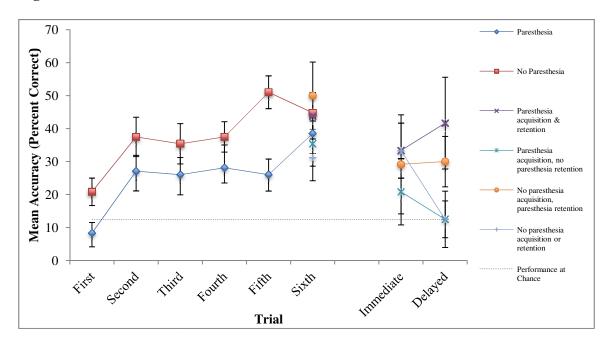


Figure 2.

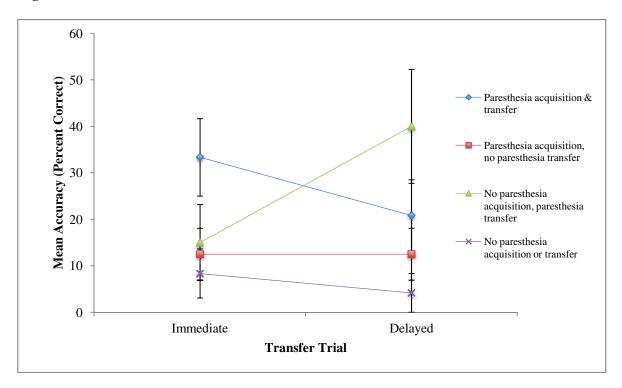


Figure 3.

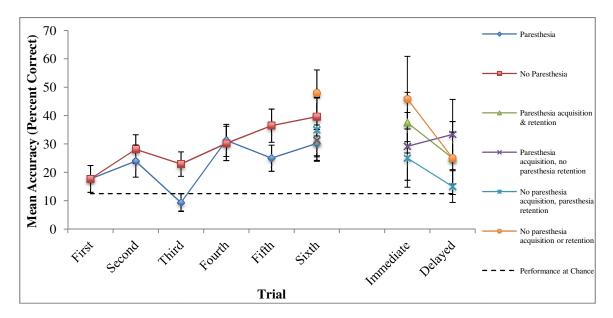
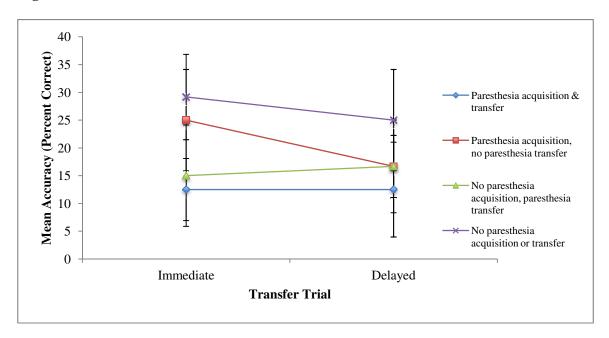


Figure 4.



DOCUMENT TWO

I was the primary investigator and major contributor for each aspect of this research project, including experimental design, testing, analyses and manuscript preparation.

This paper will be submitted to the journal Experimental Brain Research.

Running Head: SOMATOSENSORY INTEGRATION OF TACTILE INFORMATION

Somatosensory Integration and Masking of Complex Tactile Information

Steven R. Passmore^{1,2,3}, Jessica Bosse⁴, Bernadette Murphy⁴, Timothy D. Lee¹

¹McMaster University

² University of Manitoba

³New York Chiropractic College

⁴ University of Ontario, Institute of Technology

Corresponding Author Address: Steven Passmore, School of Medical Rehabilitation,

University of Manitoba, R106-771 McDermot Avenue, Winnipeg, Manitoba, Canada,

R3E 0T6

e-mail: passmore@cc.umanitoba.ca

telephone: (204) 787-1899

156

Abstract

Nerve paresthesia is a sensory impairment experienced in clinical conditions such as diabetes, and multiple sclerosis. Paresthesia may "mask" or "compete" with meaningful tactile information in the patient's sensory environment. Two purposes were the driving factors of the present study: first, to determine if radiating paresthesia produces a) a peripheral mask (b) a central mask, or (c) a combination. The second purpose was to determine if a response competition experimental design reveals changes in somatosensory integration similar to a masking context. In experiment 1 assessment of the masking impact of induced radiating ulnar nerve paresthesia (a concurrent non-target stimulus) was quantified on a vibrotactile Morse Code letter acquisition task using behavioral and neurophysiological measures in tandem. In experiment 2 a response competition design was used when the radiating paresthesia was shifted to the median nerve to alter the concurrent non-target stimulus to a location spatially removed from the target vibrotactile letter stimuli. The letter acquisition tasks remained constant, as did the application of behavioral and neurophysiological measures. The impact of induced paresthesia differentially impacted letter acquisition depending on the relative location of meaningful and non-meaningful stimulation. Paresthesia acted as a peripheral mask when presented to overlapping anatomical stimulation areas, and a central mask when stimulus presentation was at separate anatomical areas. These findings are discussed as they relate to masking, subcortical and centripetal gating.

Somatosensory integration and masking of complex tactile information

The study of dual stimulation of the touch modality is useful to accommodate for the discrepancy between competing input at sensory receptors (peripheral mask) and cortical processing overload (central mask). Competing stimuli may be two meaningful stimuli (tactile letters), or a combination of a meaningful, and not meaningful (noxious) stimuli, such as heat. Tactile sensitivity was suppressed by heat delivered to the point of creating pain in a study by Apkarian, Stea and Bolonowski (1994). In their study both tactile- and pain-provoking stimuli were presented to the base of the thumb of the right hand. Participants detected the presence of vibrotactile stimuli with and without concurrent heat-induced pain. The authors interpreted tactile-sensitivity suppression with concurrent pain to be a "gating" of the tactile system. Based on the afferent tactile pathway entering the dorsal column tracts of the spinal cord and synapsing in the dorsal column nuclei in the brainstem, they believed the disruption of tactile perception is likely to occur centrally.

The Apkarian et al., dual-touch stimulation study only considered the detection of simple vibrotactile stimuli, and not complex stimuli. The study of complex stimuli is important to allow for the communication of sophisticated information. Participants often endogenously orient to the sense of touch, and then await exogenously-driven tactile stimuli for many complex, vibrotactile-driven tasks. The lack of exploration of higher-level cognitive attention studies of complex tactile information has been identified as a priority for future research (Spence & Gallace, 2007). The primary application of

complex tactile information delivery and reception is for use when other sensory modalities are occupied. For example, workers on a noisy factory floor may need information about their task performance, or soldiers in a military context may require information about their position, or details regarding their enemy when other forms of communication are not safely possible. Spence and Gallace (2007) acknowledge the importance of looking at intramodal attention, and the impact of concurrent distracting stimuli that a participant may need to ignore, with the suggestion of exploring ecologically-valid testing conditions.

Craig (1983) determined that perturbation of a finger other than the finger required for a tactile discrimination task does not sufficiently distract the participant from the cognitive demands of the task. While changing the target finger used was unsuccessful in impacting discrimination ability, when stimulation is moved to an alternate location on the same finger performance is impacted. Kekoni et al., (1990), in their third experiment, found a decreased masking effect when the spatial location of the masker was switched to the base of the finger, and the to-be attended stimuli was shifted to the fingertip. They determined that a mask is more salient when placed over an area of dense innervation (fingertip). Their methods were unable to discern specifically whether the masking was strictly due to increased density of innervation, or possibly the larger cortical representation of the stimulated area in the brain. A limitation of Craig's (1983) results is the potential role of separate, or same peripheral innervation of the regions stimulated by the mask and the to-be-attended stimuli. If Craig's (1983) data were

reinterpreted with the concept of innervation location in mind, it would appear in general that a mask is less salient when anatomical locations with different peripheral innervation are presented with masking and meaningful stimuli. Kekoni et al., (1990) found that the masking effect was decreased when either longitudinal (distance from wrist to the fingers), or transverse (base of the second digit to base of the fifth digit) orientation distance was increased between the mask stimulus and target stimulus on the palm of the hand. Based on their findings they hypothesized that masking may have a central, not a peripheral mechanism, a topic that needs further scientific exploration.

