

EXPLORING BODY REPRESENTATIONS: EFFECTS OF VISUOTACTILE  
CONGRUENCY ON SENSORIMOTOR EEG MEASURES

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A Dissertation  
Submitted to  
the Temple University Graduate Board

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In Partial Fulfillment  
of the Requirements for the Degree  
DOCTOR OF PHILOSOPHY

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by  
Ashley Robyn Drew  
May 2017

Examining Committee Members:

Peter J. Marshall, Advisory Chair, Department of Psychology, Temple University  
Thomas F. Shipley, Examining Chair, Department of Psychology, Temple University  
Elizabeth Gunderson, Department of Psychology, Temple University  
Tania Giovannetti, Department of Psychology, Temple University  
Nora Newcombe, Department of Psychology, Temple University  
David Smith, Department of Psychology, Temple University

## ABSTRACT

There has been a recent growth of interest in exploring the complexities of multisensory processes underlying human body representation. One cross-modal aspect of body representations involves the visuotactile body mapping between tactile stimulation of a body limb and the observation of a body limb. Previous findings demonstrate that visual information influences the spatial and temporal patterning of brain responses to tactile stimulation. By manipulating the congruency of the visuotactile stimuli, the integration of visual and tactile information of the body can be investigated further.

In the current studies, electroencephalography (EEG) was used to record the neural responses to touch during congruent and incongruent visuotactile stimuli in adults and infants. Two studies investigated different characteristics of visuotactile congruency on the neural response to touch during observations of others' bodies. In Study 1, spatial congruency of visuotactile events in adults was examined by recording electrophysiological responses to tactile stimulation of the hand in different postural positions while viewing pictures of hands. In Study 2, visuotactile body mappings were explored within typically developing, preverbal infants. In the second study, infants received tactile stimulation to their hand or foot while viewing the hand or foot of another person. The findings of both studies indicate neural modulations were driven by the viewed stimuli regardless of the visuotactile congruency suggestive of attentional factors at work during late stages of somatosensory processing.

## ACKNOWLEDGEMENTS

A tremendous amount of work by numerous people was put into the writing of this dissertation. Firstly, I would like to acknowledge the lab members who helped me carry out the many steps involved in this project from data collection to analyses. Of my lab members, I would like to especially recognize Dr. Guannan Shen for thoughtful discussions and help with data analyses, Rebecca Laconi for taking responsibility of the difficult recruitment task, and Dr. Joni Saby for assisting me with setting up and analyzing my first study with infants.

I would like to convey my gratefulness to my advisor, Dr. Peter Marshall not only throughout my dissertation work, but also for his continual support throughout graduate school. Dr. Marshall gave me the opportunity to pursue my goals in his lab, and in the past five years, he has taught me a great deal about psychology, education, and mentorship.

Lastly, I would like to thank my family, who taught me the value of working hard for my achievements and who consistently provide a foundation for continuing my career. And a special thanks to my friends, who constantly encouraged me even when I expressed my own doubts. Gail, Kylie, and Rachel, you made my experience through graduate school much more fun and I am so glad to share this achievement with all of you.

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# CHAPTER 1

## INTRODUCTION

Despite the array of stimulation from multiple modalities that we receive in any given moment, our experience of the world when we interact with it is usually one of a coherent, single reality. This unitary experience is founded in a process of multimodal integration that has clear functional relevance through allowing coordinated action. Understanding this integrative process is key to understanding the central role of the body and of bodily experience in structuring the known world (Marshall, 2016). Progress in this area also requires a multilevel perspective on what can be termed “body representations”, a broad construct that encompasses experiential, implicit, and neural aspects of the body of the perceiving and acting individual.

When multimodal integration is properly coordinated, humans can move about the world seamlessly and perform guided actions. However, if the coordination between modalities is disrupted, even the simplest task can become profoundly difficult. In order to understand these processes better, the congruency between bodily stimuli in different modalities can be experimentally manipulated. While prior studies employing such methods have investigated the modulation of congruent visual information of the body part being stimulated on neural responses to tactile stimuli, no study has yet manipulated the spatial congruency between visual and tactile input of the body part being stimulated. The current document describes two studies using electroencephalographic (EEG) methods. Study 1 examined EEG responses to tactile stimulation of the hand in relation to changing spatial locations of the viewed and stimulated hand. Study 2 took a

developmental perspective on related questions to shed new light on the representation of the body in infancy (Marshall & Meltzoff, 2015).

### **Sensorimotor Body Representations**

The various ways in which “body representation” has been studied can make it difficult to pin down an exact definition of this construct. Two types of body representations have commonly been invoked in the literature: body schema and body image (Berlucchi & Aglioti, 2010). The body schema has been proposed as an implicit, sensorimotor representation of the body that guides an individual's actions. On the other hand, the construct of the body image involves other conceptual and emotional representations of the body that may be more consciously accessible, including body ownership or self-consciousness as related to the body (Berlucchi & Aglioti, 2010; de Vignemont, 2010; Marshall & Meltzoff, 2015).

One approach to the study of body representations has been to examine the neural processes involved in the organization and maintenance of body-related information in the brain. Perhaps the best-known neural representation of the body in the brain is the somatotopic representation of the body surface in the somatosensory cortex, which is sometimes referred to as a “body map”. Marshall and Meltzoff (2015) suggested that body maps in the brain may be one building block of the wider construct of the body schema and that they may be further related to other body image concepts (e.g., body ownership). As one aspect of the body schema, body maps may be closely involved in the mechanisms that register associations of the body across different modalities (e.g., across vision and touch). Marshall and Meltzoff (2015) also suggested that cross-modal coherence related to one's body might play a role in aspects of social interaction and how

one relates with others. As such, representations of one's body may be important in what can be termed "self-other correspondence" meaning the registration of similarities and differences between oneself and other people. The suggestion here is that when one is viewing the body of another, body maps in the brain may be involved in registering correspondences between the viewed body part and the corresponding body part of one's own body.

Bodily aspects of self-other correspondences have sometimes been studied under the term "interpersonal body representations" (Thomas, Press, & Haggard, 2006). It has been proposed that these bodily connections between self and other are involved in social processes and may provide a foundation on which interpersonal relationships are built (Marshall & Meltzoff, 2015; Thomas et al., 2006). One avenue for studying such interpersonal aspects of body representation is examining how vision of others' bodies influences the processing of tactile stimulation to one's own body. The current studies examine how neural responses to touch on one's own body are influenced by the vision of the bodies of others. If vision of another's body modulates the neural response to touch, this would be suggestive of a registration between the body representation of self and the representation of the body of another person.

