# INVESTIGATING TACTILE SUPPRESSION DURING GOAL-DIRECTED MOVEMENT

by

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# Abstract

When we move our ability to detect tactile events on the moving limb is reduced. This process, known as movement-related tactile suppression, prevents unimportant sensory information from bombarding our central nervous system. This thesis aimed to extend the tenets of movement-related suppression during goal-directed reaching and explore any modulation of this suppression according to task-relevance. In three experiments participants performed volitional self-driven (Experiment 1, 3) and motor-driven (Experiment 1, 2) reaching and grasping movements. Over the course of the movement, weak electrical stimulation was presented at task-relevant (i.e., index finger and thumb) and task-irrelevant sites on the moving limb. In Experiment 1, participants displayed reduced detectability during movement of a readily detectable tactile stimulus (90% resting detection). This was true for all locations on the moving limb irrespective of task-relevance and during both self and motor-driven movements. In Experiment 2 and 3 a range of stimulus amplitudes was presented to one task relevant location during both self and motor-driven movements (Experiment 2) and to a task relevant and irrelevant site during self-driven movements (Experiment 3). This slight change in methodology allowed us to get a direct estimate of perceptual thresholds and asses the magnitude of movement-related tactile suppression. During both self and motor-driven movement participants exhibited an increased perceptual threshold at the index finger (Experiment 2). The magnitude of suppression however, was greater at the forearm than at the index finger (Experiment 3). Collectively these experiments suggest that tactile suppression is a general consequence of movement. Although evident at all locations on the moving limb, we suggest that tactile suppression can be modulated in a relevance-dependent manner.

## Lay Summary

When we move a touch on the moving limb feels weaker than it actually is. This is a useful process in order to prevent irrelevant sensory information from reaching the brain. In three experiments, participants needed a stronger touch stimulus in order to feel the sensation of touch on the moving limb. This was true even at the index finger, where touch information is important in order to grasp an object. Although the stimulus had to be marginally stronger at the index finger (~12%), it had to be much stronger at the forearm in order to feel any sensation (upwards of 100%). This thesis suggests that our sensitivity to touch can be tuned in a way that meets the requirements of the task.

# Preface

Dr. Romeo Chua, Dr. Timothy Inglis and myself conceptualized the experiments of this thesis, with later contributions and development from Dr. Ian Franks. The study was approved by the University of British Columbia's Research Ethics Board [certificate H17-00132]. Dr. Romeo Chua programmed the software used during data collection and analysis. Dr. Ryan Peters also provided a psychophysics program as part of Experiment 1. I completed data collection for all three experiments. Any data analysis was done with the assistance of Dr. Romeo Chua.

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# List of Abbreviations

CNS: Central Nervous System

EMG: Electromyography

SEP: Somatosensory Evoked Potentials

MLE: Maximum Likelihood Estimation

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# Chapter 1: Introduction

When interacting and navigating everyday life, humans are presented with a multitude of sensory information from various sources. How we are able to interpret and use vast amounts of sensory information is therefore a longstanding question. Given that the environment we live in is a dynamic one in which humans are constantly interacting, investigating the use of sensory information during movement is particularly important. Models proposed about sensory processing suggest that in order to perceive the external environment, all of this information must be combined and integrated in a meaningful fashion (Ernst & Bülthoff, 2004). Moreover, our central nervous system (CNS) can reduce the amount of sensory information flooding into our sensory system by gating or downregulating less important sensory events (i.e., sensory suppression; Williams, Shenasa & Chapman, 1998; Williams & Chapman, 2000; Williams & Chapman, 2002). These ongoing processes represent a flexible motor and sensory system that allows us to continuously interact with the environment with relative ease. Consider for example washing the dishes. When performing this task, we are holding a dish that is lathered in soapy water and decreased friction exists between our fingertips and the dish compared to holding the dish when dry. In order to maintain our grip and avoid a mess, it would be advantageous for our CNS to facilitate processing of touch information from the soapy dish to the fingertips and downregulate or ignore tactile information not relevant to the task.

This thesis will focus on the up and downregulation of sensory information during goal-directed movement. Specifically, the presence or absence of tactile gating (Williams & Chapman, 2002), in which humans display a reduced ability to detect tactile stimulations on the skin before and during active or passive movement, will be explored. Although this topic has been given much attention in the existing literature, this thesis will take into account the relevance of tactile information at different sites on the moving limb while introducing a motor-driven movement condition.

## 1.1 Overview of Thesis

The overall goal of this thesis is to investigate whether tactile gating is modulated according to task relevance during goal-directed movement. What follows is a review of the literature pertaining to the uptake and integration of multiple sensory cues during action, sensory gating at both the neurophysiological and behavioural level, and the contributions of peripheral and central mechanisms to these processes. Following the literature review, three experiments will be presented. In these experiments, participants will perform goal-directed self-driven or motor-driven reaching and grasping movements. In Experiment 1, prior to, or during movement, participants received an innocuous electrical stimulation to the thumb, index finger or forearm. In this experiment, the electrical stimulation was readily detectable at rest. In Experiment 2, a wide range of electrical stimulation amplitudes were presented only at the index finger in both movement conditions. In Experiment 3, a wide range of electrical stimulation amplitudes were again presented at the index finger and forearm in only the self-driven movement condition. Where Experiment 1 and 3 investigated the presence of tactile gating at different locations on the moving and stationary limb, Experiment 2 investigated the magnitude of tactile gating at one task-relevant site on the moving limb.

# Chapter 2: Multisensory Integration and Sensory Gating

## 2.1 Multisensory Integration

In our daily interactions, our sensory receptors are rarely presented with information from one sensory modality in isolation. In turn, multiple sensory estimates are available to us in order to judge the properties of the environment. How our CNS is able to gather sensory information (from multiple modalities) and transform it into a coherent percept is thus widely investigated. One model put forward to address this question is the Maximum Likelihood Estimation (MLE) model (Ernst & Bülthoff, 2004). According to this model, the CNS integrates sensory signals in a statistically optimal fashion such that the most reliable estimate of the multisensory signal is perceived (Ernst & Banks, 2002; Ernst & Bülthoff, 2004; Sabes, 2011). The weight given to each sensory modality corresponds to the reliability of the sensory cues in which higher weight is given to more reliable cues during the integration process. Taking a weighted average of the sensory signals allows for the combination of multiple modalities in which ambiguity and variance is reduced. Further, this model has been given empirical support in which studies utilizing perceptual tasks have shown optimal or near optimal sensory integration (e.g., Ernst & Banks, 2002; Knill & Saunders, 2003).

In a seminal study conducted by Ernst and Banks (2002), participants performed an object size discrimination task using misaligned visual and haptic information (i.e., the visual size and the haptic or tactual size of the object differed). When no noise was added to the visual display (i.e., the reliability of the visual information was high) participants were biased toward the visual information when performing the object size discrimination task. When noise was added to visual display, however (i.e., the reliability of the visual information was reduced), the weighting changed from visual to haptic dominance or capture in which participants were biased toward the haptic information of the object size. This aligns with the well-documented visual dominance or visual capture literature when no noise is introduced into the visual system (e.g., McGurk & MacDonald, 1976; Rock & Victor, 1964). For example, the ventriloquist illusion posits that the location of speech is biased toward moving lips (from a dummy) as opposed to originating from the ventriloquist him or herself.

### 2.1.1 Multisensory Integration during Action

In line with the current thesis, as humans we are rarely stagnant with respect to our environment. During goal-directed movement, the uptake and continual use of sensory information is imperative to the successful completion of the task (Woodworth 1899; Elliott et al., 2010). To that end, the way in which we are able to integrate multiple sensory cues during purposeful action is of much importance. To understand the way in which sensory cues are weighted during goal-directed movement, behavioral studies have employed the use of multiple target modalities as well as the presentation of illusory percepts during movement (e.g., Cameron & López-Moliner, 2015; Sarlegna & Sainburg, 2007; Sober & Sabes, 2005; Tremblay & Nguyen, 2010).

The interaction between multiple modalities often gives rise to illusions (McGurk & MacDonald, 1976; Shams, Kamitani & Shimojo, 2000; Violentyev, Shimojo & Shams, 2005). For example, when presented with an incongruent number of visual flashes and auditory beeps, Shams et al. (2000) reported an audiovisual illusion. If participants were asked to indicate the number of perceived flashes, they were often biased by the incongruent number of auditory beeps. Specifically, if presented with one visual flash and two auditory beeps, participants reported perceiving two flashes (fission illusion). This was extended to include a fusion illusion in which the presentation of two visual flashes and one auditory beep resulted in the perception of one visual flash (Anderson, Tiippana & Sams, 2004). To test whether goal-directed action modulates the relative processing of visual and auditory information, Tremblay and Nguyen (2010) presented this audiovisual illusion during various stages of a pointing movement. The bias toward one modality over the other can provide information indicating what modality is weighted more heavily in that instance. The participant's primary task was to point to a target as quickly and accurately as possible, and as a secondary task, report how many flashes were presented during the movement. If the illusion was presented when the participant's limb was travelling around peak limb velocity (i.e., stimuli presented at 50 or 100 ms into movement), they were less susceptible to the fusion illusion (i.e., the perception of one flash when presented with two flashes and one beep) compared to if the illusion was presented when the limb was travelling at low limb velocities or not at all (i.e., stimuli presented at movement start or after peak velocity; Tremblay & Nguyen, 2010). In other words, participants were less biased by the auditory beeps when their limb was travelling at high velocities. The authors suggested that the visual signal gathered from the limb travelling at high velocities is stronger than when travelling at low velocities and thus visual information was upregulated in that instance. An alternative explanation to these results was that auditory information was downregulated or gated due to its irrelevance to the task at hand (see Chapter 2.2). Overall, this work suggests that the processing and contribution of multiple modalities to the formation of a coherent percept, and in this case visual and auditory information, can be modulated in real-time.

When interacting in daily life, we are constantly interacting with various types of environments and therefore performing movements to various types of targets. For example, these targets can range from mostly visual (i.e., a keyhole when trying to unlock a door) to mostly proprioceptive targets (i.e., one's mouth when trying to eat). That said, using multiple target modalities is another method in which the relative weighting of sensory information can be analyzed. Sober and Sabes (2005) and Sarlegna and Sainburg (2007) had participants point to either a visual (i.e., virtual target) or proprioceptive target (i.e., the fingertip of the opposite hand). These authors also manipulated the alignment of visual and proprioceptive information such that the visual representation and actual representation of the participant's fingertips were either aligned or misaligned by shifting visual feedback. In their study, Sober and Sabes (2005) showed that when pointing to a visual target, the shifted visual feedback had a significant effect on participants' pointing movements. In this case, participants relied on the shifted visual fingertip position rather than their actual fingertip position. When pointing to a proprioceptive target however, participants relied on their actual fingertip position and were less affected by the shifted visual feedback. Sarlegna and Sainburg (2007) extended this work displaying that proprioceptive information is used to plan movement distance to proprioceptive targets and visual information is used to plan movement distance to visual targets. More recently, Cameron and López-Moliner (2015) have suggested that online visual control processes are also affected by the target modality. To infer online visual control processes, the variability profile of a movement with vision was compared to the variability profile of a movement without vision (see Khan et al., 2006). If the ratio between the variabilities is relatively constant from movement start to movement end, visual processing is thought to occur offline (i.e., not during movement). If the ratio decreases as the movement progresses however, visual processing is thought to occur online (i.e., during movement). Participants made reaching movements with a stylus toward a visual, proprioceptive or both a visual and proprioceptive target while feedback of their cursor was either present or absent. When reaching toward a proprioceptive target, with or without the presence of the visual target, the variability ratio remained relatively constant from movement start to movement end. When reaching toward a visual target however, the variability ratio decreased as the movement progressed. These results suggest that when reaching to a proprioceptive target, the online visual processing of the reach was reduced compared to reaching to a visual target (Cameron & López-Moliner, 2015). Taken together, these studies suggest that our CNS is able to weight sensory signals differentially depending on the context of the task, a process integral to the successful completion of goal-directed movement.

Two explanations have been postulated to account for the aforementioned results. When performing a goal-directed movement, information from the arm position and information from the target position exist within multiple coordinate frames, in this case one visual and one proprioceptive (Sarlegna & Sainburg, 2007; Sober & Sabes, 2005). If the target is proprioceptive for example, gathering or relying on visual signals about the position of the arm would require a transformation from a visual to proprioceptive coordinate frame when comparing the arm position to the target position. This visual to proprioceptive transformation can subsequently increase the variance or noise in the system. To avoid this noise or variance, Sober and Sabes (2005) suggest that the CNS will avoid this transformation and plan the movement relying on the comparison of visual to visual or proprioceptive to proprioceptive coordinates. An alternative explanation, and not mutually exclusive from the preceding explanation, is that sensory signals are gated or downregulated in a task-dependent manner. In this case, proprioceptive information may be gated when reaching to a visual target, and vice versa, as it is less relevant to the task or to avoid the transformation of coordinate frames (Sarlegna & Sainburg, 2007; Sober & Sabes, 2005). Moving forward, the latter explanation (i.e., sensory gating) will be explored more in depth. Both neurophysiological and behavioural evidence of sensory gating during both non-goal-directed and goal-directed movement will be discussed.

## 2.2 Sensory Gating during Action

During movement it seems logical that the CNS is able to downregulate sensory information that is not pertinent to the task at hand. In turn, this may allow for the other more relevant sensory cues to be processed and used for the subsequent completion of the action (see Chapter 2.1). What follows is a discussion exploring the suppression of sensory information or sensory gating at the neurophysiological and behavioral level.

### 2.2.1 Neurophysiological Evidence for Sensory Gating

At the neurophysiological level, sensory gating has been investigated by recording electrical activity in the brain using electroencephalography (EEG). Specifically, somatosensory evoked potentials (SEP) have been used as a tool to assess the somatosensory system's functioning in a non-invasive manner (e.g., Cohen & Starr, 1987; Staines, Brooke & Mcllory, 2000; Staines, Graham, Black & Mcllory, 2002). This technique allows for the assessment of the transmission of afferent signals from the periphery to the somatosensory cortex. SEPs are measured following either brief mechanical impacts on the finger tips, using air puffs, or more commonly using electrical stimulation over a peripheral nerve (e.g., median nerve) while the amplitude of the potential corresponds to the intensity of the stimulus. Cohen and Starr (1987) recorded SEPs to median nerve stimulation at different times simultaneously and after an order to move effectors innervated by the median nerve (i.e., ipsilateral thumb, index finger and middle finger) and those not innervated by the median nerve of that forearm (i.e., ipsilateral little finger and contralateral thumb). Compared to the amplitude at rest, SEP amplitudes were reduced before the onset of electromyography (EMG), maximally reduced at the time EMG was maximal, and returned to control values when EMG activity had ceased. Further, the gating of SEPs was localized to movements innervated by the median nerve. Although this study investigated active movement, studies employing a passive upper limb movement protocol display a similar reduction in the amplitude of SEPs; however SEP suppression only occurred after passive movement onset (Jones, 1981; Rushton, Rothwell & Craggs, 1981).

In addition to active and passive movement, the relevance of the task also plays a significant role in the modulation of SEPs (Staines et al., 2000; Staines et al., 2002). Staines et al. (2000) evoked modality specific SEPs corresponding to proprioceptive (i.e., left tibial nerve stimulation at the popliteal fossa) and cutaneous afferents (i.e., left sural nerve stimulation posterior to the left lateral malleolus) during passive left foot movement. Additionally, cutaneous stimuli were applied to the dorsal side of the same foot during this movement. In a cutaneous task, participants were required to respond to the cutaneous stimuli by plantar flexing the right foot. In a position task, participants were required to respond to the movement trajectory of the left foot by matching it with their right foot. Both of these tasks, along with a no-response condition, were compared to a baseline rest condition. For the left tibial nerve, SEP amplitude was reduced in the passive movement and cutaneous task compared to rest levels. The amplitude in the position task was not different compared to rest levels and elevated in comparison to the passive movement and cutaneous task. In this case, SEP amplitude was not reduced as proprioceptive information was relevant to the position task.  For the left sural nerve, SEP amplitude was again reduced in the passive movement but was also reduced in the position task in comparison to rest levels. Further, the amplitude in the cutaneous task was elevated in comparison to the passive movement and position task. In this case, SEP amplitude was not reduced as cutaneous information was relevant to the cutaneous task. Taken together, these results suggest that the gating of SEP amplitude may be dependent on the relevance of the sensory input. In turn, sensory information that is irrelevant to task performance is suppressed while information relevant to the task may be facilitated.