Previous work successfully applied a perturbation of transcutaneously-induced paresthesia as a non-meaningful secondary stimulus that impacts the tactile system (Passmore et al., 2012). Participants in the acquisition phase of learning complex vibrotactile information (Morse Code letters) demonstrated slower total response times, and poorer accuracy scores when paresthesia was presented concurrently to the same peripheral nerve innervation region as the target letter stimuli was presented to. The results were described as evidence for a concurrent masking paradigm. No detriment to performance was noted when perturbation was applied to a separate anatomically-innervated region from the complex target stimuli, creating the context of a response competition paradigm. The conclusion was in agreement with Craig (1995) that neurophysiological studies are needed to further the understanding of the way in which complex tactile information is reflected in the nervous system and at what level it is processed.

Somatosensory evoked potentials (SEPs) reflect the neuroplasticity associated with a perceptual (Pellicciari et al., 2009), or motor task (Murphy et al., 2003) when recorded at baseline and compared to SEPs recorded following a separate perceptual, sensory or motor task. A pre-test and post-test experimental design can be used to avoid inadvertently masking the tactile system while utilizing the SEPs technique. Pellicciari et al. (2009) compared SEP recordings in the elderly and in a young population, pre- and post-exposure to paired-associative stimuli. While neuroplasticity may take place in both populations with learning, the patterns and underlying structures reflecting plastic changes may differ. Murphy et al. (2003) used pre- and post-task SEPs as a neurophysiologic measure for plasticity related to motor output. Ten individuals had SEPs recorded at baseline, then immediately after a 20-minute repetitive-typing task. Attenuation of the N13 peak, N14-18 complex, and N30-P40 complex all occurred immediately following the typing task.

The purpose of the present pair of studies is to determine if the acquisition of complex tactile-driven information elicits changes in somatosensory integration, and if those changes can be perturbed by concurrent, non-meaningful stimulation using a prepost SEPs stimulation design. Study number one investigates the masking effects of a local perturbation, concurrent with complex tactile stimulation. Study two investigates the response competition between a concurrent tactile perturbation to an region of separate peripheral innervation from the complex tactile target.

Experiment 1

The goal of experiment one was to resolve whether the masking of complex tactile information was reflective of competing input at sensory receptors (peripheral mask) a cortical-processing overload (central mask), or both. To test masking in a withinparticipant study, somatosensory evoked potentials were recorded at baseline and following the acquisition of complex tactile information (vibrotactile Morse Code letters). Letter acquisition was performed separately under both conditions of induced paresthesia as a masking perturbation, and under no perturbation. If the results of the behavioral performance measures replicate previous findings, response time should increase and accuracy should decrease with perturbation (Passmore et al., 2012). Peripheral masking will be demonstrated if no differences between sensory perturbation conditions are found upon SEP peak analysis. Central masking will be the result if only the SEPs analyses between sensory perturbation conditions differ. If there are changes between both behavioral conditions, and sensory perturbation SEPs components then both peripheral and central factors are involved in the observed complex information masking. Increases or attenuation of specific SEP peaks will reveal information about where perturbation impacts information processing. The processing locations will be predicted based on peripheral limitations, or the suspected cortical generators of the impacted SEP components.

Method

Participants.

Twelve volunteer participants (7 women, age range 19-31 years, M = 22.3 years, SD = 3.7 years) took part in the study. All were naïve regarding the purpose of the experiment, 11 were right-handed by self-report. All had normal or corrected-to-normal vision, and none reported any history of gross neurological sensory deficits. Approval by the University of Ontario Institute of Technology (UOIT) and McMaster University ethics boards was granted and informed consent was obtained from all participants.

All participants were sensory tested (Pascual-Leone & Torres, 1993), then asked to rate their knowledge of Morse code on a 5-point Likert scale (Likert, 1932), where 5 represented no knowledge, and 1 represented Morse code fluency. Only participants with no knowledge of Morse code (a score of 5) proceeded.

Design.

The study was a within-participants design and was divided into two phases, conducted over two days. Day one consisted of acquisition of one letterset, while day two consisted of acquisition of another letterset consisting of all new letters. Lettersets were counterbalanced between participants to avoid order effects and systematic effects of letter difficulty. Participants were also assigned alternately to either receive stimulation on day 1, or no stimulation first. The experiment was counterbalanced so all participants would eventually proceed to the condition opposite that which they were initially assigned in order to complete a second letterset.

Apparatus and materials.

Participants wore blindfolds and sat in a comfortable chair approximately 150 cm away from a computer monitor. Participants supinated their right hand for both two-point discrimination (Touch-Test two-point discriminator, Northcoast Medical Inc, Morgan Hill, CA), and monofilament pressure sensitivity (Touch-Test sensory evaluators, Northcoast Medical Inc, Morgan Hill, CA). Specifically, sensory testing occurred over the palmar surface of the distal aspect of their fifth digit of their right hand. Sensory testing was repeated prior to the component of the experiment that required induced paresthesia presence.

Non task specific perturbation (induced paresthesia).

Half of the participants received stimulation from a DS7A Constant Current Stimulator (Digitimer Ltd., Welwyn Garden City, Hertfordshire) for the duration of the acquisition phase of the experiment on day 1. Stimulation was delivered transcutaneously through 7 mm Ag/AgCl disposable, adhesive electrodes (Hydrospot from Physiometrix, Inc., Billerica, MA). Two electrodes were placed on the surface of dorsal medial aspect of the arm, 2 cm proximal to the ulnar notch, over the predicted course of the ulnar nerve. Custom LabVIEW (National Instruments, Austin,TX) software externally triggered the constant current stimulator, with a pulse duration of 200 μs, an interstimulus interval of 10 ms, and a voltage edge of 0.2 V.

The measurement of discrimination thresholds (sensory, radiating, premotor), served as the indicator levels to establish settings for the constant

current stimulator. Assessment of sensory threshold was the lowest stimulation level detectable by the participant, assessment of radiating threshold was the lowest stimulation level to elicit an orthodromic response from the point of stimulation along the course of the entire nerve stimulated (Zehr & Chua, 2000). Premotor threshold was the most intense signal delivered before motor contraction occurred. Participants had their sensory testing repeated on the day they received stimulation, for comparison to baseline, while being stimulated at their premotor threshold, which was the intensity used for the duration of the experiment.

Vibrotactile task.

Participants started with their right hand in a prone position with their elbow bent to 90 degrees and supported by an armrest, while the distal aspect of their left index finger rested atop the "V" key (used as the home position) on an QWERTY keyboard on their lap. The distal aspect of their right hand's 5th digit rested atop a 12mm diameter x 3.4mm thick, 200Hz vibrating disc motor (Solarbotics Ltd, Calgary, AB). Custom E-Prime software (Psychology Software Tools, Inc., Pittsburgh, PA) guided participants through the experiment, recorded dependent variables, and triggered the vibrotactile motor to create patterns representing Morse code.

Presentation of Morse code letters was achieved through patterns of vibrations (long and short pulses with spaces in between) using only letters with no more than 4 components, and no less than 3 components (e.g., Z = ``--.``; R = ``--.``). Pulse durations of 750 ms represented "dash" (-) signals, while durations of 250 ms represented

"dot" (.) signals. Spaces between letters were set to durations of 125 ms (Passmore et al., 2012; Tang et al., 2009).

Participants were exposed to a random presentation of 8 different Morse code letters until each letter was presented 6 times (48 total letter presentations). The computer screen provided a subset of 8 possible letter options and participants were then asked to indicate which letter had been presented by pressing the appropriate key on an alphanumeric keyboard with their left index finger. Augmented feedback regarding the response accuracy was provided -- the correct letter was presented visually appeared in its roman alphabetic form on the screen. The augmented information was provided retroactively to facilitate learning compared to providing the correct information before a response is made (Patterson & Lee, 2005). The participant self-selected when to depress the spacebar following feedback presentation, and returned their left index finger to the home "V" key in order to move on to the next stimulus presentation. Total response time (TRT) was the duration between when the screen requesting a letter selection appeared (immediately following vibrotactile presentation) until the response key was selected and depressed. Correctness of the response was the selection accuracy.