A central theme in the study of neural responses to touch in the mammalian brain has concerned the orderly representation of the body as exemplified through somatotopic body maps in the cortex. A vast amount of research in human adults and in non-human animals has shed light on the properties of these somatotopic maps. Most notably, classic neurological research with humans led to the description of the neural arrangement of body parts within the primary somatosensory cortex (SI), which is often depicted as a

homunculus (Penfield & Boldrey, 1937). Although much of the early work on body maps involved relatively invasive methods, research in recent decades has often employed non-invasive techniques such as functional magnetic resonance imaging (fMRI), transcranial magnetic stimulation (TMS), magnetoencephalography (MEG) and EEG. In the current document, the majority of the studies to be discussed have employed the technique of EEG.

One advantage of employing EEG in the study of body maps is the temporally fine-grained way it allows for the examination of the processing of tactile stimulation at relatively low cost and with little discomfort to the participants. Temporal precision provides a window into exploring stages of somatosensory processing. Even with their inherently limited spatial resolution, EEG techniques can pick up on the somatotopic organization of responses to tactile stimulation (Longo, Pernigo, & Haggard, 2011; Saby, Meltzoff, & Marshall, 2015; Voisin, Marcoux, Canizales, Mercier, & Jackson, 2011). Recent work has shown that EEG methods can be used to show how somatotopic maps can be blurred or sharpened across body parts on a short timescale by manipulating the congruency of visual and tactile input of the limb being stimulated (Cardini & Longo, 2016). This suggests that by altering the congruency between visuotactile events, somatotopic organization of body part representations can be modulated. The goal of the current studies is to use EEG methods to examine the influence of the congruency of the hand in space in adults (Study 1) and congruency of the limb type in infants (Study 2) between vision and somatosensation on body representations.

In the current studies, two EEG measures were used to study the influence of vision on the neural response to touch: 1) the sensorimotor alpha rhythm, which is also

often referred to as the mu rhythm and 2) somatosensory evoked potentials (SEPs). While the origins of each type of measure (mu rhythm and SEP) are different and remain partly unknown, each provide measures of neural mechanisms involved in body representations, and more specifically in processing visuotactile stimuli involving the body.

Both the mu rhythm and SEP responses are typically examined at central electrode sites overlying sensorimotor regions of the cortex. Consistent with the focus on body representations, both of the current studies examine the mu rhythm and SEP responses at the left and right central electrode sites (C3, C4), with the addition of the midline (vertex) central site (Cz) in Study 2. A diagram of the scalp locations of these electrodes is shown in Figure 1. Electrode Cz is located medially over the scalp while electrodes C3 and C4 are located laterally with C3 overlying the left hemisphere and C4 overlying the right hemisphere. Although the relatively small number of electrodes used in the current study precludes a high level of specificity in localizing of the neural responses, prior work suggests that broad somatotopic responses to tactile stimulation can be detected across central electrode sites in low-density arrays (Allison, McCarthy, & Wood, 1992; Saby, Meltzoff, & Marshall, 2013; Saby et al., 2015). In line with the somatotopic organization of somatosensory cortex, tactile stimulation of the right hand elicits the largest response in the EEG signal over the contralateral (left) electrode C3, stimulation of the left hand elicits a response over the contralateral (right) electrode C4, and tactile stimulation of the foot elicits a response at the midline central electrode (Cz) (Allison et al., 1992; Nakamura et al., 1998).

***The Sensorimotor Mu Rhythm.*** The mu rhythm oscillates in the alpha frequency range of 8-13 Hz in adults (lower in infants and children) at central electrode sites

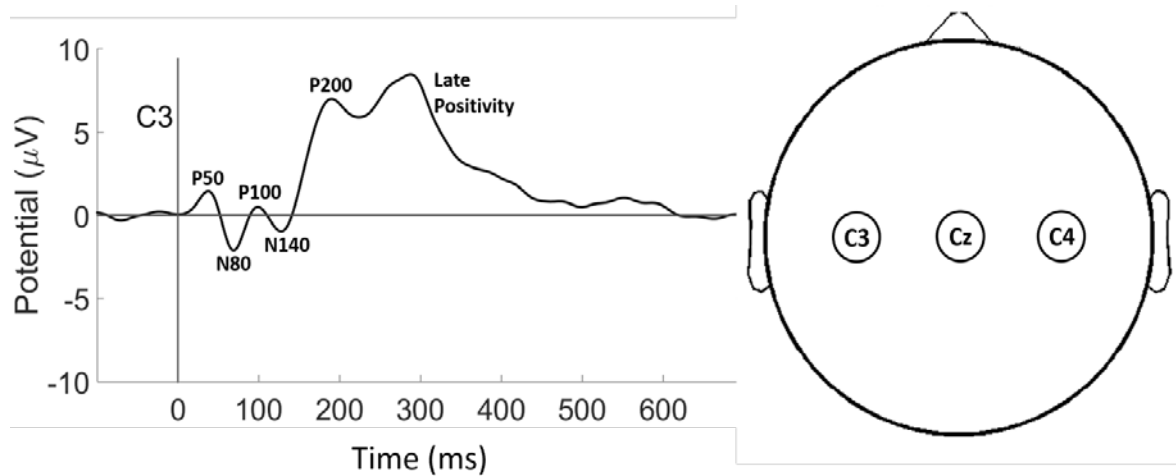


Figure 1. Somatosensory Evoked Potential (SEP) and Electrode Map. An averaged SEP response to tactile stimulation of the right finger in adults. The response shown is from electrode C3, contralateral to the tactile stimulation. The typical components of an SEP response are labeled. The diagram to the right shows the scalp location of the central electrodes (C3/Cz/C4) from which responses were analyzed in the current studies.

overlying sensorimotor regions. This rhythm is sensitive to voluntary or observed movements in both adults (Pfurtscheller & Lopes da Silva, 1999; Pineda, 2005) and infants (Marshall & Meltzoff, 2014; Marshall & Meltzoff, 2011). The response of the mu frequency band in the EEG signal is often time-locked to a specific event to gain information about the synchronous voltage changes across neuronal networks in the cerebral cortex relevant to that event (Pfurtscheller & Lopes da Silva, 1999). The reduction of mu power in response to a stimulus, often called event-related desynchronization (ERD), is generally associated with an increase in cortical activation. Likewise, an increase in mu power, often called event-related synchronization (ERS), has been associated with a decrease in cortical activation or an idling state (Pfurtscheller & Lopes da Silva, 1999; Pineda, 2005), although other work suggests ERS reflects active inhibition of underlying neural regions. Specifically, mu ERS is postulated to have a

functional role in attentional suppression of somatosensory regions (Foxe & Snyder, 2011). During an anticipation period for an upcoming tactile event, mu rhythm power decreases over sensory regions relevant to the upcoming stimulus and increases over regions that are less relevant. This pattern has been proposed to reflect attentional inhibition of distracting or irrelevant stimuli (Haegens, Händel, & Jensen, 2011; Jones et al., 2010; Shen, Saby, Drew, & Marshall, 2017; van Ede, de Lange, Jensen, & Maris, 2011).