Staines et al. (2002) extended this work by employing functional magnetic resonance imaging (fMRI) to investigate the brain areas contributing to the modulation of the SEPs according to task relevance. In Experiment 1, fMRI was recorded during unilateral vibrotactile stimulation to the left or right index finger in separate 20 second blocks. During these blocks, the frequency of the stimulation randomly changed and the participants were required to keep track of the number of changes. Thus, when presented with stimulation to either finger alone, task-relevant modulation would be represented by activity in the contralateral S1. In line with and expanding on previous work, vibrotactile stimulation enhanced blood oxygenation level-dependent (BOLD) responses in the contralateral primary somatosensory cortex (S1) and decreased the response in the ipsilateral S1. In Experiment 2, vibrotactile stimulation was presented to either the right index finger alone (unilateral) or simultaneously with the left index finger (bilateral). In half of the conditions, participants were required to keep track of frequency changes (i.e., stimuli were task-relevant) while the other half of the conditions participants were instructed to simply relax during stimulation (i.e., passive conditions). A region of interest (ROI) analysis revealed that the volume of activation increased in the right prefrontal cortex when comparing the task-relevant and passive conditions. During unilateral task-relevant stimulation to the right index finger, this corresponded to the ipsilateral side. During the bilateral stimulation condition, in which task-relevant stimulation was given to the right index finger and irrelevant stimulation was given to the left, this again corresponded to the ipsilateral side of the relevant stimulation and contralateral side to the irrelevant stimulation. In turn, these findings are consistent with a role for the prefrontal cortex in the regulation of sensory inputs at the S1 level (e.g., Knight, Scabini & Woods, 1989; Yamaguchi & Knight, 1990). For example, individuals with prefrontal cortex damage showed an impaired gating of task-irrelevant auditory or somatosensory input evidenced by an increased amplitude of middle-latency auditory evoked potentials (Knight, Scabini & Woods, 1989) and SEPs (Yamaguchi & Knight, 1990) compared to healthy controls. In line with patient data, Brown et al. (2015) reduced the excitability of the prefrontal cortex before and after recording SEPs to relevant and irrelevant stimuli. This was done using continuous theta burst stimulation (cTBS), a type of repetitive transcranial magnetic stimulation (TMS), which transiently reduces excitability in a localized cortical area (Huang et al., 2005). Consistent with previous literature, SEP amplitudes were modulated according to task-relevance. After applying cTBS however, the difference in SEP amplitudes between irrelevant or relevant stimuli was abolished and movement-related gating levels were reduced (Brown et al., 2015).

### 2.2.2 Behavioural Evidence for Sensory Gating

More relevant to the current thesis, sensory gating has also been explored at the behavioral level. Several perceptual studies during both non-goal-directed and goal-directed action will be explored. Specifically, much of the literature that will be discussed employs the perception of innocuous *tactile* stimuli and will thus be the focus of the thesis moving forward. Tactile gating as opposed to the more general sensory gating will be discussed.

#### 2.2.2.1 Tactile Gating during Non-Goal-Directed Action

At the behavioral level, studies have been conducted in which the perception of an innocuous tactile stimulus is the main dependent measure. In this section, the perception of these tactile stimuli will be discussed within the parameters of non-goal-directed movement or movement in which tactile information is not relevant to the task. Chapman et al. (1987) investigated the ability to perceive innocuous electrical stimuli in the presence and absence of active or passive elbow flexion and extension movements. The movements were either conducted with the same arm being stimulated or the contralateral arm (i.e., no stimulation on the movement arm). The authors noted that detection thresholds increased during active or passive movement as compared to the absence of movement in the ipsilateral arm. No such difference arose however, when moving the left arm while the subject was required to detect stimuli on the right arm. Thus, both central (i.e., active movement) and peripheral (i.e., passive movement) processes were thought to contribute to the diminished ability to detect weak stimuli during movement and the apparent gating was restricted to movement of the stimulated arm (Chapman et al., 1987). Moreover, this early behavioral work aligns well with the previously discussed neurophysiological work (see Chapter 2.2.1) in which SEP amplitude is reduced during active or passive movement (Cohen & Starr, 1987; Jones, 1981; Rushton, Rothwell & Craggs, 1981).

Tactile gating has since received much attention and has been explored in relation to stimulus location (Williams, Shenasa & Chapman, 1998), stimulus intensity (Williams & Chapman, 2000) and motor task (Williams & Chapman, 2002). In the aforementioned studies, participants performed rapid index finger abduction movements (Williams, Shenasa & Chapman, 1998; Williams & Chapman, 2000) or slight variations of the task (Williams & Chapman, 2002). Similar to Chapman et al. (1987), before or during these movements participants were presented with weak electrical stimuli and the ability to detect these stimuli was the main dependent measure (90% detectable at rest). Williams, Shenasa and Chapman (1998) presented these stimuli at several locations on the moving and stationary limb, as well as the ipsilateral pectoral girdle and thigh. In line with previous work on SEPs, the decrease in detection ability was greatest and occurred the earliest at stimulus locations closest to a moving finger and was weakest and occurred the latest at more proximal locations (Williams, Shenasa & Chapman, 1998). Moreover, similar tactile gating patterns were observed before and during isotonic, isometric and passive finger abduction tasks (Williams & Chapman, 2002). Although the results from the isotonic and isometric task (i.e., the index finger was already maximally abducted) suggest that this sensory attenuation was central in origin, the results from the passive movements suggest otherwise. Not only was the tactile stimulus less detectible during the passive movement, the peak decrease in detection of the tactile stimulus *preceded* the movement by an average of 38 ms (Williams & Chapman, 2002). To test whether the expectation to move (or be moved) could account for this decrease before the onset of passive movement, sham trials were introduced. These trials were integrated randomly on 20% of trials in the passive movement condition. On a given sham trial, subjects expected to be moved, but did not receive the passive movement. Detection rates during sham trials did not differ from rest trials at any of the stimulation times. The expectation of movement was therefore not a viable explanation for the aforementioned results.

Central and peripheral or postdictive (i.e., backward masking) mechanisms have been brought forth as possible explanations. The central influences on this attenuation are thought to occur due to downward projections onto the dorsal column lemniscal pathway originating from the primary motor and somatosensory cortex (Chapman et al., 1988; Chapman & Beauchamp, 2006). During active movement in monkeys, evoked responses along the dorsal column-medial lemniscal pathway to peripheral stimulation were depressed prior to and during movement (Chapman et al., 1988). Further, activation of the motor cortex in monkeys decreased the amplitude of SEPs (Jiang et al., 1990). In terms of the postdictive mechanism, Williams and Chapman (2002) suggested that backward masking, in which the detection of a weak test stimulus is prevented by a near-simultaneous administration of a stronger masking stimulus, could account for the reduction of detection preceding the movement, whether it be active or passive (Geschieder, Bolanowski & Verrillo, 1989). In the context of the task, the movement-related afferent information generated by active or passive movement masks the detection of the electrical stimulation. The contribution of central (i.e., predictive) and peripheral (i.e., postdictive) processes to the apparent sensory attenuation during movement thus remains a matter of debate.

Research supporting an integral role for a central command brings forth evidence of sensorimotor attenuation in the absence of movement (Voss, Ingram, Wolpert & Haggard, 2008; Voss, Ingram, Haggard & Wolpert, 2006). Using TMS, Voss et al. (2006) delayed the output of motor commands during voluntary movement such that a motor command was prepared but the dispatch to the periphery was delayed. Electrical cutaneous stimuli were given at rest, at the onset of movement (i.e., finger lift) and during the above described post-TMS delay period (i.e., after preparation but before movement) to the right and left index finger. The left index finger remained stationary throughout the experiment for comparative purposes. Using point of subjective equality (PSE) between the two fingers as the main dependent measure, electrical cutaneous stimulation in the movement and post-TMS delay condition had to be more than two times larger to be perceived as being of the same intensity as the stimulation to a resting finger (Voss et al., 2006). This indicates a strong sensory suppression in both conditions and a significant role for central signals related to the preparation of motor commands. Thus, it can be argued that the movement-related afferent information is not integral to exhibit tactile gating during movement.

An expectation-based mechanism has also been suggested to account for sensory attenuation during movement. In two experiments, Voss et al. (2008) delivered probe stimuli to the right index finger before a cue instructing subjects to complete either a left or right finger lift. In Experiment 1, the cue to move the left or right finger was equiprobable and random. Therefore, it was unlikely that participants could prepare a movement for the left or right finger prior to the cue to move. In turn, there was an attenuation of the signal to the right finger just before the right finger moved but no such attenuation when the left finger moved. Postdictive mechanisms likely account for these results. That said, a motor command was unlikely to contribute to the attenuation as this occurred prior to the cue to move. Further, the preparation to move was unlikely to contribute as the left or right cue were random and equiprobable and thus preparation for either left or right finger movement was not expected. In Experiment 2, the cue indicating the right finger to move was four times more probable then the cue indicating the left finger to move (i.e., the right finger was cued 80% of the time). Thus, this created a situation in which participants prepared to move the right finger as it was more likely to be cued to move. Reaction times to right cues were significantly shorter than reaction times to left cues. This finding was used as a confirmation that participants were preparing a right finger movement in advance. In this case, there was an attenuation of the signal when the right finger was cued to move but also when the left finger was cued to move. These authors suggested that the sensory system regulates sensory information based on expectations about future actions, irrespective of whether or not they are implemented.

Taken together, these studies (i.e., Voss et al., 2006 & Voss et al., 2008; Experiment 2) provide evidence that a higher, preparatory level of the motor system can account for sensory attenuation prior to movement (or lack thereof). Although this provides robust evidence for a central mechanism, the aforementioned studies are limited to single-joint movements that are non-goal-directed. Furthermore, there is no reason to believe that tactile information was particularly relevant to the employed task (i.e., finger lift).

#### 2.2.2.2 Tactile Gating during Goal-Directed Action

As humans we do not often engage in only non-goal-directed movements. The work reviewed in the previous section also only considered movements involving one joint (i.e., finger lift, finger abduction, etc.). This section will examine research in which participants are engaged in multi-joint, goal-directed movements. Thus, this recent work complements and extends the existing literature and in conjunction creates a more complete picture of the phenomenon of tactile suppression or gating. That said, tactile gating during multi-joint, goal-directed movement will be discussed with a specific emphasis on the role of central and peripheral processes as well as the relevance of the task.

Buckingham et al. (2009) sought to examine whether tactile gating is prevalent in a more complex task. Specifically, the authors extended the tactile gating literature by employing a similarly used tactile perception paradigm during visually-guided bimanual pointing movements.

Participants performed bimanual pointing movements to visual targets while a vibrotactile stimulus was presented to one of their fingertips before and during movement. Once movement ended, participants were required to indicate which finger was vibrated and their percentage of correct responses was used as a measure of tactile gating. The authors found that the percentage of correct responses, and therefore sensitivity to the vibrotactile stimulus, decreased before both movement onset and muscle activity. Further, the apparent tactile gating prevailed up to 150 ms after movement onset (i.e., the latest presentation time of the stimulus). Although tactile information may be more relevant to this task than the previously reported single-joint movements, the authors suggested that visual information may have been upregulated, and tactile information downregulated, due to the nature of the task/target (see Chapter 2.1 for review).

More recent and pertinent to the current proposal, Colino et al. (2014) and Colino and Binsted (2016) investigated tactile suppression across multiple locations of a moving limb during a task in which tactile feedback is important for successful completion (i.e., reach, grasp and lift). This task allowed for the investigation of sensory suppression at task relevant and irrelevant locations on the moving limb. Probe stimuli were placed on the mid-forearm (i.e., task-irrelevant location), index finger (i.e., task-relevant location) and fifth digit of both the left and right limb, but participants only performed the task with the right limb. The underlying assumption in this experiment was that tactile information at the index finger was relevant to a reach, grasp and lift task (e.g., regulating grip force; Johansson & Flanagan, 2009) but tactile information at the forearm was much less relevant to the task. In Colino et al. (2014; Colino & Binsted 2016), the tactile stimulus consisted of a weak vibrotactile stimulation. Further, the intensity of the stimulation was the same for all stimulus locations. This possible limitation will be discussed in more detail at the end of this section. Although the tactile stimulus was readily detectable at all locations on the left limb (i.e., consistent with previous work using single-joint movement), the detection rate was decreased before the onset of and during movement in the right forearm. Interestingly, the detection rates did not decrease at the index finger of the right limb before or during movement.

These results indicate that tactile gating dynamics are affected in a contextually dependent manner in which tactile information is not attenuated at locations where this information is important for the successful completion of the task. Colino et al. (2014) suggest that during a simple single-joint movement (e.g., finger abduction, finger lift etc.) the CNS does not predict that tactile information will be necessary for the completion of the movement and is thus more likely to be attenuated. Moreover, irrelevant sensory events become attenuated when the sensory events do not convey novel information (i.e., from the forearm; Bays & Wolpert, 2007). When we send a motor command to move, a copy of this command, termed the efference copy (Von Holst & Mittelstaedt, 1954) or corollary discharge (Sperry, 1950), is sent to higher levels of the CNS and fed into a forward model (Bays & Wolpert, 2007). It has been proposed that forward models generate estimates of sensory consequences of the movement and cancel those afferent signals that match the predicted signals, thereby preferentially processing externally generated events or exafference (Bays & Wolpert, 2007). This model has received both behavioral (e.g., Blakemore, Wolpert & Frith, 1998) and neurophysiological support (e.g., Haggard & Whitford, 2004; Voss, Bays, Rothwell & Wolpert, 2007). In the context of a reaching and grasping task, Colino et al. (2014) suggest that tactile information from the index finger will not be attenuated because tactile signals provide novel and relevant information whereas information from the forearm is redundant and therefore canceled out.

Using the concept of a forward model to account for these results does have its limitations however. For example, external stimuli are presented to participants at all locations on the moving limb. If sensory prediction/confirmation based on forward models act to highlight externally-generated events or exafference, how would this explain the sensory attenuation of external stimuli on the moving limb? Haggard and Whitford (2004) suggest an alternative optimal information-processing strategy to explain the aforementioned results. This strategy suggests that sensory information is enhanced if it is related to the action goal but is suppressed if it is related to the movement (Haggard & Whitford, 2004). In the context of Colino et al.'s (2014) results, information from the index finger was related to the action goal and was therefore not attenuated but enhanced. Further, these authors suggest that the strength of sensory pathways may be adjusted prior to action which aligns well with the modulation of SEPs according to task relevance literature presented earlier (see Chapter 2.2.1; Staines, Brooke & Mcllory, 2000; Staines, Graham, Black & Mcllory, 2002).

To further address the constituents of tactile gating during a reaching and grasping task, Colino and Binsted (2016) expanded the time course during which a stimulus could be presented. The stimulus was presented before, during and after movement end. In line with previous findings, sensitivity to the tactile stimulus was reduced before and during movement at the right forearm but was minimally reduced at the index finger. Interestingly, tactile sensitivity and detection rate at the right forearm started to return to baseline levels prior to movement completion and returned to baseline levels at and following movement completion. These results align well with a similar reaching and grasping study in which tactile gating was exhibited during execution of the movement but returned to baseline levels following movement completion (Jurvale, Deubel, Tan & Spence, 2010). Colino and Binsted (2016) suggested that prior to and early in the movement, central commands may be responsible for the apparent tactile gating (see previous paragraph), but its influence subsides later in the movement. In turn, peripheral gating sources may play a role closer to movement end. Perhaps the speed at which the limb was moving contributed to the tactile sensitivity later in the movement. Looking at the kinematic data more carefully reveals that after peak limb velocity was reached, the tactile sensitivity was not significantly different from the first presentation epoch or after movement end. Indeed, Angel and Malenka (1982) and Rushton, Rothwell and Craggo (1981) reported that movement velocity is positively correlated with detection threshold and negatively correlated with SEP amplitude, respectively. Further, using a simple abduction movement, Cybulska-Klosowicz, Meftah, Raby, Lemieux and Chapman (2011) found a critical speed for tactile gating to occur. Specifically, the critical speed at which the detection rate was above 50% corresponded to when the limb travelled at velocities greater than 200 mm/s (Cybulska-Klosowicz et al., 2011). Collectively, this would suggest that movement-related afferent information is a less potent mask of external stimuli as the limb slows toward a target, corresponding to the end stages of the movement (Cybulska-Klosowicz et al., 2011).