SEP stimulation and recording.

Participants were seated in a comfortable chair, in a quiet room with their eyes open and the lights off. Placement of stimulation electrodes was over the suspected course of the ulnar nerve of the right arm. Stimuli delivery occurred at 103% of the motor threshold, applied using a constant current stimulator (Digitimer Ltd., Hertfordshire,

Enlgand) at a rate of 4.98 Hz, a rate selected to maximize the accuracy of the N24 peak measurement (Fujii et al., 1994).

SEPs were collected in trial blocks of 1500 sweeps, and EEG signals were bandpassed filtered (3-1000 Hz), amplified (gain 100 000). Custom LabVIEW (National Instruments, Austin, TX) software controlled the data acquisition, signal averaging, and graphing functions for data analyses. The EEG signals were digitized at a sample rate of 5000 samples per second and were recorded with a sweep length of 55 ms (5 ms prestimulus and 50 ms poststimulus). All surface recording electrodes were 10mm disc, 2mm hole, gold cup EEG electrodes (Grass Technologies, West Warwick, RI) and were placed according to the International Federation of Clinical Neurophysiologists (IFCN) recommendations (Nuwer et al., 1994). IFCN recommended recording sites included electrode placement on ipsilateral Erb's point, and 2 cm posterior to contralateral central and frontal scalp sites C3/C4 (Cc') and F3/F4 (Fc') respectively. Additionally one anterior cephalic electrode was placed 6 cm anterior to Cz and 2 cm contralateral to the side of stimulation as identified by Rossi (2003). All electrodes were referenced to the ipsilateral earlobe, while a ground electrode was placed in the participant's mouth, tucked behind the lower lip.

Peripheral (N9), brainstem (N18) and cortical (N20, N24, and N30) SEPs to ulnar nerve stimulation were recorded before and after acquisition. Measurement and identification of SEP peak amplitudes was conducted according to the IFCN guidelines (Cruccu et al., 2008). All peaks were analyzed with exception of peak N9, which was

simply used as analysis exclusion criteria. Participants with N9 peaks with more then 10% variability were to be excluded from final SEP waveform analysis, no participants in the current study were impacted. The peripheral N9 peak is used to assess the stability of the signal of the peripheral afferent volley at the level of the brachial plexus.

SEP stimulation and concurrent data collection occurred at baseline, and following vibrotactile letter acquisition. Neurophysiological changes and behavioral data can be examined in tandem to create an understanding of whether learning is both demonstrated by performance and taking central nervous system electrical activity. The suspected generator of a SEP component may be used to provide insight on where central changes may occur.

Data Analysis

Sensory data analysis.

Paired Student's T-tests were performed for both two-point discrimination, and monofilament testing to compare sensory data collected at baseline to when sensory data was collected during paresthesia stimulation.

Behavioral data analysis.

Acquisition data consisting of mean total response time, and mean accuracy were each compared using within group ANOVA models. The designs were separate 2 (Sensation: Paresthesia, No Paresthesia) x 6 (Trial: Acquistion 1-6) ANOVA models with repeated measures on the both factors. Significant main effects and interactions were reported.

SEP data analysis.

SEPS data, consisting of the mean amplitude of analysed peaks, was compared between initial baseline, and following acquisition. The designs were separate 2 (Sensation: Paresthesia, No Paresthesia) x 2 (Trial Time: Baseline, Post Acquisition) ANOVA models with repeated measures on the both factors. Significant main effects and interactions were reported for each pre-identified peak.

Significance for all statistical measures was set at p < 0.05. Tukey's post-hoc analysis was applied for interpretation of results with more than two means.

Results

Sensory testing.

Significant differences were found for both two-point discrimination, t(11) = -3.08; p = 0.01, and monofilament pressure testing, t(11) = -8.48; p < 0.001. Paresthesia stimulation lead to impaired two-point discrimination (M = 3.58) compared to no stimulation (M = 2.75). Paresthesia stimulation also lead to a decrement in monofilament testing (M = 3.67) compared to no stimulation (M = 2.90).

Behavioral performance.

Analysis of mean accuracy yielded a main effect for trial, F(5,55) = 9.62; p < .001, $\eta^2 = .329$. Accuracy increased as trial number increased (Table 1). Post-hoc analysis revealed that accuracy on trial 1 (M = 15.63) was significantly less then all other trials, and trial 2 (M = 31.25) was significantly less than trial 6 (M = 45.83). There was also a main effect for sensory condition, F(1,11) = 5.32; p < .001, $\eta^2 = .156$. Letter

identification accuracy decreased in the presence of perturbation (M = 29.86) compared to no perturbation (M = 40.28). There was a 12.5% chance of guessing the correct response on each trial. Participants selected one of 8 response alternatives for consideration based on which one of the 8 possible letters they believed was presented.

Mean TRT analysis revealed a main effect was present for trial, F(5,55) = 6.98; p < .001, $\eta^2 = .132$. TRT decreased as trial number increased (Table 2). Post-hoc analysis revealed that TRT on trial 1 (M = 4595 ms) was significantly longer then all other trials.

SEP amplitude.

Significant differences were found for SEP peaks N20 and N24, but no significant differences were seen for the other peaks measured (Table 3). Peak N20 analysis included 11 participants as one participant was excluded due to a loose electrode. The analysis yielded a main effect for time, F(1,10) = 14.49; p = 0.003, $\eta^2 = .052$. Mean amplitude in microvolts was significantly greater at Time 2 (M = 1.315) than at Time 1 (M = 1.122). Peak N24 analysis also revealed a main effect for time, F(1,11) = 6.58; p = 0.026, $\eta^2 = .142$. Mean amplitude was significantly greater at Time 2 (M = 1.153) than at Time 1 (M = 0.843).

Discussion

Behavioral results reflect a successful replication of previous work (Passmore et al., 2012). Total response time increases, and accuracy decreases when paresthesia is applied to the ulnar nerve, and the site of vibrotactile Morse Code letter presentation is an ulnar innervated region compared to when no paresthesia is present.

The N20 SEP amplitude increased in response to the acquisition of complex vibrotactile information. The N20 SEP peak is recorded over the parietal cortex and is generated in the primary somatosensory cortex (S1), representing neurons within Brodmann's area 3b (Mauguiere et al., 1999; Nuwer et al., 1994; Tinazzi et al., 2000). The N20 is known to respond to tactile stimulation (Desmedt & Ozaki, 1991). The N24 component also increased in amplitude, a site considered to reflect activity in pathways involving the cerebellum and S1 (Mollinari, Restuccia & Leggio, 2009). The SEP peak changes were similar for both conditions, with no differences between sensory conditions.

The converging agreement between behavioral and neurophysiological measures provides evidence for complex tactile learning. Behavioral performance improved across the 6 acquisition trials, demonstrated by reduced time to respond and improved accuracy. The SEPs component amplitude increased after acquisition compared to baseline for both conditions. indicating tactile learning in general. Had no SEPs changes occurred compared to baseline, then no central changes would have occurred in association with the presentation of the complex tactile task. The differences between sensory conditions in behavioral results, but not in SEPs component amplitudes indicate that the detriment in behavior is explained by a peripheral masking effect. Peripheral masking has a subcortical mechanism since it occurs at a location between the actual site of tactile reception and the spinal cord.