Although anticipatory responses of the mu rhythm to upcoming tactile stimulation have been well studied, much less is known about the post-stimulus mu rhythm response immediately following delivery of a tactile stimulus. In general, the mu rhythm has been used to investigate sensorimotor brain responses to the execution and observation of overt movements, particularly hand movements (Drew, Quandt, & Marshall, 2015; Perry & Bentin, 2009; Pfurtscheller & Lopes da Silva, 1999; Quandt, Marshall, Bouquet, & Shipley, 2013). In some of these prior studies, the mu rhythm was shown to respond in a somatotopic manner when participants are performing actions as well as when they observe live-action or video-recorded actions performed by others. These findings suggest that the mu rhythm may be useful in the study of self-other correspondences mapping body-specific visual information of others onto the body representation of the self. In the same way, the mu rhythm is predicted to be a window into studying somatosensory processing of visuotactile stimuli as the mu rhythm appears to have generators in SI (Marshall & Meltzoff, 2011).

Studies reporting on the mu rhythm response to touch have generally shown an initial decrease (ERD) in mu power that is characterized by a somatotopic scalp

distribution. Mu rhythm desynchronization contralateral to the stimulated hand has been reported in MEG studies following punctate tactile stimulation (Cheyne et al., 2003; Gaetz & Cheyne, 2006), sustained tactile stimulation (van Ede, Szebényi, & Maris, 2014), and median nerve stimulation (Della Penna et al., 2004). One EEG study described a decrease in mu power in response to tactile stimulation that was then followed by an increase in mu power (ERS) around 500 ms after the onset of stimulation (Anderson & Ding, 2011). However, this study did not report statistical analyses of the ERD or ERS responses following the tactile stimulation, in part because the objective of that study was to investigate attentional processes occurring prior to the tactile stimulation. Thus, more work is needed to understand mu rhythm responses during somatosensory processing and its possible utility for studying cross-modal body mappings on the processing of visuotactile stimuli.

***Somatosensory Evoked Potentials.*** A well-studied aspect of electrophysiological responses is the SEP, which is a time-locked event-related potential (ERP) response averaged across trials to the onset of somatosensory stimulation. As with the mu rhythm, SEP responses are typically examined at central electrode sites (see Fig. 1 for an illustration of a typical SEP response recorded from central sites in adults). Generally, early components of the SEP are thought to reflect processing within primary somatosensory cortex (SI), the main receptive area for somatosensory afferent input (Hari et al., 1993). The early scalp-recorded SEP components associated with this early somatosensory processing occur within the first 100 ms after tactile onset (i.e., P50, N80) and are often examined via measurement of contralateral responses to the tactile stimulation (Allison et al., 1992). Subsequent SEP components (P100, N140, P200),

usually recorded as bilateral responses, are associated with processing in secondary somatosensory cortex (SII) (Allison et al., 1992). The role of SII in tactile processing includes feature processing such as the texture of the stimulus (Ledberg, O'Sullivan, Kinomura, & Roland, 1995) and the integration of information from the right and left sides of the body (Hari et al., 1998). Later scalp-recorded SEP components (after 250 ms post-stimulus) such as the P3 complex are less clearly identified with specific neural sources. Some work has suggested that these later components reflect a convergence of multisensory information (Longo et al., 2012) or are related to self-other distinction (Deschrijver, Wiersema, & Brass, 2015). Therefore, late SEP components may be telling of the bodily congruency between visuotactile stimuli.

### **Visuotactile Somatosensory Responses**

It may be tempting to think of the brain as registering sensory input of a tactile event, determining the bodily location from which it came, and then passing that information on as the perception of a touch to higher brain circuits, without the involvement of other sensory modalities. However, this picture is too simplistic. For instance, when you swat away an insect that landed on your body, you not only feel the insect on your skin, but you may also be able to see the insect on your body. Here, your visual sense provides additional information along with tactile information about the touch of the insect and proprioceptive input from your body posture, enabling you to quickly locate the insect and initiate an action to swat it away. Thus, even this simple action in response to a tactile stimulus depends on the successful integration of information from different modalities (de Vignemont, 2014). However, a number of questions remain as to how and when cross-modal information is integrated within the

brain. This aspect of multisensory mechanisms has often been investigated through examining the interplay between vision of the body and the perception of touch.

Various studies have demonstrated that viewing body parts while receiving tactile stimulation modulates behavioral responses to that touch (Kennett, Taylor-Clarke, & Haggard, 2001; Press, Taylor-Clarke, Kennett, & Haggard, 2004; Tipper, Lloyd, & Shorland, 1998). In one such study, adults were asked to respond as quickly as possible to tactile stimulation of various bodily locations (Thomas et al., 2006). Just prior to the stimulation, participants viewed a visual marker on a human model projected in front of them. When the location of the visual marker on the model matched the location of the tactile stimulation on the participant, participants were significantly faster at detecting the stimulation than when the visual marker was presented at a different bodily location from the tactile stimulation. Moreover, these results did not hold for a non-body visual control stimulus, suggesting that the cross-modal association between visuotactile information tested was body-specific (Thomas et al., 2006).

Work in cognitive neuroscience also supports the behavioral evidence that body-specific visual information modulates tactile processing. Using EEG techniques, a number of studies have reported modulations of the neural response to tactile stimulation of the hand or arm while participants viewed a hand or arm (Taylor-Clarke, Kennett, & Haggard, 2002; Cardini, Longo, Driver, & Haggard, 2012; Deschrijver, Wiersema, & Brass, 2015; Longo, Pernigo, & Haggard, 2011; Sambo, Gillmeister, & Forster, 2009). One of the earliest studies to show such a modulation examined the SEP at contralateral central electrodes in response to tactile stimulation of the arm (Taylor-Clarke et al., 2002). When adults viewed their own stimulated right forearm, compared to viewing an

illuminated cylinder overlying the exact location of their forearm using a mirror, there was a contralateral enhancement of the SEP component that occurs approximately 80 ms after the tactile stimulation (the N80). Subsequent studies provided more information on temporal aspects of visual influences on the SEP signal. In line with the findings of Taylor-Clarke et al. (2002), these studies examining body-specific visual influences on somatosensory responses of the hand showed evidence of effects within the first 100 ms window following the onset of tactile stimulation. Some studies reported differences arising within the first 50 ms (Cardini et al., 2012; Longo et al., 2011) although others did not find divergence until between 50 and 100 ms (Deschrijver et al., 2015; Sambo, Gillmeister, & Forster, 2009; Taylor-Clarke et al., 2002). Due to the small temporal scale scrutinized, these mixed findings may have arisen from variations in protocol such as the type or location of tactile stimulation. However, it is clear from the studies that viewing the body modulates the SEP response to tactile stimulation during a time window that likely reflects somatosensory processing within SI.