There are potential limitations that can be identified in the recent work of Colino and Binsted (i.e., Colino et al., 2014; Colino & Binsted, 2016). One possible limitation in the methods for both studies was that the same intensity of stimulation (i.e., mechanical amplitude and frequency) was given at every site. The authors addressed this by conducting a control experiment in which the detection rate was not different between any of the sites using the chosen stimulation. This still leaves the possibility that the stimulation exceeded the perceptual threshold by different amounts at different sites. That said, tactile information may have well been gated at the index finger but did not fall below the perceptual threshold at that site. On the other hand, tactile information may have been gated to the same degree at the forearm but fell below the perceptual threshold resulting in the decrease in sensitivity and detection rate. A second limitation in both studies corresponds to the relevance of the task. For example, tactile sensitivity at the index finger remained high due to its relevance when grasping a tangible object. This implies that if reaching without target contact, in which tactile information is not relevant to the goal of the movement, tactile sensitivity at the index finger should be reduced similar to other locations on the moving limb. Because a condition such as this was not included in this work, potential confounds (see previous limitation) may account for their results. A third limitation is specific to the latter study. Although Colino and Binsted's (2016) results indicate a possible role for both central and peripheral processes early and late in the movement, respectively, the methods by which they make these inferences were quite limited. For example, both a central command, and therefore efferent information, and movement-produced afferent information are involved when performing a reach to grasp movement. In turn, it is difficult to comment on the relative contribution of one process over the other throughout the time course of the task. The first and third aforementioned limitations will be addressed in the current thesis, specifically Experiment 1.

### 2.2.3 Experimental Aims and Rationale

The aim of this thesis was to investigate whether tactile suppression is modulated according to relevance of the stimulation site to the task. A secondary aim of this thesis was to further investigate central and peripheral contributions to tactile suppression. Here, participants performed both self-driven and motor-driven targeted movements. This addition of a motor-driven movement allowed us to investigate the role of movement-related afferent information in the absence of a central motor command to transport the reaching limb. Similar to recent studies (Colino et al., 2014 & 2016), tactile stimulation will be given to either task-relevant or task-irrelevant locations on the moving limb. Experiment 1 specifically investigated the presence of tactile suppression during movement. Experiments 2 and 3 examined the potential modulation of the magnitude of suppression. The related but slightly different experimental designs in these experiments were directed at helping us further understand tactile suppression in the context of goal-directed movement.

# Chapter 3: Experiment 1

## 3.1 Methods

### 3.1.1 Participants

Twenty-one right-hand dominant participants (9 female, 12 male; *M* = 26 years, *SD* = 3) with self-reported normal or corrected-to-normal vision were recruited from the University of British Columbia community. Participants had no history of neurological impairment. The total duration of the experiment was between 120-150 minutes. All participants gave informed consent prior to participating with the protocol approved by the UBC ethics board.

### 3.1.2 Apparatus

Participants were seated at a table with a wooden dowel target (Height: 24 cm, Diameter: 3cm) located 30 cm away, aligned with the participant's midline (see *Figure 3.1*). Throughout the entire experiment, the participant's right upper limb was placed in a custom-built linear slide. This allowed for smooth, relatively low friction movements along the track during both the self and motor-driven movement conditions. During the motor-driven movements, the carriage was attached to a close-looped belt driven by a computer-controlled stepper motor. Participants began each movement with the carriage resting against a micro-switch that also defined the home position. Movement onset was determined as the time at which the carriage moved away from the micro-switch. Movement end was determined as the sample at which the carriage dropped below 50 mm/s. Four surface electrodes were taped to the dorsal and palmar surface of the right thumb, right and left index finger and the ventral surface of the mid-forearm on all participants, in all conditions and thus posed as the tactile stimulus sites. The thumb and index finger of the right limb acted as the task-relevant locations and the forearm acted as the task-irrelevant location. This was based on the assumption that tactile information during a reach and grasp task is more meaningful from the digits directly involved in the grasp (Colino et al., 2014; Colino & Binsted, 2016). The left index finger was included for comparative purposes. The intensity of the stimulation was determined using a Bayesian adaptive procedure for each participant (see procedure for details). The stimulus was a 2 ms constant current pulse, generated by a 2 ms square wave voltage waveform (using a National Instruments NI USB-6002 16 bit DAQ unit) connected to an isolated constant current unit (either the AM Systems 2200 constant current stimulator, or the Digitimer DS5 constant current stimulator).  The current intensity was adjusted by varying the amplitude of the square wave voltage pulse. This was done for each participant in order to determine the intensity or level of current at which the tactile stimulus was perceived approximately 90% of the time at rest. This was used to determine the threshold at every stimulation site separately. This detection rate was chosen consistent with detection rates at rest used in previous research (Williams, Shenasa & Chapman, 1998; Williams & Chapman, 2000; Williams & Chapman, 2002).

Surface EMG across the right anterior part of the deltoid and pectoralis major were recorded for the duration of the experiment. Surface EMG was amplified (x10K) and bandpass filtered between 30 and 1000 Hz (Grass Instruments P55). This EMG signal was further bandpass filtered between 30 and 249 Hz before rectifying the signal. Once rectified, the signal was lowpass filtered using a 40 Hz cutoff frequency. EMG onset was determined as the time in which the EMG signal was 3 standard deviations above baseline. For both surface EMG and all stimulation sites, the skin was prepared using an abrasive pad over the skin area and alcohol swabs before placing the electrodes.

One infra-red light emitting diode (IRED) taped to the linear slide was used to track limb position. The IRED was sampled at 500 Hz for up to 2 seconds (Optotrak 3020, Northern Digital

Inc., Waterloo, ON, Canada). The recording window was initiated approximately 500 ms before the GO signal. A custom-written Matlab (The MathWorks, Inc.) script was used to control the Optotrak. A data acquisition board (BNC-2090, National Instruments Inc., Austin, TX, USA) was used to generate analog signals for the GO tone (piezoelectric buzzer; 50 ms tone) and mark movement onset. This allowed us to measure any relevant movement performance measures such as reaction time and movement time. These analog signals, along with the EMG signal, were recorded with the Optotrak Data Acquisition Unit (ODAU) and were sampled at 500 Hz.

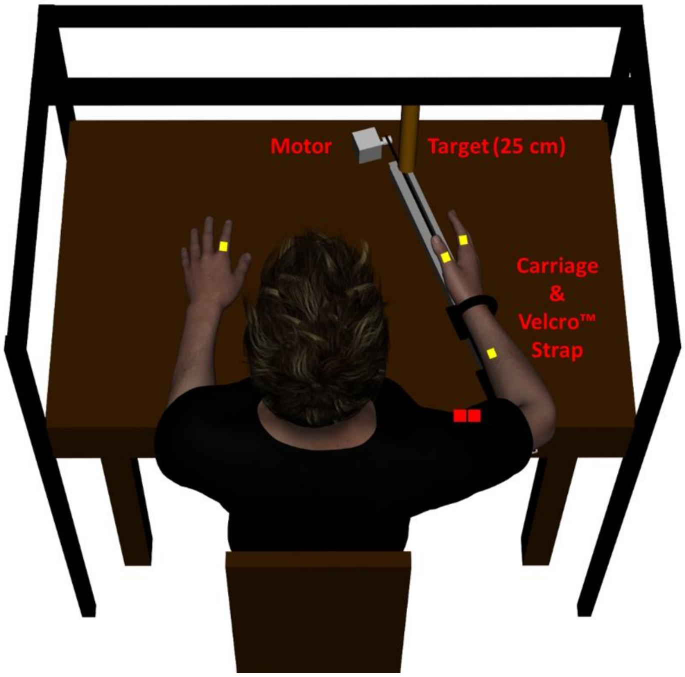

**Figure 3.1. Depiction of the tactile stimulus locations on the thumb, index finger and forearm of the right movement limb and the index finger on the left stationary limb as well as a depiction of the experimental setup. The stimulus electrodes are in yellow. Note that the electrodes were on the palmar surface of all locations. Also shown is the EMG recording site in red. Specifically this was across the anterior deltoid and pectoralis major.**

### 3.1.3 Procedures

After participants gave informed consent and the surface electrodes were attached, participants performed a Bayesian adaptive procedure. The Bayesian adaptive procedure allowed us to obtain separate psychometric curves for each stimulation site for each participant (see Peters & Goldreich, 2013). During this procedure, participants received a stimulus randomly at one of the four sites at rest. The task was then to dictate whether or not a stimulus was felt and, if so, where. Forty trials of varying intensities per site along with 16 catch trials (total trials = 176) were used to obtain separate psychometric curves.  The algorithm set in the Bayesian adaptive procedure derived an estimate of the stimulus intensity at which the participant could feel the stimulus 90% of the time. In addition, a Guessing Bayes Factor (GBF) was used as a qualification criteria for the remainder of the experiment. GBF allowed us to assess concentration levels of the participants by assessing the probability of whether their performance resulted from guessing on each trial compared to the probability that their performance could be described by a normal psychometric function (see Peters & Goldreich, 2013; Appendix A). Consistent with Peters and Goldreich (2013), we used a GBF threshold of 0.1. This value allowed us to be 10 times as confident that a participant was concentrating as opposed to randomly guessing whether they felt a stimulus. If a participant achieved a higher value at any of the four sites, the participant was dismissed from the remainder of the experiment. Nine participants achieved a threshold above 0.1 at one or more sites and therefore were excluded from the remainder of the experiment and analysis. This resulted in a total of 12 participants (3 female, 9 male; *M* = 26 years, *SD* = 3) that were included in the final analysis (see Data Analysis for details).

Once the stimulus intensity was determined, the experimental trials began. The experiment consisted of two variations of reaching and grasping movements performed with the right limb. The left limb remained stationary for the duration of the experiment. In the *self-driven* condition, the participants completed targeted reaching and grasping movements. In this condition, participants reacted to an auditory GO signal in order to initiate their movement. In the *motor-driven* condition, the participant's limb was externally guided by the motor-driven linear carriage throughout the reaching portion of the movement. In this condition, the experimenter initiated the stepper motor after the GO signal, which in turn moved the carriage on which the participant's arm was rested. The motor-driven movement was intended to simulate the kinematic characteristics of the self-driven reaching movement. Although the flight phase of the movement was driven externally, the grasping component of the two movement conditions was the same (see below).

All participants performed both conditions in a repeated-measures design. Participants performed each movement condition in a blocked fashion and the blocks were counterbalanced between participants.

Participants were instructed to perform reach to grasp movements within a 600 to 800 ms movement time bandwidth. Participants were also instructed to adopt a precision grip hand posture with their grip aperture the width of the perceived size of the target. The average movement time in the motor-driven movement condition was 718 ms (see Results for further analysis). The tactile stimulus was presented to either the thumb, index finger or forearm of the right limb or index finger of the left limb during movement preparation and before movement onset (aligned with GO signal onset); at movement onset; during movement execution (100 ms after movement onset); or after movement completion (850 ms after movement onset) in a randomized order. Participants were instructed to hold onto the target following movement completion. That said, although the movement had ended in the final presentation time, participants were still engaged in the grasping task. These stimulation times were chosen consistent with Colino and Binsted (2016). Catch trials were also included in which no stimulus was presented at all in order to calculate false alarm rates (Geschieder, 1997). Upon completion of the movement, the participants indicated whether or not a tactile stimulus was felt, and if so, at what location. Participants performed 10 trials for each stimulation time at each stimulus location and for each movement condition (320 trials). Additionally, 1 catch trial for each stimulation time at each stimulus location and for each movement condition was performed (32 trials). Thus, each participant performed 352 detection judgments altogether (see *Table 3.1*). Nine of the participants (2 female, 7 male; *M* = 26 years, *SD* = 3) also completed 44 control trials at the end of the experiment. During these trials participants were at rest and were presented with a stimulus randomly to the four sites between 100-500 ms after the auditory GO signal. In this case, 10 trials per site in addition to 4 catch trials were used. This control condition was used to reconfirm that the stimulus intensities used were indeed detected at least 90% of the time at rest.

To infer tactile gating, detection rate was used as the main dependent measure. False alarm rates (i.e., from catch trials) were also monitored in order to get an idea of the participant's ability to distinguish between a tactile stimulation and no stimulation at all. Additional variables including reaction time (RT), movement time (MT), and relative EMG onset were also monitored.

| **Stimulus Location** | **Left Index** | | | | **Right Index** | | | | **Right Thumb** | | | | **Right Forearm** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Stimulation Time (ms)** | **GO** | **0** | **100** | **Post** | **GO** | **0** | **100** | **Post** | **GO** | **0** | **100** | **Post** | **GO** | **0** | **100** | **Post** |
| **# of Stimulation Trials** | **10** | **10** | **10** | **10** | **10** | **10** | **10** | **10** | **10** | **10** | **10** | **10** | **10** | **10** | **10** | **10** |
| **# of Catch Trials** | **1** | **1** | **1** | **1** | **1** | **1** | **1** | **1** | **1** | **1** | **1** | **1** | **1** | **1** | **1** | **1** |
| **Total** | **44** | | | | **44** | | | | **44** | | | | **44** | | | |
| **Grand Total** | **176** | | | | | | | | | | | | | | | |

**Table 3.1.** Trial breakdown. Note that this showcases the trial breakdown for each movement condition. Therefore, only one-third of the trials are shown (total: 528 trials). GO indicates that the stimulus was presented simultaneously with the GO signal. Post indicates that the stimulus is presented after movement end.

### 3.1.4 Data Analysis

#### 3.1.4.1 Site Sensitivity Data

The stimulus amplitude (at which participants could feel the stimulus 90% of the time at rest) was submitted to a 4 Stimulus Location (ipsilateral thumb, ipsilateral index finger, ipsilateral forearm and contralateral index finger) one-way ANOVA.

#### 3.1.4.2 Detection Data

Detection rate was submitted to a 2 Condition (self-driven and motor-driven) by 4 Stimulus Location (ipsilateral thumb, ipsilateral index finger, ipsilateral forearm and contralateral index finger) by 4 Stimulation Time (pre-movement, movement onset, movement execution and post-movement) repeated-measures ANOVA. False alarm rates were submitted to a 2 Condition (self-driven and motor-driven) one-way ANOVA. Before analyzing any of the aforementioned data, the detection and false alarm rates were arcsine transformed. For all figures, non-transformed values are reported. As an additional analysis the post-experiment control trials (i.e., no movement), detection rate was submitted to a 4 Stimulus Location (ipsilateral thumb, ipsilateral index finger, ipsilateral forearm and contralateral index finger) one-way ANOVA.

#### 3.1.4.3 Movement-Related Measures

For reaction time and movement time, the data from active self-driven movement trials were submitted to a 4 Stimulus Location (ipsilateral thumb, ipsilateral index finger, ipsilateral forearm and contralateral index finger) by 4 Stimulation Time (pre-movement, movement onset, movement execution and post-movement) repeated-measures ANOVA. The motor-driven movement condition was not included in this analysis as the reaction was a product of the experimenter and the motor drove the movement. Relative EMG onset was submitted to a 2

Condition (self-driven and motor-driven) by 4 Stimulus Location (ipsilateral thumb, ipsilateral index finger, ipsilateral forearm and contralateral index finger) by 4 Stimulation Time (pre-movement, movement onset, movement execution and post-movement) repeated-measures ANOVA. This was used primarily to confirm that participants did not initiate their movement in the motor-driven condition.

For all analyses, a Huynh-Feldt correction was used to correct the degrees of freedom when sphericity was violated. For all effects and interactions uncorrected degrees of freedom are reported. When significance was reached, post-hoc comparisons were made using simple main effect analysis and simple t-tests where appropriate. For all tests alpha was set at $p = .05$.

## 3.2 Hypotheses

Based on the previous literature (i.e., Colino et al., 2014 & 2016), my primary hypothesis was that tactile suppression would be modulated according to the relevance of the stimulation site. In this experiment, a finding showing participants suppressing tactile information at the forearm (irrelevant site) but not the index finger or thumb (relevant sites) would be consistent with this hypothesis. If however, tactile suppression was not modulated according to the relevance of the stimulation site, there should be gating (i.e., reduced detection) at all sites on the moving limb. Further, if central and peripheral processes both contribute to tactile suppression in this task, participants should exhibit reduced detection before and during the movement in both the self and motor-driven movement conditions.