Experiment 2

The goal of experiment two was to resolve whether a response competition design

reveals changes in somatosensory integration similar to the masking context from experiment one. Response competition is suspected to be the central resolution of competing stimuli, while masking has a peripheral mechanism. Changes in the amplitudes of SEP waveforms in a response competition context compared to baseline could reveal the presence of any central processing conflicts, and possibly where they occur. To achieve the goal in a within participant study, somatosensory evoked potentials were recorded at baseline and following the acquisition of complex tactile information (vibrotactile Morse Code letters). Letter acquisition was performed separately under both conditions of induced paresthesia as a response competition perturbation, and under no perturbation. An anatomical region with innervation distinct from the location of the target stimuli presentation was selected in order to achieve a response competition paradigm. In the concurrent dual-tactile stimulation design, the participant actively ignores the secondary stimuli and focuses on the detection and interpretation of the complex target stimuli (Morse Code letter). If only the SEPs analyses demonstrate between-sensory perturbation differences then results reflect a central resolution of a response competition paradigm. Conversely, if there are no differences in SEPs analyses a subcortical mechanism is responsible.

Method

Participants.

Twelve volunteer participants (4 women, age range 20-28 years, M = 22.3 years, SD = 2.3 years) took part in the study. All were naïve regarding the purpose of the

experiment, had normal or corrected-to-normal vision, and none reported any history of gross neurological sensory deficits. Approval by the University of Ontario Institute of Technology (UOIT) and McMaster University ethics boards was granted and informed consent was obtained from all participants.

Apparatus, materials, design, procedure and analysis.

All procedures and equipment were the same as experiment 1 with the exception of the change in location of the transcutaneous electrode placement used to create radiating paresthesia. These electrodes were moved to the anterior aspect of the forearm along the midline, over the predicted course of the median nerve, 5 cm proximal to the carpal line. The DS7A Constant Current Stimulator (Digitimer Limited, Hertfordshire, England) was set to deliver stimulation as in experiment one, with the exception that radiating paresthesia was now directed to the median nerve. The median nerve innervates the first, second and third digits, and the lateral aspect of the fourth digit on the hand. The tactor was still placed under the palmer surface of the fifth digit.

For sensory testing, behavioral performance and SEPs peak analyses statistical model designs were identical to experiment 1.

Results

Sensory Performance.

Paired Student's T-tests yielded no significant differences. Median nerve paresthesia stimulation did not yield differences when compared to baseline for either two-point discrimination, or monofilament testing. No differences were found for both

two-point discrimination, t (11) = 1.88; p = 0.09, and monofilament pressure testing, t (11) = 1.48; p < 0.09. Paresthesia stimulation lead to equivalent two-point discrimination (M = 4.25) compared to no stimulation (M = 3.58). Paresthesia stimulation also yielded no difference in monofilament testing (M = 3.16) compared to no stimulation (M = 3.03).

Behavioral performance.

Analysis of mean accuracy revealed a main effect for trial, F(5,55) = 7.42; p < .001, $\eta^2 = .061$. Accuracy increased as trial number increased (Table 1). Specifically, post-hoc analysis revealed that accuracy on trials 1 (M = 17.71) and trial 3 (M = 18.75) were significantly less accurate than trials 4, 5 and 6 respectively (M = 34.90; M = 34.90; M = 36.46). Again, there was a 12.5% chance of guessing the correct response on each trial. Participants selected one of 8 response alternatives for consideration based on which one of the 8 possible letters they believed was presented.

Mean TRT analysis also yielded a main effect for trial, F(5,55) = 9.35; p < .001, $\eta^2 = .158$ TRT decreased as trial number increased (Table 2). Specifically, post-hoc analysis revealed that TRT on trial 1 (M = 4206) was significantly slower than all other trials.

SEP amplitude.

A trend approaching significance was found for peak N20, while significant differences were found for SEP peak N24. No significant differences were seen for the other peaks measured (Table 3). SEP peak N20 analysis yielded an interaction approaching significance F(1,11) = 3.90; p = 0.07, $\eta^2 = .079$. The non-significant

interaction reveals a trend that indicates the conflict between learning (amplitude increases) and paresthesia (amplitude attenuation). When there was no paresthesia present learning was demonstrated by a trend toward increased SEP component amplitude (M = 1.13; to M = 1.24). Paresthesia stimulation created a trend toward amplitude attenuation (M = 1.41; to M = 0.98). Analysis of SEP peak N24 revealed a main effect for sensory condition F(1,11) = 7.37; p = 0.02, $\eta^2 = .401$. The amplitude of the peak was attenuated in the presence of paresthesia stimulation (M = 0.764) compared to when no stimulation was present (M = 1.121).

Discussion

Behavioral results again reflect a successful replication of previous work (Passmore et al., 2012). When paresthesia is applied to the median nerve, and the site of vibrotactile Morse Code letter presentation is an ulnar innervated region total response time, and accuracy show no differences compared to when no paresthesia is present.

In response to the acquisition of complex vibrotactile information stimulation, SEP amplitude results demonstrated an interaction approaching significance for component N20. The analysis revealed a trend toward the waveform increasing in amplitude when no paresthesia was present, a finding that replicates experiment 1 in the present paper, while when paresthesia was present a trend toward waveform attenuation occurred after complex letter acquisition. An attenuation in amplitude occurred at the N24 component, a site considered to reflect the cerebellar role in somatosensory integration (Mollinari, Restuccia & Leggio, 2009). The attenuation occurred between sensory

stimulation conditions indicating that when the presence of paresthesia is in a separate region of innervation from the complex tactile stimuli there is a different level of electrical activity in the structures responsible for generation of the N24 peak.

The results provide evidence for complex tactile learning. Both sensory conditions improved in behavioral performance across the six acquisition trials compared to baseline. Attenuated precognitive cortical activity is reflected by the trend toward the differential impact of paresthesia stimulation of the N20 peak, and the significantly attenuated N24 SEP component amplitude. The somatosensory evoked potential findings indicate that when dual stimulation occurs in separately innervated regions a response competition paradigm effect occurs.

General Discussion

Both experiments demonstrated the successful acquisition of complex vibrotactile information. Tactile learning was challenging, as predicted by previous studies (Craig, 2000; Foulke & Broadbeck, 1968), since letter recognition accuracy was less than 60%. Previously, Craig (2000) noted a vibrotactile accuracy rate of 30-60% for letter learning. Similarly, Foulke and Broadbeck (1968) taught teaching Morse code letters using electrocutaneous stimulation and found a 59.4% accuracy rate. Learning was reflected in both sensory groups across trials by behavioral (accuracy increase, TRT decrease), and in experiment 1 by neurophysiological variables (the increase in cortical peak amplitude at N20 and N24). In experiment 2 when the complex vibrotactile information was spatially separated from the perturbation of induced paresthesia cortical measures recorded were

reflective of competing afferent signals attenuating cortical information processing.

The primary somatosensory cortex lies in the posterior bank of the rolandic fissure representing Brodmann's area 3b in the parietal lobe. The aforementioned anatomical region is the site of N20 peak generation (Desmedt & Cheron, 1980). It is known to respond to contralateral tactile stimuli (Hlushchuk & Hari, 2006). The parietal N20 peak is consistent and occurs contralateral to the site of stimulation (Maugueire, 2005).

Brodmann's area 3b (the primary somatosensory cortex) responds to cutaneous inputs, but not joint movement input. Desmedt and Osaki (1991) confirmed the N20 cutaneous response, and in the absence of active joint movement in a study on passive finger movement. In healthy normal participants the N20 peak is the earliest marker of cortical processing in the primary somatosensory cortex following a somatosensory stimulus (Hari et al., 1993; Kristeva-Feige et al., 1995; Rossini et al., 1997; Rossi et al., 2003).

To provide context for the significance of the SEPs findings in the present study, the origin of peak N24 is located close to the location of N20. N24 is a frontal lobe negativity that appears on the ascending slope of peak N30. Garcia Larrea, Bastuji and Mauguiere (1992) found that N24 is best revealed at high stimulus rates that selectively decrease the N30 peak. Due to its mild variability in latency the N24 peak has also been referred to as N23 (Cheron & Borenstein, 1991), or N25 (Waberski et al., 1999).