The effect on the SEP response of viewing a body part compared to a non-body control stimulus has also been reported in time windows associated with SII activity – specifically the N140 or P200 components (Deschrijver et al., 2015; Sambo et al., 2009; Taylor-Clarke et al., 2002). Unlike the unilateral (contralateral) response of components associated with SI activity, visual influences on the N140 and P200 have generally been found bilaterally. Some studies report differences in the SEP response at the N140 component as more stable in that they do not seem to be related to other task dependent conditions (i.e., observed finger movement; respond to tactile or auditory stimuli) as experiments found in the early components (P50, N80) (Deschrijver et al., 2015; Taylor-

Clarke et al., 2002). However, there is evidence from other studies that differences in the N140 between viewing a limb or another object are dependent on more general attentional factors (Cardini et al., 2012; Ohara, Lenz, & Zhou, 2006). This relates to the suggestion that the tactile N140 response is influenced by somatosensory processing occurring in frontal brain regions (Allison et al., 1992). Further work is needed to disentangle factors such as task-relevancy and attention that are influencing the SEP response in early stages of somatosensory processing.

Compared with earlier potentials, later scalp-recorded SEP components (after 250 ms post-stimulus) may reflect higher-order processing of information or multisensory integration occurring across various cortical regions. In studies reporting SEP components in the range of 200 ms after the onset of a tactile stimulus, influences of visual input on these later components depends upon congruency between the visual information of a body part or spatial attention with the location of the tactile stimulation (Deschrijver et al., 2015; Longo et al., 2012; Sambo et al., 2009). These congruency effects add another dimension to the visual modulation of the SEP at earlier processing stages. While the visual effect on early SEP components involves viewing a limb compared to not viewing a limb or a different object, the effect of congruency compares observation or attention toward the location of tactile stimulation with attention toward a bodily location not being stimulated (right or left hand; index or middle finger). Studies in this area have found that the effect of congruent visuotactile information appears to be specific to the stimulated limb (e.g., hand or foot) (Voisin et al., 2011), hand (left or right) (Sambo et al., 2009), and even finger (Deschrijver et al., 2015; Longo et al., 2012). For instance, Sambo and colleagues (2009) asked participants to covertly direct their

attention toward either their left or right hand while tactile stimulation occurred on either the attended or unattended hand. SEPs elicited during the attended and unattended tactile stimulation conditions were compared when participants either had full vision of their hands, when their hands were covered from view, or when they were blindfolded. In all three conditions, the congruency of the direction of attention to the left or right hand (congruent: attending toward stimulated hand; incongruent: attending towards the opposite hand) was found to modulate the SEP response in a time window of 200-300 ms following tactile stimulation. Additionally, attentional effects were also found in earlier SEP components (P100 & N140) when the participants had full view of their hands, suggesting that effects of attention on earlier processing stages are only apparent when visual input of the body is available.

In a related study, participants viewed pictures of right hands or feet in painful or nonpainful situations while receiving repetitive tactile stimulation of the right hand (Voisin et al., 2011). Excitability of somatosensory cortices was examined using steady-state EEG methods. Excitability was greatest while participants viewed the hand in a painful situation, providing evidence for a limb-specific modulation. While cortical excitability was not tested during foot stimulation, behavioral studies have reported improvement of tactile acuity for stimulation of the legs or feet while viewing congruent body parts (Pozeg, Galli, & Blanke, 2015; van Elk, Forget, & Blanke, 2013). Conversely, one study reported that tactile acuity of the back did not change when participants observed their backs using real-time video footage (Catley et al., 2014). A suggested reason for this finding is that upper and lower extremities are frequently within one's field of vision, whereas vision of the back is limited or nonexistent. In the case of the

back then, neural connections of visuotactile information may not be formed. In summary, the literature discussed above in general tested neural modulations of visual input of the hand (see Fig. 2 for an example; contrast between panel A and panel E) and of the congruency of the limb viewed to the limb stimulated during somatosensory processing.

While the study of neural body representations is undergoing a surge of growth, there are still a number of key questions to be addressed. One intriguing question is whether representations of one's own body map are connected with the representations of the body of others. It has been well documented in human adults that the motor and

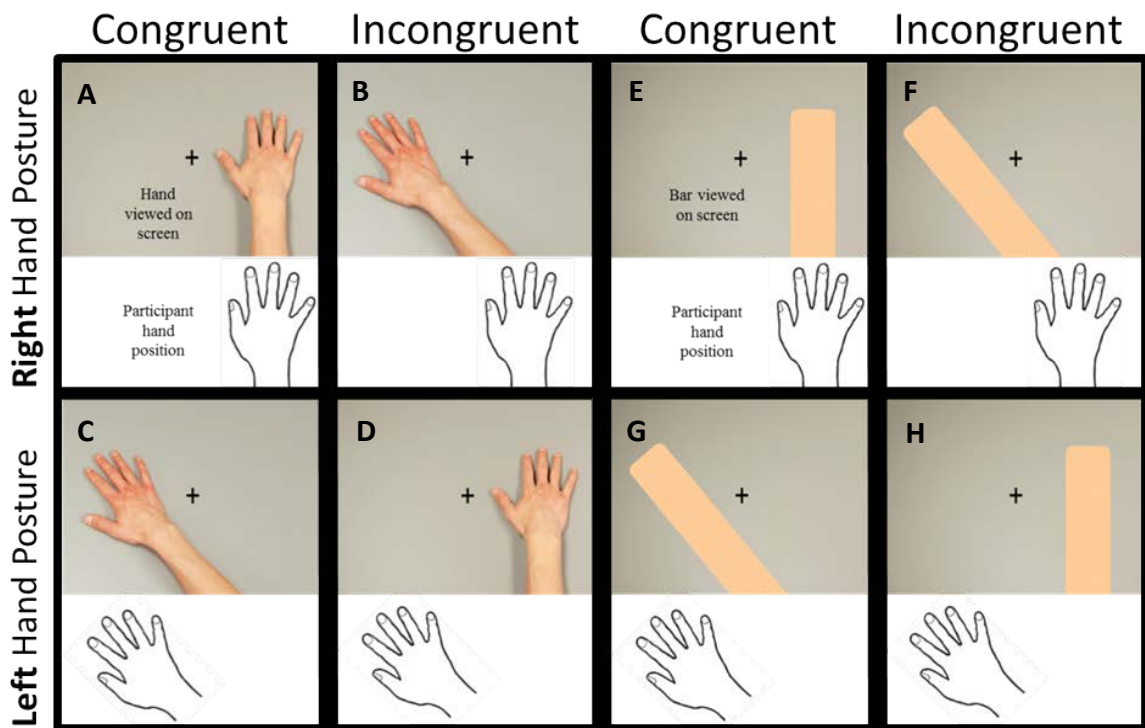


Figure 2. Eight Conditions for Study 1. The conditions vary by the pictures viewed of hands or bars (Object) on the screen in either a right or left space (Congruency). The placement of the participant's right hand varies between blocks between a right and left location (Hand Posture).

sensory cortices allowing the control of movement and the registration of touch are also involved in the processing of movements and inferring the perceptual experience of others (Keysers et al., 2004; Rizzolatti & Craighero, 2004; Singer et al., 2004). This vicarious aspect of sensorimotor processing may be based on associations between visual and tactile information, as in the case of watching someone lift an object with their hand and the activation of a corresponding representation of what it would be like to perform this action oneself (Thomas et al., 2006). As one aspect of interpersonal body representations, studying these visuotactile correspondences could provide valuable insights into the origins and maintenance of social relatedness in humans. According to the “Like-Me” hypothesis, social cognition begins in the human newborn through a process of observing that other humans are similar to me at the level of bodily actions and therefore may have goals and intentions, as I do (Meltzoff, 2013). Imitation in infancy is often taken as an early sign of this connection, since it necessarily involves a mapping of the body of another onto the infant’s body representation – a process that may involve registering correspondences between one’s own body and the body of others.