## 3.3 Experiment 1 Results

### 3.3.1 Site Sensitivity Data

The analysis of stimulus amplitude yielded a main effect of stimulus location $F$ (3, 33) = 13.15, $p < .01$, $n_p^2 = .54$ (see *Figure 3.2*). Post-hoc comparisons revealed that the stimulus amplitude for the forearm was significantly smaller than for the left and right index finger (All comparisons: $p \leq .01$). Further the stimulus amplitude to the thumb was only significantly smaller than the right index finger ($p = .03$). There were no other differences between the conditions.

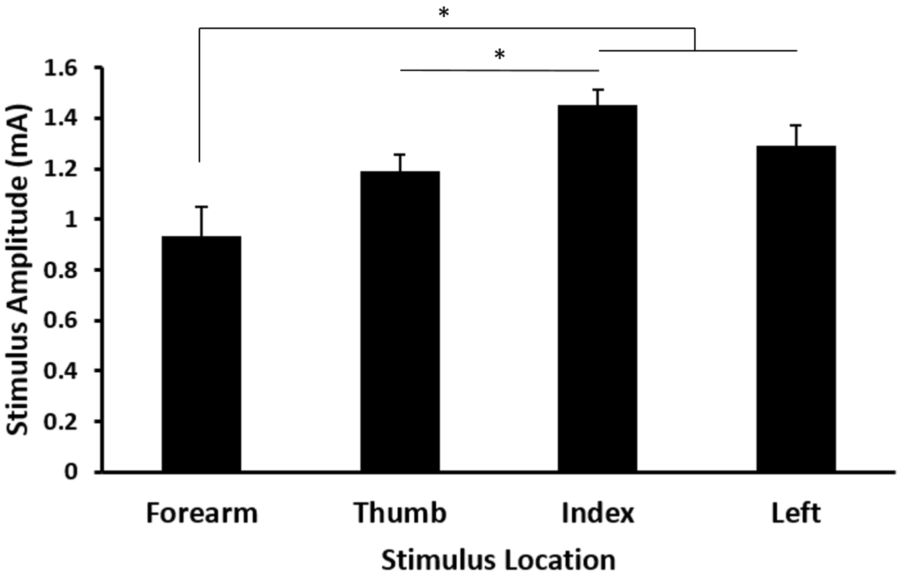

**Figure 3.2. Stimulus amplitude at which participants felt the stimulus 90% of the time at rest for each location. Error bars indicate standard error of the mean. The stimulus amplitude at the forearm was significantly weaker than the right and left index finger ($p < .01$). The stimulus amplitude at the thumb was significantly weaker than the right index finger ($p = .03$).**

### 3.3.2 Detection Data

When looking at the detection rates during the Control experiment, the main effect of stimulus location failed to reach significance ($F$ (3, 24) = 1.16, $p = .346$, $n_p^2 = .13$; see *Figure 3.3*). This implies that at rest, participants' stimulus detection rates were comparable across stimulation sites.

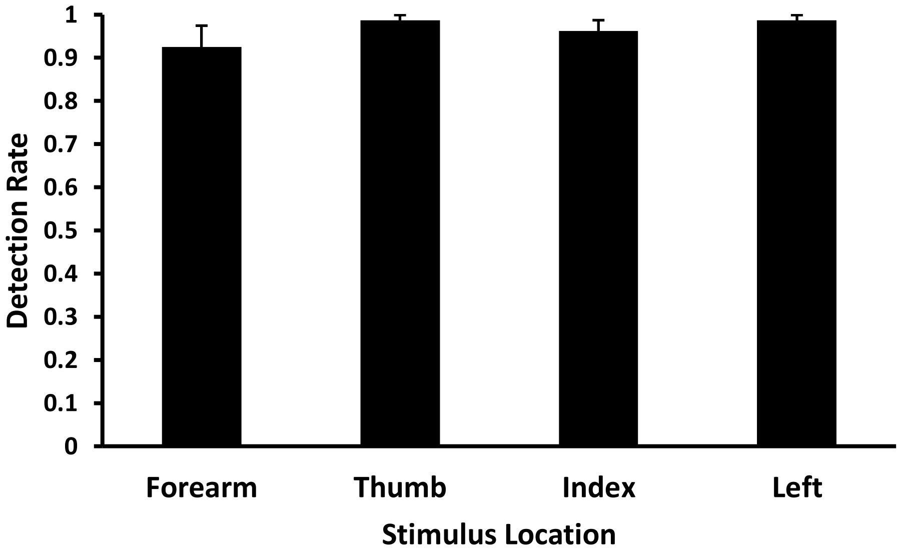

**Figure 3.3. Detection rate during the control trials (i.e., no movement). Error bars indicate standard error of the mean. Stimulation intensity was individually set such that participants were expected to detect the stimulus approximately 90% of the time.**

Analysis of detection rate during the experimental trials yielded a main effect of stimulus location (*F* (3, 33) = 10.07, $p < .01$, $n_p^2 = .48$) and stimulation time (*F* (3, 33) = 97.01, $p < .01$, $n_p^2 = .90$) but failed to yield a significant main effect of movement condition (*F* (1, 11) = 2.84, $p = .12$, $n_p^2 = .21$). Post-hoc comparisons revealed that detection rates at the forearm, thumb and right index finger were significantly smaller than at the left index finger (All comparisons: $p < .01$). This implies that participants felt the stimulus the most when it was presented at the left index finger compared to all other locations. For the main effect of stimulation time, post-hoc comparisons revealed that detection rates when stimulated at the GO signal were significantly higher than when stimulated at all other times (All comparisons: $p < .01$). Put simply, this indicates that participants felt the stimulus more when it was presented before the movement started compared to all other times.

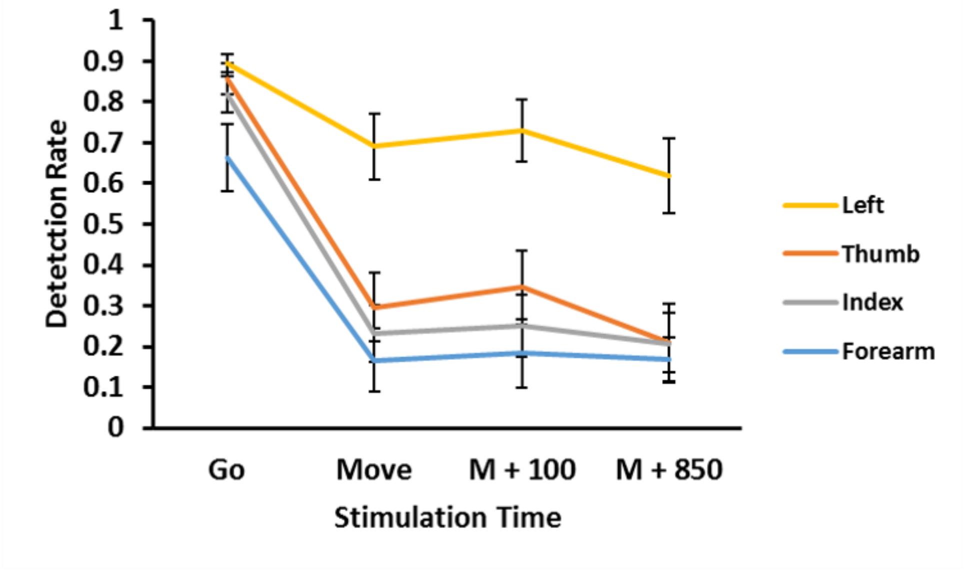

**Figure 3.4. Detection rate as a function of stimulus location and stimulation time, collapsed across movement condition. Detection rate decreased during movement of the arm (whether the movement was self-driven or motor-driven) and for the stimulation sites of the moving limb. Error bars indicate standard error of the mean. For greyscale image, from top to bottom: Left, Thumb, Index, Forearm.**

Further, the analysis yielded a stimulus location by stimulation time interaction ($F$ (9, 99) = 4.61, $p$ < .01, $n_p^2$ = .30; see *Figure 3.4*). No interactions with movement condition were present. In order to determine if there were differences in detection rate across the movement profile for each location, a simple main effect analysis of time at each location was conducted. This analysis revealed a main effect of time at all four locations (Forearm: $F$ (3, 33) = 32.27, $p$ < .01, $n_p^2$ = .75; Thumb: $F$ (3, 33) = 40.95, $p$ < .01, $n_p^2$ = .79; Right Index: $F$ (3, 33) = 25.54, $p$ <

.01, $n_p^2$ = .70; Left Index: $F$ (3, 33) = 5.08, $p$ < .01, $n_p^2$ = .32). For the forearm, thumb and right index finger, post-hoc comparisons revealed that the detection rate when stimulated at the GO signal was significantly higher than all other stimulation times (All comparisons: $p$ < .01). For the left index finger, post-hoc comparisons revealed that the detection rate when stimulated at the GO signal was only significantly greater than the detection rate when stimulated 850 ms after movement onset ($p$ = .01).

In order to determine if there were differences in detection rates between the stimulus locations at each time point, a simple main effect analysis of stimulus location at each stimulation time was conducted. This analysis revealed a main effect of stimulus location at each of the stimulation times (GO: $F$ (3, 33) = 3.16, $p$ = .038, $n_p^2$ = .22; Move: $F$ (3, 33) = 9.98, $p$ < .01, $n_p^2$ = .48; 100: $F$ (3, 33) = 9.68, $p$ < .01, $n_p^2$ = .47; 850: $F$ (3, 33) = 7.48, $p$ < .01, $n_p^2$ = .41). When stimulated at the GO signal, the detection rate at the forearm was significantly smaller than the left index finger ($p$ = .02). At all other stimulation times (i.e., move, 100 and 850), the forearm, thumb and right index finger had a significantly lower detection rate than the left index finger (All comparisons: $p \leq .01$).

### 3.3.3 Movement-Related Measures

All movement-related variables in the self-driven movement condition are displayed in *Table 3.2* and all movement-related variables in the motor-driven movement condition are displayed in *Table 3.3*. Overall, the self and motor-driven movement related variables were quite comparable (see *Figure 3*.5). Primarily, the collection of EMG was used to confirm that participants adhered to the instructions in both the self and motor-driven movement conditions. That is, in the self-driven movement condition, participants were expected to react to the GO signal and initiate their reach, and in the motor-driven condition, participants were expected to let the motor drive the movement (controlled by the experimenter). Analysis of relative EMG onset yielded only a main effect of condition ($F$ (1, 11) = 103.59, $p$ < .01, $n_p^2$ = .90). From this it is quite clear that participants adhered to the instructions and only initiated the movement in the self-driven condition (*Figure 3.5*). From the figure, we also see that some tonic EMG activity was present after movement onset in the motor-driven condition. This could be related to participants stabilizing their upper limb.

Analysis of MT failed to yield any significant main effects or interactions in the self-driven movement condition. Looking at *Table 2* and *Table 3*, it clear that the movement times in all conditions were very similar. Indeed, the mean MT in the self-driven condition was 704 ms (95% CI [683, 725]) and 718 ms (95% CI [711, 724]) for the motor-driven movement condition.

Analysis of RT in the self-driven movement condition only yielded a main effect of stimulation time, $F$ (3, 33) = 9.64, $p$ < .01, $n_p^2$ = .47. Post-hoc comparisons revealed that the RT when stimulated at the GO was significantly shorter than when stimulated at any other stimulation time (All comparisons: $p$ < .01).

**Table 3.2.** Means and between subject standard deviations for Reaction Time (RT; ms), Movement Time (MT; ms) and Relative EMG Onset (Rel.EMG; ms) in the self-driven movement condition.

| | **Forearm** | | | | **Thumb** | | | | **Right index** | | | | **Left Index** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **GO** | **MOVE** | **M+100** | **M+850** | **GO** | **MOVE** | **M+100** | **M+850** | **GO** | **MOVE** | **M+100** | **M+850** | **GO** | **MOVE** | **M+100** | **M+850** |
| **RT** | | | | | | | | | | | | | | | | |
| ***mean*** | 327 | 370 | 361 | 381 | 321 | 360 | 352 | 356 | 342 | 369 | 356 | 359 | 324 | 357 | 374 | 353 |
| ***sd*** | 50 | 77 | 49 | 74 | 53 | 40 | 52 | 52 | 53 | 50 | 58 | 65 | 59 | 54 | 71 | 67 |
| **MT** | | | | | | | | | | | | | | | | |
| ***mean*** | 715 | 708 | 706 | 699 | 698 | 707 | 692 | 695 | 725 | 703 | 708 | 700 | 706 | 700 | 704 | 699 |
| ***sd*** | 27 | 49 | 42 | 47 | 34 | 38 | 47 | 39 | 35 | 41 | 32 | 33 | 41 | 43 | 33 | 43 |
| **Rel.EMG** | | | | | | | | | | | | | | | | |
| ***mean*** | -110 | -114 | -105 | -113 | -109 | -104 | -108 | -106 | -113 | -113 | -108 | -109 | -110 | -113 | -108 | -108 |
| ***sd*** | 19 | 36 | 21 | 20 | 23 | 19 | 19 | 22 | 22 | 21 | 21 | 24 | 15 | 28 | 26 | 37 |

**Table 3.3** Means and between subject standard deviations for Reaction Time (RT; ms), Movement Time (MT; ms) and Relative EMG Onset (Rel.EMG; ms) in the motor-driven movement condition.

| | **Forearm** | | | | **Thumb** | | | | **Right index** | | | | **Left Index** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **GO** | **MOVE** | **M+100** | **M+850** | **GO** | **MOVE** | **M+100** | **M+850** | **GO** | **MOVE** | **M+100** | **M+850** | **GO** | **MOVE** | **M+100** | **M+850** |
| **RT** | | | | | | | | | | | | | | | | |
| ***mean*** | 643 | 627 | 630 | 648 | 668 | 653 | 647 | 645 | 678 | 622 | 644 | 639 | 668 | 651 | 648 | 646 |
| ***sd*** | 84 | 62 | 73 | 81 | 78 | 84 | 87 | 75 | 102 | 69 | 78 | 81 | 89 | 87 | 93 | 68 |
| **MT** | | | | | | | | | | | | | | | | |
| ***mean*** | 716 | 717 | 719 | 717 | 719 | 716 | 718 | 719 | 718 | 713 | 716 | 717 | 719 | 722 | 718 | 718 |
| ***sd*** | 8 | 10 | 11 | 9 | 15 | 8 | 12 | 11 | 11 | 5 | 8 | 9 | 11 | 15 | 10 | 12 |
| **Rel.EMG** | | | | | | | | | | | | | | | | |
| ***mean*** | 190 | 204 | 198 | 206 | 208 | 215 | 203 | 203 | 203 | 204 | 210 | 215 | 193 | 200 | 206 | 207 |
| ***sd*** | 111 | 116 | 113 | 114 | 133 | 123 | 108 | 110 | 118 | 118 | 119 | 117 | 119 | 109 | 112 | 114 |