Waberski et al., (1999) used source localization to identify to the posterior wall of the central sulcus in area 3b of the somatosensory cortex as the site of N24 generation. In order for the pathway to be completed the input sent to the somatosensory cortex travels

through the cerebellar cortex and deep cerebellar nuclei (Molinari, Restuccia, & Leggio, 2009). The N24 amplitude is enhanced if the cerebellar cortex is disrupted. N24 is reduced or absent, but all preceding peaks are left intact if the cerebellar cortex and deep cerebellar nuclei are lesioned (Restuccia et al., 2001). The characteristics of N24 are linked directly to the integrity of the cerebellum through its cortex and its deep nuclei. Experiment 2 yielded an attenuation of the N24 amplitude only with paresthesia. These findings provide evidence that the somatosensory integration created by a tactile response competition context is resolved in the cerebellar cortex and its deep nuclei.

The results of experiment 1 provide support for the phenomena known as subcortical gating (Gandevia, Burke & McKean, 1983). Subcortical gating implies that the interference of multiple stimuli presented concurrently interacts neurologically downstream from the cortex. The increases seen in activation at peaks N20, and N24 occurred after learning complex tactile information were equivalent between both sensory conditions. The lack of differences between the SEPs waveforms generated under different sensory conditions, but the different behavioral results attained provide evidence for a peripheral masking paradigm.

The results of experiment 2 provide support for the phenomena known as centripetal gating (Rossini et al., 1999; Cheron & Borenstein, 1991; Gandevia, Burke & McKean, 1983; Jones & Power, 1984; Jones, Halonen & Shawkat, 1989). Centripetal gating is the attenuation of short latency (less than 60 ms) SEPs as a result of passive vibration or cutaneous sensory stimulation, which leads to interference between

somatosensory inputs (Rossini et al., 1999). The results of experiment 2 provide evidence for the selective attenuation of a specific SEP component. Conditions creating attenuation in single cortical peaks, but not impacting behavioral measures between conditions reveal a cortical interference in information processing. The behavioral measures revealed no peripheral masking occurred, and the design allowed for the neurophysiological study of a response competition paradigm. The experimental conditions applied were successful in creating an interference effect that may have had ramifications for the suspected cortical generator of the N24 peak. Paresthesia presented concurrent with meaningful tactile information at separate anatomical locations supressed peak N24. If all cortical SEP peaks were supressed with dual stimulation the mechanism would be predicted to be subcortical (Rossi et al., 2003). N24, is the site considered to reflect the cerebellar role in somatosensory integration particularly the spatial predictions or deivations of sensory input (Mollinari, Restuccia & Leggio, 2009), and a significant central change occurred with the response competition design. At the cortical level the conflict regarding response selection was observed.

A possible limitation of the neurophysiological aspect of the study design was the SEPs stimulus rate of 4.98 Hz. While it enhances the accuracy of measuring cortical peak N24, it may do so by attenuation of other SEPs peaks (Fujii et al., 1994), particularly peak N30, which may be why no N30 changes were found for the present experiments. However, Yamada, Yeh and Kimura (2004) found that for SEPs with latencies occurring at or before 30 ms, a stimulus rate up to 8 Hz does not significantly affect latency (or

amplitude).

According to Maugueire (2005) early SEPs waveform components (<40 ms) generated by upper limb stimulation should not be impacted by voluntary attention. Therefore, the present study's findings address early plastic changes associated with tactile learning concurrent with competing paresthesia stimulation at spatially different locations, not changes in volitional attention. The waveform changes reflect neuroplastic changes that are evidence of response competition independent of attention.

It is not yet possible to infer if the detected neurophysiological activations result in an overall net faciliatory or inhibitory effect on behavior. Future studies building upon the knowledge generated by the presented experiments may use the SEP peak's suspected cortical origin as a starting point to indicate regions to study paresthesia competing with complex tactile information acquisition on imaging and activation studies using fMRI and MEG. These experimental findings may also serve as a future model for clinician scientists to quantify the masking of information acquisition and the ramifications of altered somatosensory processing of individuals with disorders that manifest clinical paresthesia.

Acknowledgements

The lead author was initially supported with fellowships from the Foundation for Chiropractic Education and Research (FCER), and New York Chiropractic College. Subsequently, support was provided from the Ontario Graduate Scholarship (OGS) program and the Natural Sciences and Engineering Research Council of Canada.

References

- Apkarian, A.V., Stea, R.A., & Bolonowski SJ. (1994). Heat-induced pain diminishes vibrotactile perception: a touch gate. *Somatosensory and Motor Research*, 11, 259-67.
- Arezzo, J.C., Schaumburg, H.H., & Spencer, P.S. (1982). Structure and function of the somatosensory system: a neurotoxicological perspective. *Environmental Health Perspectives*, 44, 23-30.
- Cheron, G., & Borenstein, S. (1991). Gating of the early components of the frontal and parietal somatosensory evoked potentials in different sensory-motor interference modalities. *Electroencephalography & Clinical Neurophysiology*, 80, 522-530.
- Craig, J.C. (1983). The role of onset in the perception of sequentially presented vibrotactile patterns. *Perception & Psychophysics*, *34*, 421-432.
- Craig, J.C. (1995). Vibrotactile masking: the role of response competition. *Perception & Psychophysics*, *57*, 1190-1200.
- Craig, J.C. (2000). Vibratory temporal integration as a function of pattern discriminability. *Perception & Psychophysics*, 62, 596-606.
- Cruccu, G., Aminoff, M.J., Curio, G., Guerit, J.M., Kakigi, R., Mauguiere, F., Rossini, P.M., Treede, R.D., & Garcia-Larrea, L. (2008). Recommendations for the clinical use of somatosensory-evoked potentials. *Clinical Neurophysiology*, 119, 1705-1719.
- Desmedt, J.E., & Cheron, G. (1980). Central somatosensory conduction in man: neural

- generators and interpeak latencies of the far-field components recorded from neck and right or left scalp and earlobes. *Electroencephalography & Clinical Neurophysiology*, *50*, 382-403.
- Desmedt, J.E., & Osaki, I. (1991). SEPs to finger joint input lack the N20-P20 response that is evoked by tactile inputs: contrast between cortical generators in areas 3b and 2 in humans. *Electroencephalography & Clinical Neurophysiology*, 80, 513-521.
- Foulke, E., & Broadbeck, A.A. (1968). Transmission of Morse code by electrocutaneous stimulation. *The Psychological Record*, *18*, 617-622.
- Fujii, M., Yamada, T., Aihara, M., Kokubun, Y., Noguchi, Y., Matsubara, M., & Yeh,
 M.H. (1994). The effects of stimulus rates upon median, ulnar and radial nerve somatosensory evoked potentials. *Electroencephalography & Clinical Neurophysiology*, 92, 518-526.
- Gandevia, S.C., Burke, P., & McKean, B. (1983). Convergence in the somatosensory pathway between cutaneous afferents from index and middle finger in man. *Experimental Brain Research*, 50, 415 – 425.
- Garcia Larrea, L., Bastuji, H., & Mauguiere, F. (1992). Unmasking of cortical SEP components by changes in stimulus rate: a topographic study.

 Electroencephalography & Clinical Neurophysiology, 84, 71-83.
- Hari, R., Karhu, J., Hamalainen, M., Knuutila, J., Salonen, O., Sams, M., Vilkman, V. (1993). Functional organization of the human first and second somatosensory

- cortices: a neuromagnetic study. European Journal of Neuroscience, 5, 724–734.
- Hlushchuk, Y., & Hari, R. (2006). Transient suppression of ipsilateral primary somatosensory cortex during tactile finger stimulation. *The Journal of Neuroscience*, 26, 5819-5824.
- Jones, S.J., & Power, C. (1984). Scalp topography of human SEPs: the effect of interfering tactile stimuli applied to the hand. *Electroencephalography & Clinical Neurophysiology*, 58, 25 36.
- Jones, S.J., Halonen, J.P., & Shawkat, F. (1989). Centrifugal and centripetal mechanisms involved in the "gating" of cortical SEPs during movement.