Although many of the studies discussed above have focused on the visuotactile events involving one’s own body, of particular interest here are studies of tactile processing involving the vision of the bodies of others. A few studies have provided behavioral evidence for an improvement in tactile acuity when participants viewed an artificial or rubber hand or foot (Pozeg et al., 2015; Thomas et al., 2006; van Elk et al., 2013). There has also been a limited number of studies examining SEPs while participants viewed videos of another’s hands or face (Adler, Schabinger, Michal, Beutel, & Gillmeister, 2016; Deschrijver et al., 2015). Informally combining the results of these

studies, the SEP components elicited during viewing of another person's hands appear to resemble the SEP components when participants viewed their own hand (Deschrijver et al., 2015). However, the studies using video of hands and face of another person involved synchronies between the observed and felt tactile events (i.e., viewing tactile stimulation such as a rod touching a hand at the same time that stimulation occurs on the participant's body). Since synchrony of visual and tactile stimulation is likely to increase an individual's sense of body ownership over the observed body part (see below), whether or not these studies show SEP response to viewing another's body is uncertain as participants may begin to have feelings of ownership over the visual. Thus, more research is needed to substantiate and clarify these findings in order to understand the role of cross-modal correspondences in interpersonal contexts.

***Body Ownership.*** Body ownership is the subjective experience of owning a body and alone having ownership over that body (Tsakiris, 2010). By manipulating multisensory contingencies related to the body, illusions such as the Rubber Hand Illusion (RHI) can deceive a person into claiming body ownership over fake body parts (Botvinick & Cohen, 1998; Grivaz, Blanke, & Serino, 2017). The RHI and related illusions involve synchronizing tactile input with the observation or sensation of touch (Ehrsson, Holmes, & Passingham, 2005). This is similar to studies examining visuotactile stimuli while observing one's own body, as discussed above (Cardini et al., 2012; Longo et al., 2011; Sambo et al., 2009; Taylor-Clarke et al., 2002). What these studies have in common is the observation of a body part and the tactile stimulation of a congruent limb. However, studies examining visual influences on SEP responses have not generally reported on feelings of ownership, since participants are usually viewing their own body.

However, body ownership may be an important factor to consider in studies where participants are observing body parts other than their own while receiving tactile stimulation to their own bodies.

Specific cortical areas involved in cross-modal integration and also important to representations of body ownership have been identified, including the premotor cortex and cerebellum (Ehrsson et al., 2005; Serino et al., 2013). Activity in these areas is positively related to participant report of body ownership during the RHI illusion (Ehrsson et al., 2005). One study used EEG and synchronized visuotactile stimuli of the hand to explore neural measures of body ownership (Evans & Blanke, 2013). As feelings of body ownership increased, stronger mu ERD was observed in a somatotopic pattern. In this case, the mu rhythm may be reflective of neural signatures of a state of body ownership. In terms of SEP responses, a recent study explored SEP responses to synchronized touches on the face comparing observations of a touch occurring on the self or another's face (Adler et al., 2016). In addition, there were also trials in which a rod was seen next to the face (but not touching) in the picture of the self or another's face even when the participant still received tactile stimulation to their face. Differences in the SEP were observed in touch vs. no touch trials of both the self and other prior to 100 ms, likely reflecting SI involvement. However, self-related events seemed to precede other-related events with differences observed in the P45 component when viewing one's own face and differences observed in the N80 component when viewing another's face. Additionally, this study was the first to report individual differences of synchronized visuotactile events in SEPs based on participants' self-reported depersonalization character – feelings of detachment from one's self or body. Participants were split

between high and low depersonalization groups depending on their self-reported answers to a depersonalization scale. Crucially, the SEPs of participants in the high depersonalization group did not show touch vs. no touch differences for the P45 component while observing their own face, as was found in the low depersonalization group. The response of the N80 to viewing other's faces was the same in both groups. Therefore, feelings of connection to one's bodily self appear to modulate SEP responses to visuotactile stimuli, which suggest that patterns of visuotactile processing may influence, and be influenced by, a sense of body ownership over the viewed body part.

### **Spatial Frames of Reference**

Using a combination of visual and proprioceptive input, information about one's current body positioning (i.e., posture) is also important for the localization of touch and for somatosensory processing. Taking an earlier example, imagine that an insect lands on your hand and you need to localize the bodily location it landed in order to swat it away. In order to achieve this, you must take into account two different spatial reference frames of bodily locations (Heed, Buchholz, Engel, & Roder, 2015). First is the anatomical frame of reference, or the specific body part or area of your body in which the event is occurring. For instance, the insect may have landed on your right as opposed to your left hand. The second frame of reference concerns where your body part is in space. Even though the insect landed on your right hand, your right hand may currently be located across the midline of your body (i.e., on the left side of your body). In terms of the two frames of reference, the insect landed anatomically on your right hand; however, it landed externally in your left space. Alternatively, if your right hand happened to be located (as it usually would be) in your right space, the insect would be in your right

space both anatomically and externally speaking. Clearly, the combination of visual and proprioceptive information about your body in space must contribute in some way to the representation of your body.

In order to parse apart the relation between these two frames of reference in tactile processing, a crossed hands method is often utilized in conjunction with a tactile localization task (Aglioti, Smania, & Peru, 1999; Bartolomeo, Perri, & Gainotti, 2004; Groh & Sparks, 1996). In this technique, participants either have their hands resting in front of them in an uncrossed position, with their right hand in the right space (and left hand in left space), or a crossed position, with their right hand in the left space (and left hand in the right space). Responses to tactile stimulation can then be compared when the anatomical and external frames of reference are either matching (uncrossed) or not matching (crossed). One common task in these studies involves tactile temporal order judgments (TOJs) (Heed & Azañón, 2014). In a TOJ task, participants receive two tactile stimuli on different hands but in close temporal succession to one another. The task of the participant is to identify the hand to which the first tactile stimulus of the pair was delivered. Along with reaction time and localization accuracy of the participants, the necessary time between the two stimuli in order for participants to achieve a certain level of accuracy can be determined. When participants' arms are in a crossed position, their response times and accuracy are significantly impaired and a longer time window between the two stimuli is needed in order for participants to correctly localize the hand of the first stimulus compared to an uncrossed position (Heed & Azañón, 2014). These TOJ studies show that both anatomical and external frames of reference are encoded when processing tactile stimulation. Several theories purport to explain the localization

impairment in the crossed arm position (Badde, Heed, & Röder, 2014; Shore, Spry, & Spence, 2002; Takahashi, Kansaku, Wada, Shibuya, & Kitazawa, 2013; Yamamoto & Kitazawa, 2001). Importantly, all of the theories propose the occurrence of a spatial remapping in order for correct localization of touch to occur informed by the anatomical localization and information of the body in space (Heed, Buchholz, Engel, & Röder, 2015).