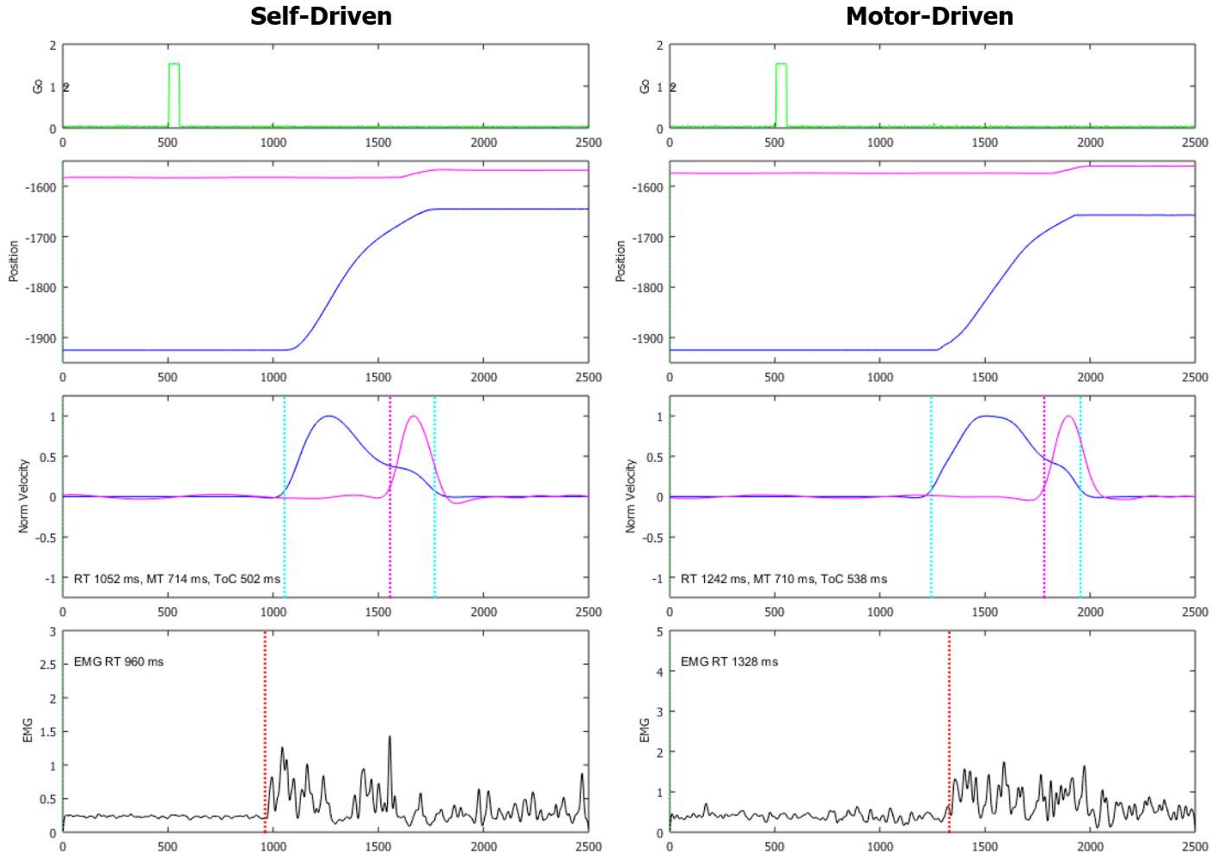

**Figure 3.5. Raw movement related measures in the self-driven (left panels) and motor-driven (right panels) movement conditions for one trial across one participant. From top to bottom: Onset of GO signal, displacement profile of the carriage (blue) and target (pink), velocity profile of carriage (blue) and target (pink), filtered rectified EMG profile (black). Notice that the velocity profile of both movement conditions are similar with a longer tail after peak velocity. Also notice the later onset of EMG activity in the motor than the self-driven movement condition.**

## 3.4 Experiment 1 Discussion

In Experiment 1, participants performed self-driven or motor-driven reaching and grasping movements toward a stationary target. Before, during or after movement, participants were presented with an electrical stimulation to the right and left index finger, the right thumb or the right forearm. While the electrical stimulation was readily detectable at rest, the main dependent measure was the participants' ability to detect this tactile stimulation across the movement profile.

### 3.4.1 Movement-Related Measures

Before speaking to the detection data, it is first important to consider the movement-related variables. If we look at reaction time in the self-driven movement condition, participants displayed a shorter reaction time when stimulated at the GO signal than when stimulated at any other stimulation time. This result is consistent with recent work employing a similar task, displaying that the earlier a stimulation was given before movement onset, the shorter the reaction times (Voudouris & Fiehler, 2017: Experiment 1). Participants had the highest detection rate when stimulated at the GO and suggests that the tactile stimulation might have served as an additional cue to begin the movement (Voudouris & Fiehler, 2017). Indeed, intersensory facilitation studies have shown shorter reaction times when responding to multisensory stimuli compared to when responding to either unimodal stimuli alone (e.g., visual and auditory: Gielen, Schmidt & Van Den Heuval, 1983; visual and tactile: Forster et al., 2002). When examining movement times, it is important to note that no differences arose across the stimulation times or stimulus locations. Further, the movement times for both movement conditions were quite similar. This suggests that participants adhered to the prescribed movement time bandwidth and also shows that, at least in terms of movement time, the self-driven and motor-driven movements were comparable. Lastly, relative EMG onset was used to confirm that participants were not initiating their movements in the motor-driven movement condition. Not surprisingly, this was the case as the EMG activity preceded movement in the self-driven movement condition but followed movement in the motor-driven movement condition.

### 3.4.2 Sensitivity and Detection Data

The aim of thesis was to investigate the modulation of tactile suppression according to the relevance of the stimulation site during goal-directed movement. Further, this experiment addressed some limitations in recent similar studies. Specifically, recent work (Colino et al., 2014; Colino & Binsted, 2016) employed the same single stimulus intensity across multiple locations on the upper limb. Here, a Bayesian adaptive procedure and a strict GBF threshold (Peters & Goldreich, 2013) allowed us to determine, with confidence, the stimulus intensity at which the tactile stimulation was felt 90% of the time at rest. This allowed us to be more consistent with earlier, seminal work on tactile suppression (e.g., Williams & Chapman, 2000; Williams & Chapman, 2002). When analyzing stimulus amplitude, the main effect of stimulus location confirmed a difference in sensitivity across the four sites. The forearm and thumb, although not different from each other, were significantly more sensitive than the right index finger. That is, a smaller stimulus amplitude was needed to elicit 90% detection rate at the forearm and thumb compared to the right index finger. This was again confirmed by the control experiment in which 9 participants performed additional detection trials at rest. At all four locations, mean detection rates were above 90% and critically, were not different from each other. The differing sensitivities across stimulation sites highlights the importance of using relative intensities in a detection task such as this.

The main effect of stimulation time displayed that participants were significantly poorer at detecting tactile electrical stimulation during and after movement compared to before movement onset. This result is partially at odds with the tactile suppression literature displaying tactile suppression before movement and a lack thereof after movement completion (Colino & Binsted, 2016). Here, we show high detection rates when the stimulation was presented at the GO signal. This can be accounted for by participants' reaction times. In the self-driven movement condition, the mean reaction time when stimulated at the GO signal was 328 ms (*SD* = 45 ms). Consistent with previous research, if a stimulation is given 250 ms before movement start, tactile suppression may not be present (Colino et al., 2014; Colino & Binsted, 2016). The movement preparation interval in the motor-driven condition when stimulating at the GO signal was 664 ms (*SD* = 83 ms). Again, earlier work has shown that backward masking only took place if the stimulus was presented up to 150 ms before movement onset, albeit for a simple finger abduction task (Williams & Chapman, 2002). For stimulations presented after movement completion, we expected tactile detection to come back up to control levels due to the fact the participant was at rest. However, this was not the case and differs from Colino and Binsted's (2016) findings (see *Figure 3.6*). After movement completion in our task, participants were still grasping the target and were engaged in an isometric contraction. Indeed, early work has shown no differences between an isotonic and isometric movement in terms of tactile suppression (Williams & Chapman, 2002). In the task employed by Colino and Binsted (2016) movement end was not defined and was therefore ambiguous as to whether or not participants were still holding the object when the stimulation was given.

In terms of tactile suppression, there were no differences when comparing the self and motor-driven movement condition. Overall, gating across the movement, irrespective of the movement condition, suggests that both central and peripheral processes contributed to tactile gating. This is consistent with literature which displays tactile gating during both active (Williams & Chapman, 2000; Williams & Chapman, 2002; Voss et al., 2006) and passive movement (Williams & Chapman, 2002). During active movement, sensory attenuation is thought to occur at the level of the dorsal column-lemniscal pathway (Chapman et al., 1988). That said, evoked responses to peripheral stimulation along this pathway were depressed during active movement in monkeys (Chapman et al., 1988). In humans, neurophysiological evidence also showcases a reduction in SEP amplitude corresponding with EMG onset during active movement (Cohen & Starr, 1987) and movement onset during passive upper limb movement (Jones, 1981; Rushton, Rothwell & Craggs, 1981). In our motor-driven movement condition, the afferent information gathered from the movement itself likely masked the detection of the tactile stimuli. Consistent with the SEP work, tactile suppression was evident from movement onset. Although the literature defines a role for both central efferent signals and peripheral afferent signals in tactile suppression, we cannot dissociate the two processes in the current experiment. These results cannot rule of the possibility that peripheral processes accounted for the suppression displayed during movement, regardless of being self or motor-driven. That said, the current design is limited by employing one pre-movement stimulation time in conjunction with relatively long intervals between the Go signal and movement onset.

Where this study differs from recent literature (Colino et al., 2014; Colino & Binsted, 2016) is that in this experiment we do not show a difference in tactile modulation according to the relevance of the stimulation site. When performing the self-driven movement, participants suppressed tactile information during movement at all locations on the moving limb. That is, even at the task-relevant stimulus locations (i.e., the right thumb and index finger) tactile information was gated in line with the task-irrelevant stimulus location (i.e., right forearm). This result suggests that participants did not attenuate the tactile suppression at locations where tactile information may be important to the task. One possible explanation is that the weak electrical stimulation was well below the stimulus intensity of what would be received by the actual target. That is, when we contact the target the tactile stimulus or information we receive is much more salient. In that case, gating a weak electrical stimulus would not, and did not, hinder the success of the task. While this result is opposite to that of Colino et al.'s work (2014 & 2016), we suggest that presenting different stimulus amplitudes to the four sites, according to site sensitivity, may potentially account for these differences. Here, we show that each site was presented with a different stimulus amplitude. Further, this was done separately for each participant. Therefore, we can be confident that the relative intensity at each site was the same. In Colino et al.'s work (2014 & 2016) one (mechanical) vibration amplitude was used for all sites and for all participants. We suggest that their results may have been confounded by differing relative intensities across all the stimulus locations and when you control for this limitation, no difference in tactile suppression arises. In both of their studies, the index finger showed no signs of tactile suppression with very low variability around the mean values (see *Figure 3.6*). If this was a suprathreshold stimulus it is possible that participants felt the stimulus as weaker but still felt the stimulus, although this was not directly measured. What further differentiates the current experiment and the aforementioned work is the use of electrical stimulation as opposed to vibration. Although both stimuli are likely to activate cutaneous receptors, we chose to use electrical stimulation because it has been validated in the past (e.g., Williams, Shenasa & Chapmam, 1998; Williams & Chapman, 2000; Williams & Chapman, 2002; Voss et al., 2006; Voss et al., 2008) and it allows for easy manipulation of stimulus parameters (i.e., depending on thresholds). Vibration however, is variably used across the literature with stimulus parameters differing from study to study, partially due to the poor flexibility in stimulus parameters. For example, Jurvale and Spence (2010) used a 250 Hz, 660 ms tactile pulse while Colino et al.

(2014 & 2016) used a 7.5 ms pulse without specifying the frequency parameter. This lack of consistency across studies using vibrotactile stimuli make it difficult to compare across studies. We therefore feel that using electrical stimulation, with stimulus parameters that match early seminal work in this field, allowed us to be confident in our results.

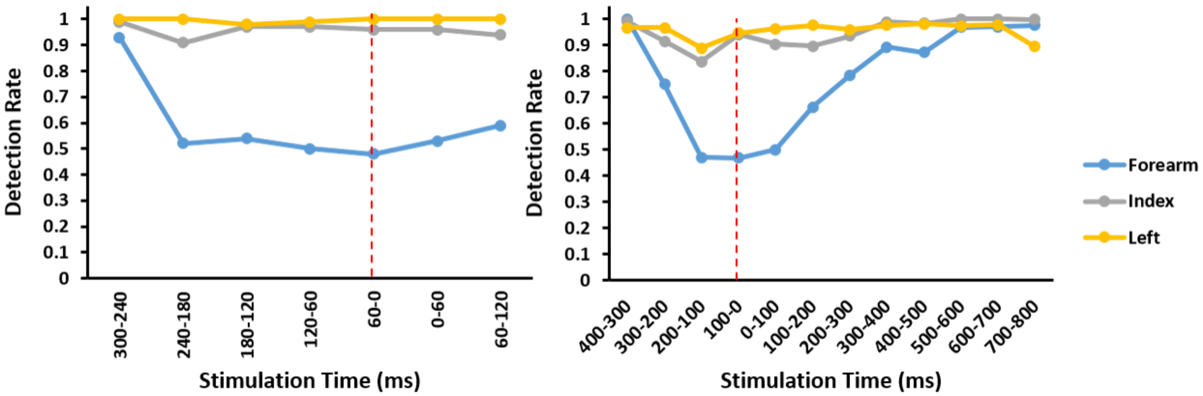

**Figure 3.6. Detection rate as a function of stimulation time at the right forearm, right index finger and left index finger. The graph on the left is recreated from Table 3 in Colino et al. (2014) and the graph on the right is recreated from Figure 3 in Colino and Binsted (2016). The stimulation times are relative to the onset of movement (defined by the red vertical line). To the left of the red line denotes pre-movement and to the right denotes during or after movement. For greyscale image, from top to bottom: Left, Index, Forearm.**

Attention also likely played a role in tactile suppression for the stationary limb. Throughout the entirety of the experiment the left limb remained stationary. During movement of the contralateral limb however, participants detected the stimuli less than during resting control conditions. In the experiment overall, the stimuli were given to the left stationary index finger only 25% of the trials. In addition to this low probability, participants were likely attending to the right limb as it was involved in the targeted movements as well as being sent a stimulation on 75% of the trials. This attentional shift away from the stationary limb likely accounts for these results. When stimulating numerous proximal locations to the index finger during a finger abduction task, Williams, Shenasa and Chapman (1998) also showed a similar effect. That is, although the suppression was decreased the further away the stimulation was from the moving effector, every stimulus location showed a decrease in detection rate compared to control levels. Collectively, this corresponds well with previous studies that show an increase in perceptual thresholds according to the number of possible stimulation sites (Meyer et al., 1963).

Tactile suppression during movement on all locations on the moving limb does however align well with other literature employing goal-directed movement. When reaching and grasping a computer mouse, for example, Jurvale and Spence (2010) showed an increase in perception thresholds during movement execution as compared to the motor preparation period. In this task, tactile information is also arguably important for successful completion of the reach. Further, a more recent study employed pointing movements to a visual target or the participant's own opposite index finger (Voudouris & Fiehler, 2017). In their third experiment, Voudoris and Fiehler (2017) show that for the pointing index finger, not only was there significant tactile suppression during movement but, there was no difference in perceptual thresholds to a vibratory stimulus whether they were pointing to a visual target or their own finger. This suggests that even though tactile information may have been more important when pointing to their own finger, participants displayed the same level of tactile suppression compared to when pointing to a visual target. Consistent with these findings, the current results show no change in tactile gating dynamics according to task relevance. In summary, the results of the present study suggest that we do not attenuate the typically observed suppression during movement (cf. Colino et al., 2014; Colino & Binsted, 2016), whether the movement is under one's control or under external control.

To complement the current work, I sought to further investigate the degree of tactile suppression using slightly different methodology. In this experiment, participants detected the stimulus less during movement, irrespective of stimulus site or relevance; however, I cannot speak to any changes in participants’ perceptual thresholds. Based on the tactile suppression literature, one can only assume that the perceptual threshold to a tactile stimulus will increase when performing movement. That is, a stronger stimulus is needed to detect that a stimulation occurred when moving as opposed to at rest. But for example, the perceptual threshold may have increased to a different degree during the differing movement conditions or stimulation sites.

# Chapter 4: Experiment 2

Recent work has suggested another useful method for investigating tactile gating during goal-directed movement. Voudouris and Fiehler (2017) had participants point to either a somatosensory/proprioceptive target (i.e., their own opposite index finger) or a visual target (i.e., a circle on a screen). Rather than giving only one stimulus amplitude which was readily detectable at rest, they provided a wide range of intensities either before or during movement. For each stimulation time, the authors were able to obtain separate psychometric functions. In turn, these functions provide an estimate of the perceptual threshold at rest and during movement. This methodology provides a new way to quantify tactile suppression. Expanding on Experiment 1, Experiment 2 and 3 will use the aforementioned methodology in order to directly obtain perceptual thresholds and thus the magnitude of tactile suppression.

Experiment 2 of the thesis was designed in order to directly assess shifts in perceptual thresholds during movement. Participants performed the same reaching and grasping movements but with multiple stimulus amplitudes presented before and during the movement. This design mirrored that of recently published studies (Gertz et al., 2017; Voudouris & Fiehler, 2017) and allowed for separate psychometric curves to be made before and during the movement. In this experiment, the tactile stimuli were presented to one task relevant stimulation site on the moving limb (i.e., right index finger) during either self or motor-driven movements. Using one stimulation site also eliminates any confounding effect of attention in which multiple stimulation sites may have contributed to an increase in perceptual threshold or a decrease in detectability. Comparing the shifts in perceptual thresholds allows us to investigate any differential tactile suppression between self and motor-driven movements at one task relevant site.