 *Electroencephalography & Clinical Neurophysiology, 4, 36–45.
- Kekoni, J., Tikkala, I., Pertovarra A., & Hamalainen, H. (1990). Spatial features of vibrotactile masking effects on airpuff-elicited sensations in the human hand. *Somatosensory & Motor Research*, 7, 353-363.
- Kristeva-Feige, R., Rossi, S., Pizzela, V., Tecchio, F., Romani, G.L., Erne, S., Edrich, J., Orlacchio, A., Rossini, P.M. (1995). Neuromagnetic fields of the brain evoked by voluntary movement and electrical stimulation of the finger. *Brain Research*, 682, 22-28.
- Leeman, S.A. (2007). SSEPs: from limb to cortex. *American Journal of Electroneurodiagnostic Technology*, 47, 165-177.
- Likert, R. (1932). A technique for the measurement of attitudes. *Archives of Psychology*, 22, 55.
- Mauguiere, F. (2005). Somatosensory evoked potentials: normal responses, abnormal

- waveforms, and clinical applications in neurological diseases. In E. Niedermeyer, & F.H. Lopes da Silva (Eds.), *Electroencephalography: basic principles, clinical applications, and related fields* (pp. 1067-1120). Philadelphia: Lippincott, Williams & Walkin.
- Molinari, M., Restuccia, D., & Leggio, M.G. (2009). State estimation, response prediction, and cerebellar sensory processing for behavioral control. *Cerebellum*, 8, 399-402.
- Murphy, B.A., Haavik Taylor, H., Wilson, S.A., Oliphant, G. & Mathers, K.M. (2003).

 Rapid reversible changes to multiple levels of the human somatosensory system following the cessation of repetitive contractions: a somatosensory evoked potential study. *Clinical Neurophysiology*, 114, 1531-1537.
- Nuwer, M.R., Aminoff, M., Desmedt, J., Eisen, A.A., Goodin, D., Matsuoka, S., Mauguiere, F., Shibasaki, H., Sutherling, W., & Vibert, J.F. (1994). IFCN recommended standards for short latency somatosensory evoked potentials: report of an IFCN committee International Federation of Clinical Neurophysiology. *Electroencephalography & Clinical Neurophysiology*, 91, 6-11.
- Pascual-Leone, A., & Torres, F. (1993). Plasticity of the sensorimotor cortex representation of the reading finger in Braille readers. *Brain*, *116*, 39-52.
- Passmore, S.R., Bosse, J., Murphy, B., & Lee, T.D. (2012). The impact and specificity of nerve perturbation on novel vibrotactile sensory letter learning. *Manuscript submitted for publication*.

- Patterson, J.T., & Lee, T.D. (2005). Learning a new human-computer alphabet: the role of similarity and practice. *Acta Psychologica*, 120, 267-287.
- Pellicciari, M.C., Miniussi, C., Rossini, P.M., & De Gennaro, L. (2009). Increased cortical plasticity in the elderly: changes in the somatosensory cortex after paired associative stimulation. *Neuroscience*, *163*, 266-276.
- Restuccia, D., Valeriani, M., Barba, C., Le Pera, D., Capecci, M., Filippini, V., & Molinari, M. (2001). Functional changes of the primary cerebral cortex in humans. *Brain*, *124*, 757-768.
- Rossi, S., della Volpe, R., Ginanneschi, F., Ulivelli, M., Bartalini, S., Spidalieri, R., & Rossi, A. (2003). Early somatosensory processing during tonic muscle pain in humans: relation to loss of proprioception and motor 'defensive' strategies.

 *Clinical Neurophysiology, 114, 1351-1358.
- Rossini, M., Babiloni, C., Babiloni, F., Ambrosini, A., Onorati, P., Carducci, F., & Urbano, A. (1999). "Gating" of human short-latency somatosensory evoked cortical responses during execution of movement. A high resolution electroencephalography study. *Brain Research*, 843, 161-170.
- Rossini, M., Babiloni, F., Babiloni, C., Ambrosini, A., Onorati, P., Urbano, A. (1997).

 Topography of spatially-enhanced short-latency somatosensory evoked potentials,

 NeuroReport, 8, 991-994.
- Spence, C., & Gallace, A. (2007). Recent developments in the study of tactile attention.

 Canadian Journal of Experimental Psychology, 61, 196-207.
- Tang, K., Staines, W.R., Black, S.E., & McIlroy, W.E. (2009). Novel vibrotactile

- discrimination task for investigating the neural correlates of short-term learning with fMRI. *Journal of Neuroscience Methods*, 178, 65-74.
- Waberski, T.D., Buchner, H., Perkuhn, M., Gobbele, R., Wagner, M., Kucker, W., & Silny, J. (1999). N30 and the effect of explorative finger movements: a model of the contribution of the motor cortex to early somatosensory potentials. *Clinical Neurophysiology*, 110, 1589-1600.
- Walsh, P., Kane, N., & Butler, S. (2005). The clinical role of evoked potentials. *Journal of Neurology Neurosurgery and Psychiatry*, 76(Supplementary II), ii16-ii22.
- Yamada, T., Yeh, M., & Kimura, J. (2004). Fundamental principles of somatosensory evoked potentials. *Physical Medicine and Rehabilitation Clinics of North America*, 15, 19-42.
- Zehr, E.P., & Chua, R. (2000). Modulation of human cutaneous reflexes during rhythmic cyclical arm movement. *Experimental Brain Research*, *135*, 241-250.

Table 1

Mean Accuracy (percent correct) by Condition During Acquisition Experiments 1 and 2

Tables

		Acquisition Trial											
		1		2		3		4		5		6	
Experiment	Condition	M	SD	М	SD								
1	Paresthesia	11.5	16.4	26.0	18.0	31.3	21.7	36.5	23.5	31.3	21.0	42.7	16.4
	No Paresthesia	19.8	15.5	36.5	21.6	38.5	24.1	40.6	17.0	57.3	18.0	49.0	22.9
2	Paresthesia	17.7	17.2	27.1	18.3	11.5	11.3	35.4	23.1	27.1	19.1	32.3	20.3
	No Paresthesia	17.7	16.4	32.3	22.3	26.0	18.8	34.4	24.5	42.7	23.5	40.6	24.5

Table 2

Mean Total Response Times (TRT in Milliseconds) by Condition During Acquisition in

Experiments 1 and 2

		Acquisition Trial											
			1		2		3		4		5		6
Experiment	Condition	M	SD	М	SD	M	SD	М	SD	М	SD	М	SD
1	Paresthesia	4823	1940	3674	1498	4272	2011	3608	1456	3331	1412	3364	1511
	No Paresthesia	4368	1817	3411	1101	3174	1005	3572	1186	3167	1090	2906	771
2	Paresthesia	4287	1590	3584	2039	3603	1448	2877	1096	2914	1146	2773	739
	No Paresthesia	4124	1507	3220	1215	3279	846	2820	805	3018	1093	3123	1348

Table 3

Mean Early SEP Component Amplitudes (in microvolts) by Condition in Experiments 1

and 2

	Early SEP Component									
	N18		N20		N24		N30			
Condition	M	SD	M	SD	M	SD	M	SD		
Paresthesia										
Baseline	0.51	0.53	0.95	0.51	0.81	0.49	1.09	0.66		
Post Learning	0.56	0.29	1.23	0.68	1.06	0.63	1.13	0.46		
No Paresthesia										
Baseline	0.55	0.47	1.30	0.69	0.87	0.46	1.00	0.63		
Post Learning	0.56	0.31	1.40	0.61	1.25	0.74	1.29	0.76		
	Paresthesia Baseline Post Learning No Paresthesia Baseline	Condition M Paresthesia Baseline 0.51 Post Learning 0.56 No Paresthesia Baseline 0.55	Paresthesia Baseline 0.51 0.53 Post Learning 0.56 0.29 No Paresthesia Baseline 0.55 0.47	N18 N2 Condition M SD M Paresthesia 0.51 0.53 0.95 Post Learning 0.56 0.29 1.23 No Paresthesia 0.55 0.47 1.30	No ParesthesiaNo ParesthesiaBaseline0.510.530.950.51Post Learning0.560.291.230.68No Paresthesia0.550.471.300.69	N18 N20 N Condition M SD M SD M Paresthesia 0.51 0.53 0.95 0.51 0.81 Post Learning 0.56 0.29 1.23 0.68 1.06 No Paresthesia 0.55 0.47 1.30 0.69 0.87	N18 N≥0 N≥4 Condition M SD M SD M SD Paresthesia 0.51 0.53 0.95 0.51 0.81 0.49 Post Learning 0.56 0.29 1.23 0.68 1.06 0.63 No Paresthesia 0.55 0.47 1.30 0.69 0.87 0.46	N18 N20 N24 N Condition M SD M SD M Paresthesia 0.51 0.53 0.95 0.51 0.81 0.49 1.09 Post Learning 0.56 0.29 1.23 0.68 1.06 0.63 1.13 No Paresthesia		