In addition to behavioral studies, the specific time course of the remapping of reference frames has been investigated by combining the crossed hands technique with the temporal accuracy of EEG recordings (Heed & Röder, 2010; Soto-Faraco & Azañón, 2013). One study by Rigato and colleagues (2013) examined SEPs elicited by tactile stimulation to hands in a crossed or uncrossed posture. Regardless of whether the participants were able to view the position of their hands, differences in the SEP were found for the N140 component such that the crossed hands condition was associated with a larger negative peak. This finding is consistent with other studies reporting differences occurring 100-140 ms post-stimulus (Heed & Röder, 2010; Ley, Steinberg, Hanganu-Opatz, & Röder, 2015). The difference in the SEP waveform between the two hand postures suggests the occurrence of a spatial remapping as the external reference frame of the touch was the only change between conditions. Since evidence of a spatial remapping of the tactile pulse appeared within the P100 to N140 component range of the SEP, the reference frame mapping may be related to activity in SII during a relatively early stage of somatosensory processing. Although, one study has suggested that remapping may start earlier, in the time frame of the N80 component (Soto-Faraco & Azañón, 2013).

The study of Rigato et al. (2013) also examined how viewing the hands (compared to not being able to see one's hands) within a crossed or uncrossed position affects the SEP response. When participants were able to view their hands, differences in N140 amplitude between the two hand positions were observed within the hemisphere contralateral to the tactile stimulation. However, when participants could not view their hands and were made to rely solely on proprioceptive input, the N140 differences between hand positions occurred in the ipsilateral hemisphere to the touch. While the appearance of these hemispheric differences was not fully addressed, this lateralization effect may reflect the addition of visual information improving spatial remapping in some manner for accurate tactile localization. This suggests that body representations are being informed by multiple modalities used functionally to enhance processing. While the prior literature discussed in the current section has generally examined modulations of the hand posture (see Fig. 2 for an example; contrast panel A and panel C), the spatial congruency of the viewed hand in a particular space and the space of the hand being touched has never before been tested (Fig. 2; contrast panel A and panel B). The testing of the spatial congruency of visuotactile events would be telling of whether space is a factor for coherent body representation.

### **Body Representation Development**

While the amount of research on body representations in adults has steadily increased over the past decade, relatively little attention has been paid to the development of body representations in early human development. This is beginning to change, with interest arising in how infants come to understand or represent the bodies of others. Identifying self-other correspondences is important for social interactions throughout life,

but this ability is critically important for infants as it may lay the foundation for emerging social capacities (Meltzoff, 2007a, 2007b). During the first year of life, infants vastly progress in their ability to communicate, imitate, and learn from others. In order for infants to imitate someone, it has been theorized that they must begin with an identification of their own body part that corresponds with the body part being used by the other person (Meltzoff & Moore, 1997). This identification may involve correspondences between the observed body part of another and the body part of the infant. Behavioral studies examining cross-modal associations in infancy report developmental changes in the first year of life of the use of both visual and tactile information in the formation of early body representations (Bremner, 2016). Therefore, the manipulation of visuotactile events may be one way of studying the mechanisms through which infants might register correspondences between body parts of self and other.

A series of recent studies have provided evidence of a neural mapping between infants' representations of their own body and the bodies of others using EEG. In a live observation protocol, 14-month-old infants observed actions of an adult reaching toward and touching a toy (Saby et al., 2013). These actions were performed by the experimenter using her hand or her foot. The neural response recorded displayed a somatotopic pattern during the observation of the hand and foot actions, with greater desynchronization of the mu rhythm occurring over sensorimotor areas corresponding to the observed body part (i.e., a lateralized ERD response for hands and a medial response for feet). A similar somatotopic response was found during infant's own production of hand and foot actions (Marshall, Saby, & Meltzoff, 2013). The study provides neuroscientific evidence of a

neural correspondence of body parts between the self and other during infancy, with the implication that these correspondences may play a role in early social engagement.

In terms of developmental aspects of somatosensory processing in the infant brain, there is an established body of literature investigating SEP responses in infants. Many of these studies have focused on an early N1 component that is particularly detectable during median nerve stimulation and likely reflects the arrival of afferent information in SI. Individual differences in the N1 response to tactile stimulation have proven useful in detecting early signs of dysfunction in infants at risk of impairment for treatment or rehabilitation purposes (Pihko & Lauronen, 2004; Saby, Meltzoff, & Marshall, 2016). It should be noted that stimulation of the median nerve elicits a slightly different SEP response than tactile stimulation (Saby et al., 2016). Of the limited number of studies that have reported on the SEP response to tactile stimuli relative to median nerve stimulation, a large positivity occurs between 100-300 ms post-stimulus with the peak latency occurring slightly later in newborns than in later infancy (Gondo et al., 2001; Nevalainen et al., 2008; Pihko, Lauronen, Kivistö, & Nevalainen, 2011; Saby et al., 2015). Using MEG methods, which provide superior localization of neural sources compared to EEG, the early positivity seen in the SEP may correspond to activity occurring in SII (Nevalainen, Lauronen, & Pihko, 2014). The early positivity between 100-300 ms in the infant SEP has been shown to follow a somatotopic pattern, as seen in adults. Examining 7-month-old infants, Saby and colleagues (2015) observed a peak in the SEP at 175 ms post-stimulus onset (Fig. 3). Following a somatotopic pattern, largest mean amplitude responses of the early positivity were found overlying the foot region of the sensorimotor cortex (electrode Cz) during foot stimulation. During hand stimulation,