## 4.1 Methods

### 4.1.1 Participants

Fourteen right-hand dominant participants (7 female, 7 male; *M* = 24 years, *SD* = 3) with self-reported normal or corrected-to-normal vision were recruited from the University of British Columbia community. Participants had no history of neurological impairment. The total duration of the experiment was between 60-90 minutes. All participants gave informed consent prior to participating with the protocol approved by the UBC ethics board.

### 4.1.2 Procedure

The experimental setup was the same as Experiment 1 in which participants performed self and motor-driven reaches toward a target in a blocked and counterbalanced fashion. Here, rather than four stimulus locations and four stimulation times, participants were only stimulated at the right index finger either before or during movement. Again, participants were instructed to perform reaching and grasping movements within a 600 – 800 ms movement time bandwidth. One tone was used as a ready signal followed by an auditory tone which acted as a GO signal (1000 ms apart). Here, a tactile stimulus was presented in between the two auditory tones (prior to movement) or during movement execution (100 ms after movement onset). Rather than using one stimulus amplitude throughout the experiment, 20 stimulus amplitudes (0.35 – 2.25 mA in equal 0.1 mA steps) were presented. In the self and motor-driven movement conditions, the stimulation time and stimulus amplitude were presented in a randomized order. Participants performed 5 trials per stimulation amplitude per stimulation time. This resulted in a total of 200 trials for the self-driven and 200 trials for the motor-driven movement condition. In addition, 10 catch trials, in which no stimulation was given, were included in each movement condition. In total participants performed 420 trials.

If participants were able to readily detect the lowest stimulus amplitude (0.35 mA) or were not able to detect the largest stimulus amplitude (2.25 mA) they were excluded from the analysis. In these cases, an accurate perceptual threshold could not be obtained. This resulted in the exclusion of four participants. Therefore, 10 participants were included in the final analysis (5 female, 5 male; *M* = 23 years, *SD* = 3).

We calculated the proportion of stimuli detected for each participant, in each stimulation time and movement condition. We then fitted these proportions to a psychometric curve using the *glmfit* function in Matlab with a logit link function (Wichmann & Hill, 2001). From the function, we were able to obtain the detection threshold as the stimulus intensity that was detected 50% of the time (Gescheider, 1997). Further, the precision of stimulus detectability was the difference in stimulus intensities between the 50% and 84% point of the function (Gertz et al., 2017; Voudouris & Fiehler, 2017). This measure gives us insight into the slope of the psychometric function. That is, a steeper slope would suggest that a small change in stimulus amplitude is easily detectable. A more gradual slope however, would suggest that a bigger change in stimulus amplitude is needed in order to elicit a change in detectability. For each movement condition (i.e., self and motor-driven) the difference in detection threshold and precision between the two stimulation times (i.e., before movement and during movement) was taken. This resulted in a detection threshold difference and a precision difference in the self and motor-driven movement condition for each participant. These difference scores represent the strength of tactile suppression during movement. That is, a positive difference from zero is representative of tactile suppression, zero represents no tactile suppression, and a negative difference is representative of tactile enhancement.

### 4.1.3 Data Analysis

#### 4.1.3.1 Detection Data

To infer whether tactile suppression was evident during movement, a one sample t-test was performed comparing the mean detection threshold differences to zero. This was done for both the self and motor-driven movement conditions. To infer whether there was a difference in the magnitude of gating during the two movement conditions, paired samples t-tests (between self and motor-driven) were used to compare the detection threshold and precision difference scores. In total, this resulted in 4 separate t-tests.

#### 4.1.3.2 Movement-Related Measures

MT and RT values were compared using a paired samples t-test between the two stimulation times in the self-driven movement condition. Relative EMG onset was submitted to a 2 Condition (self and motor-driven) by 2 Stimulation Time (pre-movement and movement execution) repeated measures ANOVA. For all tests alpha was set at $p = .05$.

## 4.2 Hypothesis

If central and peripheral processes contribute to tactile gating, I expected the detection threshold differences to be significantly different than zero when performing both self and motor-driven movement. If tactile gating is attenuated during self-driven reaching and grasping movements, then participants should exhibit a lesser magnitude of tactile suppression in the self than the motor-driven movement condition. If, however this tactile suppression is not modulated at the index finger or modulated to the same degree in both movement conditions, then I expected that participants would not exhibit differences in the magnitude of tactile suppression between the self and motor-driven movement conditions.

## 4.3 Experiment 2 Results

### 4.3.1 Detection Data

For both the self-driven and motor-driven movement conditions the perceptual threshold difference scores were significantly greater than zero (self-driven: $t$ (9) = 3.97, $p < .01$, 95% CI [0.08, 0.30]; motor-driven: $t$ (9) = 2.74, $p = .02$, 95% CI [0.02, 0.21]; see *Figure 4.1*). The two movement conditions however, were not significantly different from each other ($t$ (9) = 1.38, $p$ = .20, 95% CI [-0.05, 0.20]). Further, when analyzing the precision difference scores, the two movement conditions were also not different from each other ($t$ (9) = -0.85, $p$ = .42, 95% CI [-0.19, 0.09]; see *Figure 4.2*).

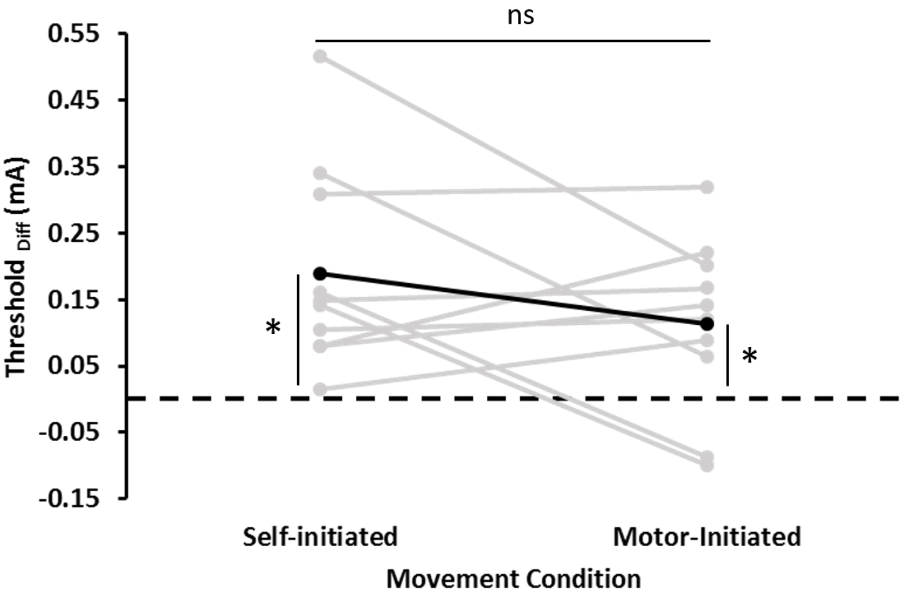

**Figure 4.1. Perceptual threshold difference as a function of movement condition. The black line represents the mean values and the grey lines represent individual participant values. A positive non-zero difference score indicates that perceptual thresholds were higher during the movement relative to the period preceding the Go signal. The vertical asterisk bar beside the means indicates a significant difference from zero.**

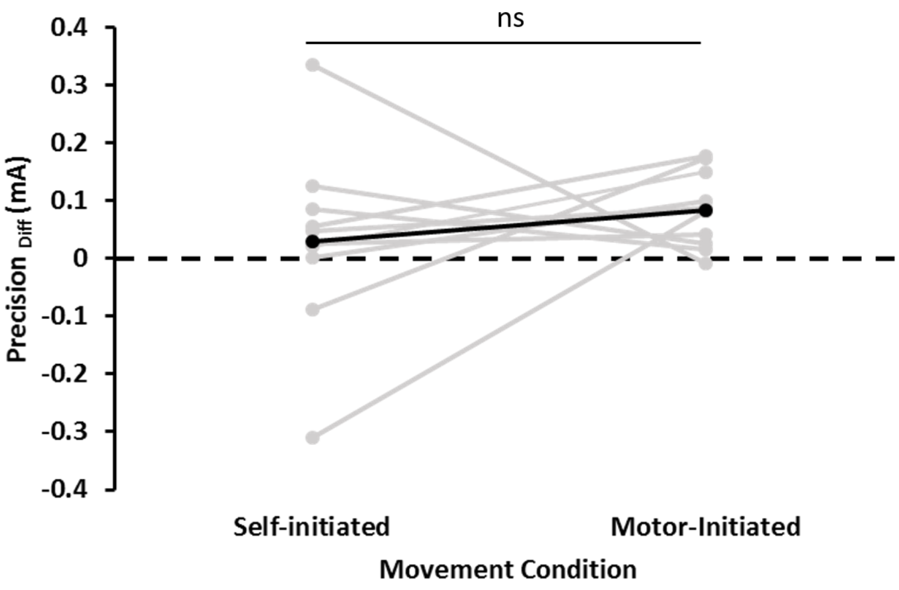

**Figure 4.2. Precision difference as a function of movement condition. The black line represents the mean values and the grey lines represent individual participant values. The precision score reflects the slope of the psychometric function.**

### 4.3.2 Movement-Related Measures

All movement-related variables are displayed in *Table 4.1.* The analysis of RT revealed that participants had shorter (i.e., faster) reaction times when stimulated in the pre-movement condition compared to the movement-execution condition ($t$ (9) = -7.12, $p$ < .01; self-driven: 95% CI [266.24, 364.24]; motor-driven: 95% CI [309.51, 419.06]. The analysis of MT revealed no differences between stimulation times. The analysis of relative EMG onset yielded a main effect of movement condition ($F$ (1, 9) = 368.54, $p$ < .01, $n_p^2$ = .98) and main effect of stimulation time ($F$ (1, 9) = 5.44, $p$ = .045, $n_p^2$ = .38) but failed to yield an interaction between the two. The main effect of movement condition revealed that the EMG onset was earlier (and prior to movement onset) in the self-driven compared to the motor-driven movement condition (see *Table 4.1*). The main effect of stimulation time revealed that the EMG onset was earlier in the pre-movement compared to the movement-execution stimulation time.

**Table 4.1** Means and between subject standard deviations for Reaction Time (RT; ms), Movement Time (MT; ms), and Relative EMG Onset (Rel.EMG; ms) in both movement conditions.

| | Self-Initiated | | Motor-Initiated | |
|---|---|---|---|---|
| | **Pre** | **Movement** | **Pre** | **Movement** |
| **RT** | | | | |
| ***mean*** | 315 | 364 | 242 | 239 |
| ***sd*** | 68 | 77 | 91 | 92 |
| **MT** | | | | |
| ***mean*** | 729 | 732 | 718 | 718 |
| ***sd*** | 25 | 26 | 26 | 27 |
| **Rel.EMG** | | | | |
| ***mean*** | -131 | -137 | 128 | 120 |
| ***sd*** | 31 | 32 | 42 | 44 |

## 4.4 Experiment 2 Discussion

In Experiment 2, participants performed self-driven and motor-driven reaching and grasping movements toward a stationary target. Before or during these movements, participants were presented with a range of electrical stimulation amplitudes to the right index finger. As in Experiment 1, the main dependent measure was the detectability of the stimulations. The aim of this experiment was to investigate whether there are any shifts in perceptual thresholds during self or motor-driven movement at one task relevant location (i.e., index finger).

### 4.4.1 Movement-Related Measures

Consistent with experiment 1, participants displayed shorter reaction times when the stimulus was presented before the movement began as opposed to during the movement. This provides further support for a facilitatory effect of the tactile stimulus in terms of reaction time and aligns with the findings from Experiment 1 (Voudouris & Fiehler, 2017). As in the previous experiment, movement times for the self and motor-driven movement were similar (self-driven: *M* = 731 ms, *SD* = 25; motor-driven: *M* = 718 ms, *SD* = 26). This confirms that, at least in term of movement times, the self and motor-driven movement conditions were similar. With the relative EMG onset measure, we also confirmed that participants initiated their movement in the self-driven condition whereas EMG activity only occurred after the movement began in the motor-driven condition. The earlier EMG onset in the pre-movement compared to the movement-execution stimulation time is likely related to the significantly shorter reaction times when comparing said conditions.

### 4.4.2 Detection Data

This experiment was designed to extend the findings of the first experiment and more directly investigate the amplitude of tactile suppression. In both the self and motor-driven movement conditions participants displayed an increased perceptual threshold during movement compared to baseline rest levels. That is, a stronger tactile stimulation was needed for detection during movement as compared to rest. These findings are in line with previous research showing a similar decrease in detection rate or increase in perceptual threshold during movement (e.g., Juravle & Spence, 2010; Vodouris & Fiehler, 2017; Williams & Chapman, 2002).

The current findings also align well with previous studies employing single-joint active or passive movements. Although these studies could not speak to the amplitude of tactile suppression, Williams and Chapman (2002) and Williams and Beachamp (2006) also showed reduced detection rates and sensitivity during active and passive finger abduction or elbow extension movements, respectively. In the current experiment, as in the first, our motor-driven movement condition does not exactly mirror that of the passive movement conditions in previous studies. Although muscle activity is present in the motor-driven condition, and therefore cannot be deemed completely passive, we suggest that the delayed EMG onset compared to the onset of movement suggests that participants did not initiate the movement themselves and likely did not send a motor command to initiate the movement. EMG activity displayed in the motor-driven condition may have been postural in nature as opposed to related to the movement goal (see *Figure 3.5*). Regardless, this experiment, along with Experiment 1, is the first to employ motor-driven reaching and grasping movement in the context of tactile suppression.

Along with the first experiment, these findings conflict with those of Colino et al. (2014 & 2016; see *Figure 3.6*). Here, we show that even at a task relevant stimulation site (i.e., the index finger) perceptual thresholds increase during movement as compared to rest. This extends the findings of the first experiment in which the detection of a readily detectable stimulus at rest was sparsely felt during movement. Based on the current findings, I suggest that perceptual thresholds may also have increased at all sites on the moving limb in Colino et al.'s work (2014 & 2016). Because they used one stimulation amplitude at all sites, irrespective of differences in sensitivity, their methodology may not have been sensitive enough to display this shift. In turn, at the index finger, the tactile stimulus detectability was never reduced during movement. I believe that the methodology used in these two experiments more accurately depicts the dynamics of tactile suppression at the index finger.

Not only were perceptual thresholds higher than baseline in both the self and motor-driven movements, but the amplitude of the perpetual threshold shift was not different between the two conditions. Further, the amplitude of the precision differences was also not different between the two conditions. This means that the psychometric curve was shifted to the right to the same degree and that the slope of the curves also did not differ between the two movement conditions. In conjunction, these findings suggest that in the self-driven movement condition, participants did not attenuate tactile suppression at a site where tactile information may be important. This also suggests that using a forward model to account for these results may not be sufficient. That is, when we move a copy of our motor command (i.e., the efference copy) can be fed into a forward model in order to make a prediction of the sensory consequences of the movement (Bays & Wolpert, 2007). Predicted and therefore attenuated reafferent information is thought to help highlight any external stimuli and classify self and externally-generated movement (see Cullen & Roy, 2004 for review). In non-human primates, while active and passive head movements are similarly encoded at the level of the vestibular afferent, the vestibular nuclei selectively encode passive head rotations and attenuate active rotations (Cullen & Roy, 2004; Roy & Cullen, 2001). In contrast, evoked responses are reduced at the first major relay along the dorsal-column medial lemniscal pathway during movement (Ghez & Pisa, 1972; Seki & Fetz, 2012; see Chapter 6). In the context of this experiment, a reduction in stimulus detectability in both movement conditions suggests that it is unlikely that an internal model/reafference principle can completely account for these results. Indeed, detection of an external stimuli was reduced regardless of whether a motor command was employed.

As in the first experiment, participants were still able to complete the task (i.e., successfully grasping the target). Perhaps the salience of target object may account for these results. That is, the tactile information from the target itself may be more salient than the weak electrical stimulation delivered in this experiment. Although, tactile information is suppressed the salience of the target still exceeds the new increased threshold levels. In this case, this level of tactile suppression would not compromise the success of the movement.