2 Paresthesia

Baseline	0.49	0.37	1.41	0.74	0.88	0.60	1.21	1.05
Post Learning	0.60	0.38	0.98	0.70	0.65	0.37	1.18	0.83
No Paresthesia								
Baseline	0.57	0.31	1.13	0.47	1.05	0.51	0.98	0.59
Post Learning	0.67	0.51	1.23	0.64	1.19	0.56	1.08	0.71

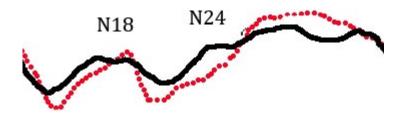
Figure Captions

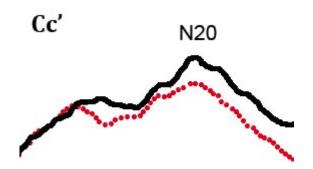
Figure 1. An example of the significant SEP amplitude increases (N20, N24) from the averaged waveform of a single participant from experiment 1 between baseline and post tactile learning (a). An example of the significant SEP amplitude attenuation (N24) from the averaged waveform of a single participant from experiment 2 between paresthesia, and no paresthesia conditions (b).

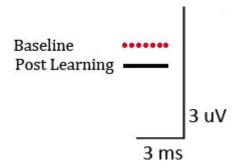
Figure 1.

a.

Rossi Site

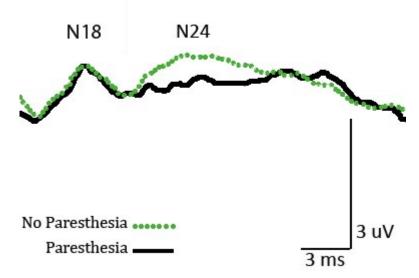






b.

Rossi Site



GENERAL CONCLUSION

The purpose of this dissertation was to examine the effects of interference during complex tactile information transmission. To achieve the purpose, four experiments were conducted to provide evidence regarding sensory and information processing demands in the early stages of complex tactile learning. Tactile information processing was examined through changes in the spatial location of a perturbation to the acquisition and subsequent application of vibrotactile Morse code letters (document 1). To examine possible central changes during the acquisition of complex tactile information neurophysiological measurement was applied (document 2) while also replicating the behavioural results of document 1.

Experiment 1 in document 1, compared learning in two contexts: i) a concurrent masking paradigm, and ii) a no perturbation stimulation control group. In the stimulation group experimentally induced paresthesia was directed to the same nerve pathway required to detect vibrotactile Morse code letters. Stimulation presence resulted in decreased accuracy and increased response time, but lead to improvements in transfer performance. Acquisition performance under stimulation reflected results consistent with a masking phenomenon (Craig, 1985; Verrillo, 1985), while the retention and transfer results demonstrated an enhancement paradigm (Verrillo & Gescheider, 1976; Verrillo, 1983). Even though experimental conditions were designed to maximize the possibility for masking effects, a response competition paradigm (Craig & Evans, 1995) could not be ruled out. To determine whether the results of experiment one could be attributed to

masking or response competition paradigms a second experiment was conducted.

Experiment 2 in document 1, was structured in an identical manner to experiment 1, with the exception that the current perturbation was applied to a different spatial location. The paresthesia was applied to a median nerve pathway, while the target stimulation was again applied to an ulnar nerve pathway. Spatial separation of the target and non-target stimulation eliminated the possibility of the peripheral receptor masking by the dual concurrent stimulation, setting up a response competition context (Craig & Evans, 1995). As predicted the masking effect seen during letter acquisition from experiment 1 was eliminated. However, in addition no advantage was seen for retention of transfer of learning. What remained unresolved at the conclusion of document 1 was whether the masking and response competition paradigms from experiments 1 and 2 could be resolved with further neurophysiological evidence for the behavioral results, which Craig (1995) identified as a future research priority. Specifically how the spatial change in stimulation resulting in masking and response competition effects respectively impacted the peripheral or central components of complex tactile information processing.

Dissertation experiments 3 and 4 (document 2) served to replicate behavioural acquisition data from experiments 1 and 2 (document 1). They also built upon the first two experiments by neurophysiological measurement associated vibrotactile information acquisition under the two perturbation location conditions. At baseline and following information acquisition somatosensory evoked potentials were elicited and analyzed. The study discerned whether the masking and response competition paradigms from

experiments 1 and 2 were predominantly impacting the peripheral or central components of information processing. It was determined that in a masking context equal cortical activity changes were found post learning for both the paresthesia and the control group. This provided evidence that the behavioral findings reflecting a masking paradigm occurred as a result of a subcortical or peripheral mechanism (Gandevia, Burke & McKean, 1983). In contrast, when a response competition context was tested, cortical activity changes were differentially impacted when receiving paresthesia. The presence of paresthesia at a peripheral site spatially separated from the target Morse code letters yielded an attenuation of neural activity. This attenuation reflects changes in cortical processing associated with the perturbation. The cortical gating in a response competition paradigm is an example of centripetal gating (Rossini et al., 1999).

The results of experiment 3 provide support for the phenomena known as subcortical gating (Gandevia, Burke & McKean, 1983). Subcortical gating implies that the interference of multiple stimuli presented concurrently interacts neurologically downstream from the cortex. The increases seen in activation at peaks N20, and N24 occurred after learning complex tactile information were equivalent between both sensory conditions, the increased activity reflected learning (Hoffken et al., 2007). The lack of differences between the SEPs waveforms generated under different sensory conditions, but the different behavioural results attained provide evidence for a peripheral masking paradigm. Peripheral masking is predicted by previous research that associates masking as a phenomenon that reflects the overwhelming of specific cutaneous tactile receptors

(Gescheider & Wright, 2012).

Results from experiment 4 support a centripetal gating phenomena (Rossini et al., 1999; Cheron & Borenstein, 1991; Gandevia, Burke & McKean, 1983; Jones & Power, 1984; Jones, Halonen & Shawkat, 1989). Centripetal gating is short latency (less than 60 ms) SEP attenuation from passive vibration or cutaneous sensory stimulation, creating interference between somatosensory cortical inputs (Rossini et al., 1999). Experiment 4 attained results that are evidence for the selective attenuation of a specific SEP component. When conditions attenuate single cortical peaks, but do not impact behavioural measures between conditions they reveal interference in cortical information processing. Behavioural measures revealed the absence of peripheral masking, and the design fascilitated neurophysiological study of a response competition paradigm. The applied experimental conditions successfully created an interference effect on the suspected cortical generator of the N24 peak. Suppression of peak N24 occurred with concurrent paresthesia and meaningful tactile information presentation to separate anatomical locations. Suppression of all cortical SEP peaks with dual stimulation would indicate a subcortical predicted mechanism (Rossi et al., 2003). The cerebellar role in somatosensory integration is considered to be reflect in the N24 peak. It is the site particularly identified as managing spatial predictions or deviations of sensory input (Mollinari, Restuccia & Leggio, 2009). A significant N24 change occurred with the response competition design, which reflects cortical interference.

The 4 experiments conducted in the presented dissertation aid our understanding

of complex tactile learning. Specifically, that neutral concurrent masking of complex tactile stimuli impacts the system subcortically. The masking phenomenon yields poor initial performance, but only during information acquisition. In terms of the ability to apply tactile information the challenging masking condition leads to enhanced learning demonstrated by the improved transfer of the tactile acquired information. The target stimuli and concurrent masking technique used in this dissertation achieved some of the proposed "future" directives set out by Craig (1995).