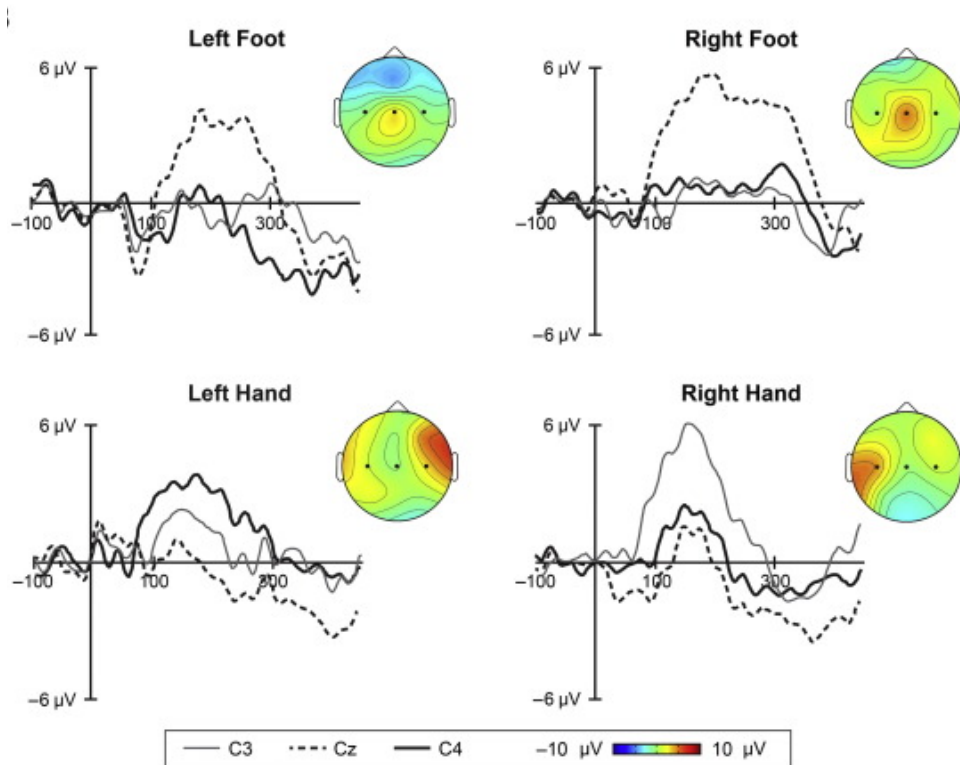


Figure 3. Infant SEP Responses. SEP responses to tactile stimulation of 7-month-old infants (Saby et al., 2015). Each plot shows the response at central sites for stimulation of the right or left hand or foot. Greater responses for feet were recorded at electrode Cz and greater responses for hands were recorded at electrodes C3 and C4 following a somatotopic pattern.

largest responses were found at the more lateral hand regions (electrode C3 for right hand stimulation and electrode C4 for left hand stimulation).

While the study of Saby et al. (2015) did not consider reference frames in relation to the tactile stimulation, a related study specifically examined the SEP response in infants when the external frame of reference of the tactile stimulation was altered (Rigato, Begum Ali, van Velzen, & Bremner, 2014). In this study, 200 ms of sustained vibrating tactile stimulation was applied to the palms of infants' hand, and SEP responses were compared when hands were either in a crossed or uncrossed position. SEP responses of

6.5-month-old infants showed no differences when the hands were in a crossed position compared to an uncrossed position. By 8 months of age, differences began to emerge in some infants and by 10-months of age, differences in the SEP response to hand stimulation were consistently present. Rigato et al. (2014) found that the postural differences observed in 10-month-old infants were dependent on the visual input of their arm position, as the differences were not found when their hands were hidden from view. This suggests that at the later ages in the study, visual information was a stronger modulator of SEP responses and may play a large role in informing body representations.

Missing from the research on infant body representations is work specifically investigating visual influences of tactile events as seen in the SEP response of somatosensory processing. As mentioned previously, adult studies have shown that viewing a body part modulates SEP responses to tactile stimulation while viewing the same part of one's own body (Cardini et al., 2012; Longo et al., 2011; Sambo et al., 2009; Taylor-Clarke et al., 2002) and perhaps while viewing the relevant part of another person's body (Adler et al., 2016; Deschrijver et al., 2015). A similar body-specific visual modulation of neural responses to touch have been demonstrated in a study of 3- to 4-year-old children using MEG (Remijn et al., 2014). In this study, children received tactile stimulation on their index finger while they viewed video clips of either a hand or foot of another person being touched. There was an increase in neural activation over sensorimotor hand regions while viewing the video clips of a hand being touched, but not while viewing video clips of a toe being touched. This study provides evidence of a limb-specific visual effect on somatosensory processing in young children. Evidence of self-other bodily mappings was also provided as the video clips watched by the children were

of others' hand and feet, not their own. Visuotactile stimuli could be further explored in infants to understand better ontogenetic aspects of neural body maps and how body representations may be a building block to an early social concept of the self and others. Moreover, knowledge of the development of body representations in infancy could be useful to recognizing early signs of atypical development such as autism (Casco, Foss-Feig, Burnette, Heacock, & Cosby, 2012; Kaiser et al., 2016; Schauder, Mash, Bryant, & Casco, 2015).

### **The Current Studies**

One promising path towards a better understanding of body representations focuses on the multisensory integration of bodily information. Of specific interest here is the interaction between vision and somatosensation. Prior work has demonstrated that viewing a stimulated body part modulates the neural response to stimulation of that body part (Taylor-Clarke et al., 2002). The current studies manipulated the congruency of visuotactile events in order to examine specificities of visuotactile body mappings during somatosensory processing, mappings thought to be important to body representation. In adults, modulations of the spatial congruency (hand posture of viewed and touched hand) of visuotactile events on the neural responses to touch were examined. Furthermore, turning toward a gap in the literature, interpersonal body representations were explored in infants by examining brain responses to tactile stimulation during viewing of another person's hand or foot. It is postulated that partly through these body correspondences, one may come to recognize a likeness between the self and others. In this way, an individual might come to have a social understanding of others as psychologically similar beings with goals and intentions (Meltzoff, 2007a).

***Question 1: Does spatial congruency between viewed and stimulated body parts modulate somatosensory processing in the adult brain?***

*By modulating the spatial congruency of the viewed and stimulated body part, the neural responses to the tactile stimuli are expected to be altered. If true, there would be evidence that human body representation is informed by a congruency between the body in space and the view of the body in space.*

In Study 1, undergraduate participants received tactile stimulation to their right hand across different postural conditions, while they viewed images of a right hand that was either congruent or incongruent with the position of their own hand. During the recording of the EEG signal, undergraduate participants received tactile stimulation to their right index finger while viewing a picture of a right hand within right or left space. The participant's hand was placed either in right or left space. If spatial congruency of the body between visuotactile stimuli influenced somatosensory processing, different EEG patterns would occur for congruent and incongruent trials of viewed and stimulated space. In addition, a control condition was used to confirm whether the results were body-specific or space-specific by replacing the pictures of hands with bars. The SEP and mu rhythm response were derived from the EEG signal to evaluate modulations of somatosensory processes. Lastly, participant self reports were obtained on their feelings of ownership over the viewed hand within each condition.