Participants performed targeted movement in both the self and motor-driven tasks. That being the case, tactile information at the index finger was important to grasp the target object regardless of the movement condition. Perhaps, the amplitude of tactile suppression was similar due to the presence of the target. Indeed, when recording modality-specific evoked potentials during passive foot movement, Staines et al. (2000) displayed task dependent modulation. In their experiment, they recorded from the tibial nerve (corresponding to proprioceptive afferents) and the sural nerve (corresponding to cutaneous afferents). Consistent with SEP literature (e.g., Jones, 1981; Rushton et al., 1981), during passive foot movement SEP amplitude was reduced at both recording sites. Interestingly, when performing a task in which proprioceptive information was important (i.e., limb matching with the opposite foot), the SEP amplitudes evoked via the tibial nerve were higher than passive movement alone. Further, when performing a task in which cutaneous information was important (i.e., plantar flexing the opposite foot when cutaneous stimuli were felt), the SEP amplitudes evoked via the sural nerve were higher than passive movement alone. In all cases however, suppression was evident when comparing to baseline and the amplitude of suppression was modulated. Collectively, this suggests that even during passive limb movement, task dependent modulation can occur. That said, in the current experiment it is not directly clear whether participants did not attenuate movement-related tactile suppression or whether in both the self and motor-driven movement condition participants modulated tactile suppression to the same degree due to the presence of the target.

# Chapter 5: Experiment 3

Experiment 3 was designed to extend the results of Experiment 1. Whereas Experiment 2 explored one task relevant site during a self and motor-driven movement, this experiment explored a task relevant and irrelevant site during a self-driven movement. In this experiment, participants performed volitional self-driven targeted movement and were given weak electrical stimulation to either one task relevant site (index finger) or one task-irrelevant site (forearm). Employing the same methodology as Experiment 2, Experiment 3 was aimed at assessing shifts in perceptual thresholds during movement as a function of task relevance. That said, this experiment allowed us to explore whether the degree of suppression is modulated differently at the index finger compared to the forearm.

## 5.1 Methods

### 5.1.1 Participants

Ten participants (one left-handed; 6 female, 4 male; *M* = 27 years, *SD* = 8) with self-reported normal or corrected-to-normal vision were recruited from the University of British Columbia community. Participants had no history of neurological impairment. The total duration of the experiment was between 60-90 minutes. All participants gave informed consent prior to participating with the protocol approved by the UBC ethics board.

### 5.1.2 Procedure

The apparatus and procedure was similar to Experiment 2. Participants reached and grasped the target while being presented with a weak electrical stimulation to the index finger or forearm in a blocked and counterbalanced fashion. For the index finger, the range of stimulus amplitudes for both the pre-movement and movement-execution stimulation times was 0-1.95 mA. For the forearm, the range of stimulus amplitudes for the pre-movement condition was 0-

1.95 mA and for the movement execution stimulation time it was 0.65-2.55 mA. Pilot testing determined that the range of stimulus amplitudes needed to be shifted for the movement execution stimulation time for the forearm stimulus location. Participants performed 5 trials per stimulation amplitude per stimulation time. This resulted in a total of 200 trials for the index finger and 200 trials for the forearm stimulus location. In addition, 10 catch trials, in which no stimulation was given, were included for each stimulus location. In total participants performed 420 trials.

As in Experiment 2, we calculated the proportion of stimuli detected for each participant, in each stimulation time and movement condition. We then fitted these proportions to a psychometric curve using the *glmfit* function in Matlab with a logit link function (Wichmann & Hill, 2001). From the function, we were able to obtain the detection threshold as the stimulus intensity that was detected 50% of the time (Gescheider, 1997). Further, the precision of stimulus detectability was the difference in stimulus intensities between the 50% and 84% point of the function (Gertz et al., 2017; Voudouris & Fiehler, 2017). For each stimulus location (i.e., index finger and forearm) the difference in detection threshold and precision between the two stimulation times (i.e., before movement and during movement) was taken. This resulted in a detection threshold difference and a precision difference at the index finger and forearm for each participant. These difference scores represent the strength of tactile suppression during movement.

### 5.1.3 Data Analysis

#### 5.1.3.1 Detection Data

To infer whether tactile suppression was evident during movement, a one sample t-test was performed comparing the mean detection threshold differences to zero. This was done for both the index finger and forearm stimulus locations. To infer whether there was a difference in the magnitude of gating at both locations, paired samples t-tests (between index finger and forearm) were used to compare the detection threshold and precision difference scores. In total, this resulted in 4 separate t-tests.

#### 5.1.3.2 Movement-Related Measures

MT and RT values were submitted to a 2 Stimulus Location (index finger and forearm) by 2 Stimulation Time (pre-movement and movement execution) repeated measures ANOVA. For all tests alpha was set at $p = .05$.

### 5.2 Hypothesis

If tactile suppression is modulated according to the relevance of stimulation site, then I expected that there would be differences in shifts in perceptual threshold at the index finger compared to the forearm. Specifically, I hypothesized that tactile suppression would be attenuated at the index finger compared to the forearm. This would be represented by a smaller difference in perceptual thresholds between movement and pre-movement for the index finger compared to the forearm. Based on the findings of the previous experiments, I expected some degree of tactile suppression to remain evident at the index finger.

## 5.3 Experiment 3 Results

### 5.3.1 Detection Data

For both the index finger and forearm stimulus locations, the perceptual threshold difference scores were significantly greater than zero (index: *t* (9) = 2.73, *p* = .02, 95% CI [0.01, 0.14]; forearm: *t* (9) = 5.17, *p* < .01, 95% CI [0.51, 1.30]; see *Figure 5.1*). Further, the two stimulus locations were significantly different from each other (*t* (9) = -4.6, *p* < .01, 95% CI [-1.24, -0.42]). When analyzing the precision difference scores, the two movement conditions were also different from each other (*t* (9) = -3.0, *p* = .01, 95% CI [-0.22, -0.03]; see *Figure 5.2*). For both the perceptual threshold and precision, the difference scores at the index finger were significantly smaller than at the forearm.

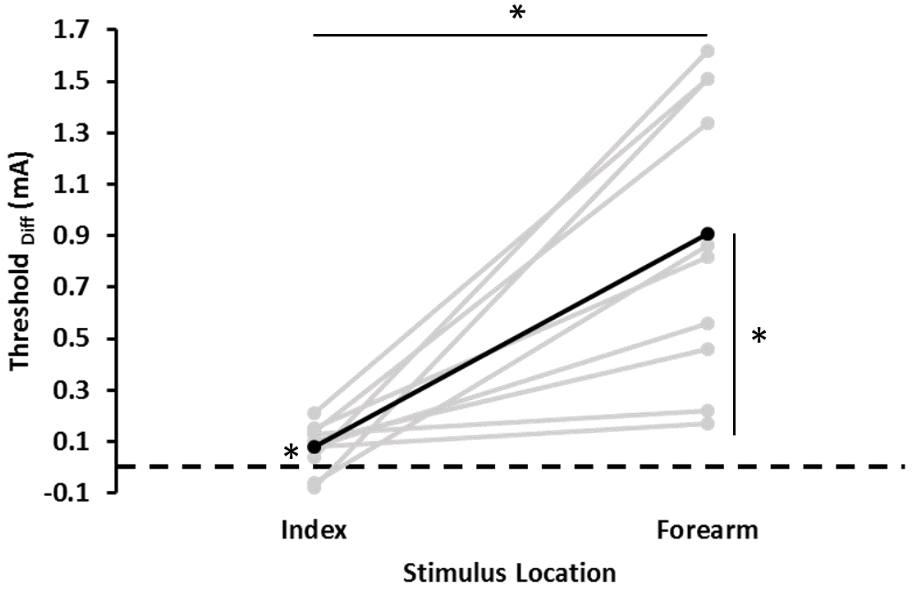

**Figure 5.1. Perceptual threshold difference as a function of stimulus location. The black line represents the mean values and the grey lines represent individual participant values. A positive non-zero difference score indicates that perceptual thresholds were higher during the movement relative to the period preceding the Go**

**signal. The vertical asterisk bar beside the stimulus location means values indicated a significant difference from zero. The asterisk between the mean values indicates a significant difference between the stimulus locations.**

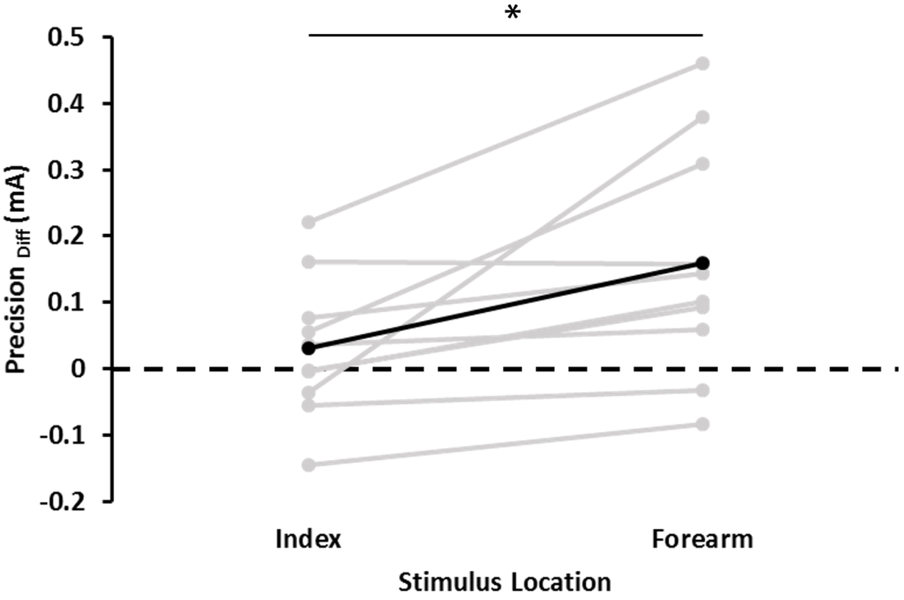

**Figure 5.2. Precision difference as a function of stimulus location. The black line represents the mean values and the grey lines represent individual participant values. The precision score reflects the slope of the psychometric function. A positive non-zero difference score indicates that the slope of the function was more gradual during the movement relative to the period preceding the GO signal. The asterisk between the mean values indicates a significant difference between stimulus locations.**

### 5.3.2 Movement-Related Measures

All movement-related variables are displayed in *Table 5.1.* The analysis of RT yielded a main effect of Stimulation Time ($F$ (1, 9) = 7.02, $p$ = .03, $n_p^2$ = .44) but failed to yield a main effect of Stimulus Location or any interaction between the two. The main effect of Stimulation Time revealed a significantly shorter reaction time in the pre-movement compared to the movement stimulation time (see *Table 5.1*). The analysis of MT failed to yield any main effects or interactions.

**Table 5.1** Means and between subject standard deviations for Reaction Time (RT; ms) and Movement Time (MT; ms) for both stimulus locations.

| | **Index Finger** | | **Forearm** | |
|---|---|---|---|---|
| | **Pre** | **Movement** | **Pre** | **Movement** |
| **RT** | | | | |
| ***mean*** | 344 | 369 | 340 | 381 |
| ***sd*** | 53 | 65 | 70 | 83 |
| **MT** | | | | |
| ***mean*** | 710 | 714 | 697 | 702 |
| ***sd*** | 22 | 24 | 30 | 28 |

## 5.4 Experiment 3 Discussion

In Experiment 3, participants performed self-driven reaching and grasping movements toward a stationary target. Before or during these movements, participants were presented with a range of electrical stimulation intensities to either the right index finger or right forearm in a blocked fashion. As in the previous experiments, the main dependent measure was the detectability of the stimulations. The aim of this experiment was to investigate whether there are any differential shifts in perceptual thresholds according to the relevance of the stimulation site.

Consistent with Experiment 1 and 2, participants displayed a shorter reaction time when the stimulus was delivered prior to movement onset compared to after movement onset. This confirms the facilitatory effect of the tactile stimulus in terms of reaction time found in Experiments 1 and 2 and aligns with the findings of previous research using a similar methodology (Voudouris & Fiehler, 2017). Further, similar movement times across conditions confirms that any differences in movement time did not affect the perception data.

When performing self-driven reaches toward a stationary target, participants displayed an increase in perceptual threshold compared to rest irrespective of the stimulus location. This result is indicative of tactile suppression at both a task relevant (i.e., index finger) and irrelevant site (i.e., forearm) on the moving limb during movement. In terms of the index finger, a shift in perceptual threshold during movement aligns well with both previous experiments. More importantly, a significant shift in the perceptual threshold replicates the findings of Experiment 2. This replication further validates the use of multiple stimulus intensities as opposed to one 90% threshold stimulus (Gertz et al., 2017; Voudouris & Fiehler, 2017). If the shift in perceptual threshold was relatively small (*M* = 0.08 mA), how does this account for the drastic reduction in detectability at the index finger in Experiment 1? Based on the results on Experiment 2 and 3, the 84% detection threshold during rest at the index finger roughly equated to the 50% detection threshold during movement (not reported). This implies that the stimulus used in Experiment 1 was around the perceptual threshold during movement for the index finger. With the additional attentional demands of the task in Experiment 1 it is not surprising that this resulted in a very low detection rate. In terms of the forearm, an increase in perceptual threshold during movement also aligns well with Experiment 1. That is, participants could not detect a previously readily detectable stimulus during movement in Experiment 1. With the current experiment, it is clear that participants could not detect the stimulus during movement due to a shift in their perceptual threshold. Although the magnitude of suppression was different (see below) the shift in perceptual thresholds was enough to reduce detectability and therefore failed to yield any differences according to task relevance in Experiment 1.

Along with Experiment 2, a significant shift in perceptual thresholds at both sites on the moving limb conflicts with the findings of Colino et al. (2014 & 2016). That is, this experiment again shows significant tactile suppression at the index finger and forearm, whereas the aforementioned work only shows this effect at the forearm. With all three experiments of this thesis displaying tactile suppression, it seems that a lack of suppression found in Colino et al.'s (2014 & 2016) work resulted from the use a suprathreshold vibratory stimulus. That said, tactile suppression during movement, even at task relevant locations, is consistent with previous research employing multi-joint, goal-directed movement (e.g., Juravle & Spence, 2010; Voudouris & Fiehler, 2017).

The magnitude of tactile suppression was greater at the forearm compared to the index finger (see *Figure 5.1*). On average, participants only felt a stimulus at the forearm during movement when the stimulus amplitude was 0.9 mA (*SD* = 0.55) larger than at rest corresponding to a 135% increase in perceptual threshold. At the index finger however, a 0.08 mA (*SD* = 0.09) increase in stimulus amplitude was necessary in order to elicit a correct detection corresponding to a 7% increase in perceptual threshold. Further, the precision change was larger at the forearm than at the index finger. Collectively, a larger increase in stimulus intensity was necessary in order elicit a correct detection at the forearm and larger steps in stimulus intensity were necessary in order to detect that any differences in stimulus intensity occurred.

The magnitude difference across stimulation sites provides evidence for the modulation of tactile suppression according to the relevance of sensory information at the stimulation site. Indeed, at a location in which tactile information may be important to the task, tactile information was suppressed to a lesser extent than a location in which tactile information is not important to the task. In their work using somatosenosry evoked potentials, Staines et al. (2000) showed less attenuation of SEP amplitude during passive limb movement when either cutaneous or proprioceptive information was relevant to the task compared to passive movement alone. This work suggests that the specific relevance of information can be used to selectively attenuate the degree of movement-related suppression. Recent behavioral work, in which participants pointed to either a visual target or their own opposite index finger, also suggest a flexible modulation of tactile sensitivity according to the relevance of sensory information, albeit on the non-moving target finger (Voudouris & Fiehler, 2017). When pointing to a visual target, there was no change in perceptual threshold at the static index finger. When pointing to the static index finger however, perceptual thresholds were decreased when compared to resting perceptual thresholds at the static finger. In this case, tactile sensitivity was enhanced at a task-relevant site although this finger was not involved in any movement.