First, paresthesia served as a neutral stimulus, one that required no specific response and was used as a masking stimulus. A neutral stimulus is one that could not by its physical nature be confused with the response required by the target stimulus (Craig 1995). Second, Craig (1995) noted the need to include the delivery of more complex stimuli to the same spatial area of the skin as the non-target stimuli. Vibrotactile Morse code is a method of communicating complex meaningful information and the fingertip (Tang et al., 2009). Since the paresthesia was elicited distally and radiated into the fingertips, the design of our studies allowed for the mechanical target stimulus to be presented to the desired, and perturbed, area of the fingertip.

Third, Craig (1995) recommended that if an energy mask is used, it should not be delivered in a manner where sharp edges of a mask pattern could be perceived, as they could be confused with target stimuli characteristics. The superiority of the paresthesia application to previous techniques is that it did not have harsh "edges". Edges such as that which could directly impact sensory perception in the immediate vicinity of the target

stimulation. Previously applied masking systems using TVSS technology could not concurrently present target and masking stimuli, nor could they present stimulation that did not have rigidly defined edges.

A fourth and final important contribution made by this dissertation regarding the concerns proposed by Craig (1995) is that experiments 3 and 4 specifically addressed how the target stimuli impacts the central nervous system, and how a response competition and masking paradigm differ in their central representation. Using SEPs as a neurophysiological technique, changes in the electrical activity that were consistent with learning complex tactile information (experiment 3) and the impact of perturbation (experiment 4) were observed.

The experimental effects attained provide evidence that a masking phenomenon reflects subcortical or peripheral gating. The attenuation of the SEPs waveforms during paresthesia in a response competition context provides evidence for centripetal gating. Centripetal gating is the central-competition of afferent stimuli at the cortical level. Specifically, the presented results support the view that centripetal gating induced by cutaneous stimuli act on cortical SEP generators (Cheron & Borenstein, 1991).

Tactile learning of complex information the presented studies was challenging, since at best letter recognition accuracy was less than 60%. The poor accuracy finding with tactile learning is congruent with previous studies (Craig, 2000; Foulke & Broadbeck, 1968). Craig (2000) noted vibrotactile letter learning accuracy rates of 30-60%. Foulke and Broadbeck (1968) found a 59.6% accuracy rate when teaching Morse

code letters using electrocutaneous stimulation. Both sensory conditions demonstrated learning across trials evidenced by behavioural variables (accuracy increases, TRT decreases), and in document 2 additionally by neurophysiological variables (SEP amplitude increases).

One of the limitations of this dissertation is that we still do not know how the observed effects of paresthesia, and vibrotactile Morse code apply to specific cutaneous tactile reception channels. Gescheider and Wright (2012) propose that tactile learning is specific to individual receptor types and their processing channels. This dissertation focused specifically on how perturbation impacted complex learning, as opposed to the distinct peripheral information detection at the level of the cutaneous receptor. A second limitation is that from the results of the presented studies we are not able to completely discern if the detected neurophysiological activations result in an overall net facilitory or inhibitory effect on behaviour.

Future studies building on the knowledge generated by the presented experiments may use the suspected cortical origins of SEP peaks to indicate target brain regions.

Imaging and activation studies using fMRI and MEG could target where paresthesia competes with complex tactile information acquisition. Additional future studies could explore how the observed changes in tactile information acquisition, and knowledge usage, are impacted in clinical populations. Specifically, clinical populations who are forced to rely on their tactile sense although it may be impeded. For example, patients with advanced unmanaged diabetes may also suffer from vision loss (diabetic

retinopathy), in addition to distal extremity impaired sensation (peripheral neuropathy) (Marks & Zukerberg, 2004). In a training context in may be advantageous to present a masking stimulus, to challenge the system, with the intended result of enhanced future learning.

In summary, the collective results from this dissertation serve as an advancement of our understanding of masking and response competition phenomenon as they pertain to complex tactile learning. Extrapolation of the information derived from the results can be a catalyst to further studies regarding the tactile nature of human-technology interfaces. Particularly, the results can serve as a conduit to the future exploration of tactile knowledge transfer to sensory impaired populations. Challenged populations, whose lives may be positively influenced by our advances in understanding their potential abilities, and not simply their disabilities.

References

- Cheron, G., & Borenstein, S. (1991). Gating of the early components of the frontal and parietal somatosensory evoked potentials in different sensory-motor interference modalities. *Electroencephalography & Clinical Neurophysiology*, 80, 522-530.
- Craig, J.C. (1995). Vibrotactile masking: the role of response competition. *Perception & Psychophysics*, *57*, 1190-1200.
- Craig, J.C. (2000). Vibratory temporal integration as a function of pattern discriminability. *Perception & Psychophysics*, 62, 596-606.
- Craig, J.C. & Evans, P.M. (1995). Tactile selective attention and temporal masking.

 *Perception & Psychophyics, 57, 511-518.
- Foulke, E., & Broadbeck, A.A. (1968). Transmission of Morse code by electrocutaneous stimulation. *The Psychological Record*, *18*, 617-622.
- Gandevia, S.C., Burke, P., & McKean, B. (1983). Convergence in the somatosensory pathway between cutaneous afferents from index and middle finger in man. *Experimental Brain Research*, 50, 415 – 425.
- Gescheider, G.A., & Wright, J.H. (2012). Learning in tactile channels. *Journal of Experimental Psychology: Human Perception & Performance*, 38, 302-313.
- Hoffken, O., Veit, M., Knossalla, F., Lissek, S., Bliem, B., Ragert, P., Dinse, H.R., Tegenthoff, M. (2007). Sustained increase of somatosensory cortex excitability by tactile coactivation studied by paired median nerve stimulation in humans correlates with perceptual gain. *Journal of Physiology*, 584, 463-471.

- Jones, S.J., & Power, C. (1984). Scalp topography of human SEPs: the effect of interfering tactile stimuli applied to the hand. *Electroencephalography & Clinical Neurophysiology*, 58, 25 36.
- Jones, S.J., Halonen, J.P., Shawkat, F. (1989). Centrifugal and centripetal mechanisms involved in the "gating" of cortical SEPs during movement.

 Electroencephalography & Clinical Neurophysiology, 4, 36–45.
- Marks, P.W., & Zukerberg, L.R. (2004). Case records of the Massachusetts General Hospital. Weekly clinicopathological exercises. Case 30-2004. A 37-year-old women with paresthesias of the arms and legs. *New England Journal of Medicine*, 351, 1333-1341.
- Molinari, M., Restuccia, D., & Leggio, M.G. (2009). State estimation, response prediction, and cerebellar sensory processing for behavioural control. *Cerebellum*, 8, 399-402.
- Rossi, S., della Volpe, R., Ginanneschi, F., Ulivelli, M., Bartalini, S., Spidalieri, R., Rossi, A. (2003). Early somatosensory processing during tonic muscle pain in humans: relation to loss of proprioception and motor 'defensive' strategies.

 *Clinical Neurophysiology, 114, 1351-1358.
- Rossini, M., Babiloni, C., Babiloni, F., Ambrosini, A., Onorati, P., Carducci, F., Urbano, A. (1999). "Gating" of human short-latency somatosensory evoked cortical responses during execution of movement. A high resolution electroencephalography study. *Brain Research*, 843, 161-170.
- Tang, K., Staines, W.R., Black, S.E., & McIlroy, W.E. (2009). Novel vibrotactile

- discrimination task for investigating the neural correlates of short-term learning with fMRI. *Journal of Neuroscience Methods*, 178, 65-74.
- Verrillo, R.T. (1983). Vibrotactile subjective magnitude as a function of hand preference. *Neuropsychologica*, 21, 383-395.
- Verrillo, R.T. (1985). Psychophysics of vibrotactile stimulation. *Journal of the Acoustical Society of America*, 77, 225-232.
- Verrillo, R.T., & Gescheider, G.A. (1976). Effect of double ipsilateral stimulation on vibrotactile sensation magnitude. *Sensory Processes*, *1*, 127-137.