Context dependent modulation of tactile suppression also aligns with Colino et al. (2014 & 2016) work. Although the current results demonstrate tactile suppression at all locations on the moving limb, tactile information is suppressed less at the index finger than at the forearm during a reaching and grasping task. Therefore, the current work provides support for the findings of differential suppression according to relevance of the stimulation site (Colino et al., 2014, 2016). From this work, we suggest that these authors presented a suprathreshold stimulus. The relatively large attenuation at the forearm and relatively small attenuation at the index finger likely accounted for their results. Even though the perceptual threshold likely increased at the index finger, the stimulus was too strong to elicit any decrease in detection rate. At the forearm however, the perceptual threshold shift was large enough to elicit a large decrease in detection rate. Although our results cannot lend support for a lack of tactile suppression at task relevant locations, the current experiment can help clarify their results.

In the context of the current experiment, it is likely that the prefrontal cortex contributed to the level of tactile suppression according to task relevance. SEP results suggests that any modulation according to the relevance of sensory information was accompanied by activation of the dorsolateral prefrontal cortex (Staines et al., 2002). When the excitability of the dorsolateral prefrontal cortex is inhibited using continuous theta-burst stimulation, SEP modulation according to task relevance is no longer evident (Brown et al., 2015). This is also corroborated by patient data in which damage to the prefrontal cortex results in an inability to filter out irrelevant sensory stimuli (e.g., Knight, Scabini & Woods, 1989; Yamaguchi & Knight, 1990). In the context of this experiment, I suggest that the prefrontal cortex may have facilitated sensory information from the index finger during the reach and grasp movement, although this was not directly measured.

# Chapter 6: General Discussion and Conclusions

The aim of this thesis was to investigate whether tactile gating is modulated according to task relevance during goal-directed movement. A secondary aim was also to investigate the role of central and peripheral processes to this suppression. In the current thesis, three experiments are presented in which participants performed targeted self-driven (Experiment 1-3) and motor-driven movement (Experiment 1-2). Before or during said movement, they were given a weak electrical stimulus to multiple relevant and irrelevant stimulation sites (Experiment 1, 3) or a single task relevant site (Experiment 2). In all experiments, stimulus detectability was the main dependent measure of interest.

Experiment 1 was intended to address some limitations in the experimental protocols of previous research employing similar methodology. Specifically, Colino et al. (2014 & 2016) had participants reach and grasp an object while presenting vibrotactile stimulation to the left and right index finger, little finger and forearm. The stimulus they presented however, was the same intensity at all sites and therefore differential sensitivity across stimulus locations was not controlled or accounted for. Further, the limited use of vibrotactile stimuli in the literature makes it difficult to compare these studies to other tactile suppression literature. In their experiments, tactile gating was evident at the forearm (i.e., a task irrelevant location for tactile information) but no such effect was found at the index finger (i.e., a task relevant location for tactile information). Of particular concern was the apparent lack of any suppression accompanied by low variability at the index finger (see *Figure 3.6*). In the current experiment however, when differential sensitivity across sites was controlled for and the same relative intensity was used, tactile gating was evident at all locations on the moving limb. Indeed, the forearm was significantly more sensitive than the index finger in our experiment, so scaling the intensity of the stimulus was necessary. In Experiment 2, this work was extended by directly investigating the shift in perceptual thresholds during movement as compared to rest. When only stimulating one task relevant stimulus location, tactile suppression remained evident in both the self and motor-driven movement condition and further, to the same degree. In Experiment 3, the magnitude of tactile suppression was greater at a stimulation site in which tactile information was not deemed important to the task (i.e., forearm) than a stimulation site in which tactile information was important to grasping (i.e., index finger).

In Experiment 1 and 2, the motor-driven condition was introduced to explore peripheral contributions to tactile gating during a reaching and grasping task. In the context of tactile suppression, this novel condition extends previous work exploring tactile suppression during passive single joint movement (e.g., Chapman & Beachamp, 2006; Williams & Chapman, 2002). In the context of these experiments, we support the notion that the perception of the tactile stimulus was likely masked by peripheral re-afferent information (Williams & Beachamp, 2006; Williams & Chapman, 2002). During the motor-driven movement, in which an efferent signal was likely not involved during the transport portion of the reach, several muscle and joint receptors are activated giving information about the movement onset as well as joint and limb position. This inflow of sensory information is likely stronger than the weak electrical stimuli used in these experiments and therefore masked the perception of this exafferent information. This result is also consistent with SEP work in monkeys in which the amplitude of SEP at various levels of the dorsal-column medial lemniscal pathway is reduced in line with the onset of movement (Chapman, 1994). We do not however show direct evidence for backward masking - that is, tactile suppression evident prior to the onset of movement (Williams & Chapman, 2002). In Experiment 1, the earliest stimulation time was in line with the GO signal. Looking at the reaction times reveals that the difference (in time) between the presentation of the stimulus and the onset of movement likely accounts for these results. Based on previous literature, tactile suppression begins approximately 50 ms prior to the onset of movement, depending on the task (Williams & Beachamp, 2006; Williams & Chapman, 2002). In Experiment 2 and 3, the earliest presentation time was specifically chosen to remove any effects backward masking might have on participants' perceptual thresholds.

We cannot rule out the possibility that movement-related masking accounted for the results in both the self and motor-driven conditions (Experiments 1 and 2). That is, even in the self-driven movement condition we found no evidence of suppression before the movement began. As in the motor-driven condition, the earliest presentation time was approximately 300 ms before the onset of movement. Again, based on the literature (Colino et al., 2014; Colino & Binsted, 2016; Williams & Chapman, 2002), you would not expect to see tactile suppression at times greater than 150 ms prior to movement onset. In both experiments, during movement it is likely that both the motor command and the movement-related afferent activity contributed to the reduced perception of the tactile stimulus. However, with the current experimental design it is difficult to parse out any differential contribution.

It is clear that in the self-driven movement condition, in which an efferent command is sent to move, that task relevant information cannot completely attenuate tactile suppression. This initial hypothesis was based on the assumption that tactile information is important in a reach and grasp task. Although these experiments were unimodal in nature, research exploring the weighting of sensory information in multisensory tasks suggest that sensory information is weighted according to the context of the task. For example, when pointing to a proprioceptive target participants will rely on proprioceptive information and when pointing to a visual target they will rely on visual information (even if this information leads to error; Sarlegna & Sainburg, 2005; Sober & Sabes, 2005). In the context of this experiment, we sought to explore whether the possible upregulation of tactile information would abolish tactile suppression during movement. In this study however, a readily detectable tactile stimulus was sparsely felt during movement (Experiment 1) accompanied by a shift in perceptual threshold (Experiment 2 and 3). A motor command in isolation has been shown to be enough to shift perceptual thresholds compared to rest (Voss et al., 2006, 2008). Further, SEP amplitudes are reduced prior to movement onset in active movements (Chapman, 1994; Cohen & Starr, 1987). In the self-driven movement, it is possible that the combination of the efferent motor command and the movement-related afferent information created a stronger masking stimulus than in the motor-driven task. If this is the case, then we would expect tactile suppression in both movement conditions. That said, the presence of a target in both conditions may limit the clarity of our conclusions (see Chapter 4.4). From Experiment 2, we cannot conclude whether similar amplitudes of tactile suppression occurred between the two conditions or whether they both attenuated some degree of tactile suppression.

Experiment 3 provides evidence that tactile suppression can be modulated according to task-relevance. Although participants suppressed tactile information at index finger (i.e., task relevant stimulation site; see above), the magnitude of suppression was significantly less than that of the forearm. The results of this experiment provide support for recent work displaying differential suppression according to task relevance (Colino et al., 2014, 2016; Voudouris & Fiehler, 2017). Although Colino et al. (2014, 2016) showed a lack of suppression, it is likely that the use of a supratheshold stimulus can account for their results. Indeed, the perceptual threshold likely increased at the index finger (Experiment 2 and 3) but the stimulus was still strong enough to elicit high detectability.

It is postulated that the purpose of movement-related sensory suppression is to reduce the vast amounts of sensory information that accompanies movement. This seems intuitive as we cannot uptake and attend to all of the possible sensory signals that flood our central nervous system. Prior to movement onset, evoked responses are suppressed at the level of the dorsal column nuclei (Ghez and Pisa, 1972) and the dorsal horn in the spinal cord (Seki, Perlmutter and Fetz, 2003; Seki and Fetz, 2012). This represents suppression at the first main relay to the somatosensory cortex. Further along the dorsal-column medial lemniscal pathway however, the magnitude of evoked responses is suppressed to a greater extent (i.e., at the sensory thalamus and S1; Chapman, 1994). These decreases in the magnitude of evoked responses are likely central in origin as they occur before the onset of movement, aligned with EMG activity, in active movement and aligned with movement onset when moved passively (Chapman, 1994). The smaller decrease in magnitude at the earlier stages during passive movement (i.e., medial lemniscus) may also implicate the role of the motor command at early as opposed to late stages in the pathway. Behavioural responses also align well with this work showing decreases in detectability of a readily detectable stimulus at EMG onset in active movement and slightly before movement onset during passive movement (Williams and Chapman, 2002).

The aforementioned work may represent a general suppression of sensory information prior to and during movement that is likely both central and peripheral in nature. The results of all three of the experiments provide behavioural support for this notion as participants displayed tactile suppression at all locations on the moving limb during both self and motor-driven movements. We extend this work by also providing evidence that although suppression may be a general consequence of movement, the amplitude of the suppression may be modulated according to task-relevance. In their work using evoked potentials, Staines et al. (2000) provided evidence that the amplitude of suppression can be attenuated depending on the relevance of the sensory information during passive limb movement. Further work (Brown et al., 2015; Staines et al, 2002) has implicated the prefrontal cortex in relevance-based filtering of sensory information. For example, when the excitability of the dorsolateral prefrontal cortex is reduced, any attenuation of suppression according to the relevance of the sensory information no longer exists (Brown et al., 2015). In the context of Experiment 3, perhaps the prefrontal cortex contributed to attenuation of tactile suppression at the index finger and the lack thereof at the forearm. Indeed, the results of Experiment 3 add to the growing literature suggesting modulation of tactile sensitivity according to task-relevance (Colino et al., 2014; Colino & Binsted, 2016; Voudouris & Fiehler, 2017).

Comparing behavioural work to physiological work does have its limitations however. Recent work suggests that sensory attenuation at the perceptual and physiological levels have different underlying neurophysiological correlates (Palmer, Davare & Kilner, 2016). In their study, these authors had participants perform a force matching paradigm while concurrently presenting median nerve stimulation in order to obtain SEPs. Not surprisingly, the force matching paradigm revealed that participants' overestimated force in the self condition compared to the external condition. During movement, SEP amplitudes were reduced compared to rest levels but this reduction was not modulated by task condition. That is, there was no effect of task (self or external) when looking at the primary and secondary components of the SEP. Further, the perceptual measures of sensory attenuation (i.e., force matching) significantly correlated with delusional ideation whereas physiological measures showed no such correlation (Palmer et al., 2016). Although this work explored sensory attenuation in the domain of self-produced stimuli, future work on movement-related sensory attenuation to external stimuli should work on directly comparing physiological and perceptual measures.

We cannot rule out an effect of attention when interpreting these results. Although attention likely has a role in attenuation of sensory information (e.g., Meyer et al., 1963; Williams, Shenasa & Chapman, 1998), we did our best to control for this confound in Experiments 2 and 3. Using a blocked as opposed to random presentation schedule (in terms of stimulation site) ensured that participants had prior knowledge of where the stimulation was presented. That said, we can assume that participants attended to that specific stimulation site. One caveat here is that participants may have also been attending to the index finger for the entire duration of the experiment as information here is relevant to the grasp. When stimulating the forearm, this may have resulted in a division of attentional resources leading to an increase in perceptual threshold during movement. Although we cannot dissociate attention and task-relevance, Experiment 1 may help rectify this result. When examining the stationary left index finger, a small but significant reduction in detectability was observed during movement (see *Figure 3.4*). The high attentional demands of the protocol likely accounted for this reduction. The reduction, presumably based on attention, was quite small however (approximately 20% decrease from rest). Considering that a small shift in perceptual threshold at the right index finger (Experiment 2 and 3 $M = 0.12$ mA) resulted in such a large decrement in detectability (approximately 60% decrease from rest), we can assume that the perceptual shift based on attention alone is less than 0.12 mA. The magnitude of tactile suppression at the forearm was 0.9 mA ($SD = 0.55$). Therefore, even if we subtract the effect of attention from this perceptual threshold shift, the magnitude of suppression at the forearm would still be much greater than at the right index finger. It is not clear however if attention affects perception in an additive or super additive nature.

Overall, this thesis provides novel findings in the context of tactile suppression during goal-directed movement. Perhaps the most important finding from this thesis is that tactile information is suppressed during movement at all locations on the moving limb. Where this work differs from other similar methodology is that this work (Experiment 1 in particular) accounts for any differences in sensitivity at different parts of the upper limb. When this integral confound is taken into account, it is clear that the detection of a relatively readily detectable stimulus is reduced during movement. We confirmed this result in Experiment 2 and 3 in which shifts in perceptual thresholds were directly assessed. Here, stronger stimuli were needed in order to obtain a perceptual threshold at a task-relevant site. Further, using a novel motor-driven movement condition showed a similar magnitude of suppression as a volitional self-driven movement condition. As far as we know, this is the first experiment to directly compare the two conditions in a goal-directed task. In Experiment 3, we used the more direct measure from Experiment 2 in order to further investigate any modulation of suppression according to task-relevance. On the moving limb, this is the first experiment to show differential shifts in perceptual thresholds according to the relevance of the stimulation site.

### 6.1.1 Future Directions

From this work, it is clear that when using multiple stimulation sites a randomized design may introduce attention as a confounding variable. That said, it is important that future work employs a blocked presentation schedule. In experiments such as these, participants are already performing a dual task (i.e., movement and perception). Using this methodology, any changes in perceptual thresholds will avoid any bias introduced by the increased attentional demands of a randomized schedule. It is also evident that future work employs the presentation of multiple stimulation amplitudes. This allows for a more direct assessment of perceptual threshold shifts. Ideally, both of these methods can be used in conjunction to make conclusion regarding reduced detectability (i.e., single amplitude method) and a corresponding shift in perceptual thresholds and or slope of the psychometric function (i.e., multiple amplitude method).

This thesis allows for much more research to be done investigating questions related to tactile suppression. The design of Experiment 2 and 3 in particular, will allow us to explore differential amplitudes of tactile suppression. Building off Experiment 1 and 3, we can further investigate the contribution of task-relevance to tactile suppression. For example, we can further probe this question by imposing a situation in which tactile information is not important to the task as opposed to being not important at specific stimulation sites on the limb. In this case, we can employ a pantomime or no target condition as compared to a target condition. During a targeted reach and grasp, tactile information at the fingers is important to grasp and hold the object. When performing a reach without the grasp component, this tactile information no longer seems relevant. Again, we would expect to see suppression in both the targeted and pantomime task, but the degree of suppression should differ. That is, tactile suppression at the index finger should be greater during a non-targeted reach compared to a targeted reach and grasp movement. This experiment would test any modulation at the index finger itself allowing for a robust effect of task relevance.

Future work should also explore tasks in which other parts of the moving limb are relevant. In the current thesis, and much of the existing literature, is it clear that during a reaching and grasping task tactile information is important at the effector grasping the object. Can we modulated tactile suppression at different sites in the same way we see modulation at the index finger? One way to address this question would be to employ a reaching movement in which the tactile stimulation determines the target location. For example, participants would plan to reach to a target in line with their midline. If they feel an electrical stimulation at the forearm however, they would be tasked with reaching toward a different rightward target. In this scenario, tactile information at the forearm is inherently important for the successful completion of the task. Compare this condition with a condition in which tactile information from the index finger determines the target location and any corresponding modulation would be indicative of task-relevance changing the suppression dynamics. In conjunction with the current thesis, these proposed experiments will allow for more robust conclusions in regards to tactile suppression during goal-directed movement.

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# Appendices

## Appendix A  Guessing Bayes Factor Calculation

### Guessing Bayes Factor (GBF)

$$GBF = \frac{(0.5)^t}{\iiint\limits_{a,b,\delta} P(r_1, r_2, \ldots r_t | \Psi_{a,b,\delta}) P(\Psi_{a,b,\delta}) d_a d_b d_\delta}$$

where $r_i$ refers to the participant's response (correct or incorrect) on the $i^{th}$ trial, $t$ is the total number of non-discarded trials in the testing block, and P($\Psi_{a,b,\delta}$) is the prior probability density over the psychometric function characterized by parameters $a$, $b$, and δ.