Based on the prior research outlined earlier, visual influences of viewing a hand compared to viewing an object (bar) on the SEP to tactile stimulation were expected to be found for components in the first 100 ms post-stimulus (P50, N80), a time period associated with somatosensory processing in SI. Similarly, a greater mu rhythm

desynchronization was expected while viewing of the hand compared to viewing the bar, as information about an observed hand may be more relevant to tactile processing of a hand touch. These differences were expected to occur contralateral to the tactile stimulation. An effect of congruency was also expected at later processing stages, after 250 ms post-stimulus, where greater mu desynchronization and SEP amplitudes for congruent compared to incongruent trials would be observed. These modulations were postulated to be bilateral and specific to the observation of hands (not bars) as prior associations are expected to be body-specific and not simply relevant to spatial location in general. As seen in previous studies, an effect of participants' hand in space was also expected to occur for the SEP components associated with SII activity (P100 or N140) such that there would be a difference in mean amplitude when the participant's hand was located in left compared to right space. Lastly, self-reported body ownership scores were expected to be greatest for body-specific, congruent conditions.

***Question 2: Is there evidence of limb-specific visual influences on the neural response to tactile stimulation at 7 months of age?***

*By modulating the congruency of the viewed and stimulated limb, the neural responses to the touch are expected to be altered. If true, this would provide evidence for a bodily mapping of visuotactile events at 7-months including interpersonal bodily mappings that may lay a foundation for early social cognitive development.*

Study 2 employed a between-subjects design with 7-month-old infants to examine the effect of correspondences between the location of tactile stimulation (hand vs. foot) and a live presentation of an experimenter being touched on either the hand or the foot. Prior work examining the reactivity of the sensorimotor mu rhythm to the observation

others' actions and the actions of the infant have primarily been carried out using infants between 8-18 months (Marshall & Meltzoff, 2014). Older infants were used in prior work so that infants were reliably able to carry out back-and-forth exchanges with an experimenter in order to study self-other linkages between observed and executed actions. By instead studying the response to tactile stimulation, self-other linkages observed in SEP and mu rhythm responses can be studied earlier in the development of the infant, as executed actions are not necessary. Therefore, 7-month-old infants were chosen for the current study to examine self-other correspondences of observed and felt limb stimulation.

Infants received tactile stimulation to their hand or foot. These pulses occurred while infants viewed an experimenter's hand or foot being touched with a feather duster. If limb-specific congruency between tactile stimulation of the infant's body and observed body limbs were present, there would be differences in SEPs elicited to congruent compared to incongruent visuotactile events. Examining this question extends the work of Saby et al. (2015) who reported somatotopic responses to tactile stimulation to the hand and foot in the SEP response of 7-month-old infants. In the current study, greater SEP mean amplitudes were expected for congruent trials within a positive peak occurring 100-300 ms post-stimulus, which was the period examined in Saby et al. (2015). Furthermore, these differences were expected to be largest overlying the central electrodes following a somatotopic pattern of limb stimulation (i.e., a lateralized response to hand stimulation and more medial response to foot stimulation). Due to low statistical power in infant EEG work from a limited number of useable trials where the infant was attending to the stimuli, not making large limb movements, and noise in the EEG was

minimal, the infant mu rhythm was not analyzed in Study 2. In order to calculate changes in mu power, a larger time window for trial epochs is needed compared to SEP calculations. By increasing the time of the epoch, there becomes a greater occurrence of less attention, limb movements, and EEG signal noise that would in turn increase the number of trials removed from further analyses.

## CHAPTER 2

### STUDY 1

#### **Method**

***Participants.*** Forty undergraduates received course credit in return for participation. Data from four participants were excluded from analyses due to technical issues. An additional two participants were excluded due to excessive motor and/or eye movement artifacts that contaminated more than 25% of trials. The final analyzed sample included 34 participants (mean age = 21.29 years;  $SD = 3.92$ ; 28 females). All participants were right-handed ( $M = 87.65$ ;  $SD = 13.72$ ) according to the Oldfield Handedness questionnaire (Oldfield, 1971), were neurologically healthy, and had normal or corrected vision.

***Tactile Stimulation.*** Tactile stimulation was delivered using an inflatable membrane mounted in a plastic casing (10 mm diameter; MEG International Services). A similar device for producing tactile stimulation was used in prior EEG studies within our lab (Saby et al., 2015; Shen et al. 2017) and in MEG studies from other research groups (Pihko & Lauronen, 2004; Pihko, Nevalainen, Stephen, Okada, & Lauronen, 2009). Using a flexible polyurethane tubing (3 m length, 3.2 mm outer diameter), the membrane was inflated by a short burst of compressed air controlled by STIM stimulus presentation software and a pneumatic stimulator unit (James Long Company). One membrane was attached to the back of the participant's right hand using a double-sided adhesive electrode collar. Another membrane mounted to a finger clip was placed on the right index finger (Fig. 4).



Figure 4. Study 1 Tactile Stimulation. An inflatable membrane mounted in a plastic casing (10 mm diameter; MEG International Services) and surrounding clip placed on the index finger of an adult for Study 1.

For each tactile stimulus, a trigger from the STIM presentation software opened the solenoid on the pneumatic stimulator unit for 10 ms. This elicited an expansion of the membrane that began 15 ms after trigger onset and peaked at 2 newtons (N) around 35 ms after trigger onset. The total duration of membrane movement was around 100 ms. The 15 ms delay between trigger and membrane movement was corrected for in the timing of the events such that the time of 0 ms was the onset of the membrane movement. The pneumatic stimulator was located in an adjacent room behind a closed door and within a Styrofoam ice chest to prevent solenoid operation being audible to the participant.

**Procedure.** Participants were fitted with a mesh EEG cap (ANT Neuro) and the hand stimulators. During EEG collection, the participant sat at a table with a 15" tablet monitor (Wacom Cintiq 15X) placed on top so that participants looked down toward the table (~ 38 cm from screen) at the visual stimuli, which were approximately overlying their own right hand under the table. Participants were instructed to watch the visual

stimuli appearing on the monitor while they receive tactile stimulation on their right index finger or on the back of their right hand. Participants were instructed to respond verbally when stimulation occurred on the back of their hand.

The experiment consisted of 440 trials divided into 10 blocks of 44 trials each. Trials in which participants received stimulation on the back of their hand were infrequent (40 total; 4 per block). Each block contained four conditions determined by the visual stimuli and four infrequent trials (one with each visual stimulus). The four conditions included a picture of a right hand or a bar in either the right or left external body space. Trials in each condition were presented in a random order within each block. While participants received stimulation, their right hand either rested on their right leg (in right space) or left leg (in left space). The position of the participant's hand alternated between blocks; giving a total of eight possible conditions (see Figure 2).

A schematic in Figure 5 shows the sequence of one trial. First, a fixation cross in the center of the screen was displayed (image appearance varied between 600-1000 ms). Next, a picture of a right hand or a bar appeared either in a right or left external body space configuration. Exactly 600 ms after the onset of the appearance of the hand or bar, participants received tactile stimulation on either their right index finger or on the back of their right hand. 1200 ms after onset, The visual display of the hand or bar was replaced by the fixation cross 1200 ms from the onset of the tactile stimulation. The fixation cross remained on the screen for 600 ms before the next trial began.

Participants verbally responded to trials in which the back of their right hand was stimulated. An experimenter was seated behind participants recording their response to

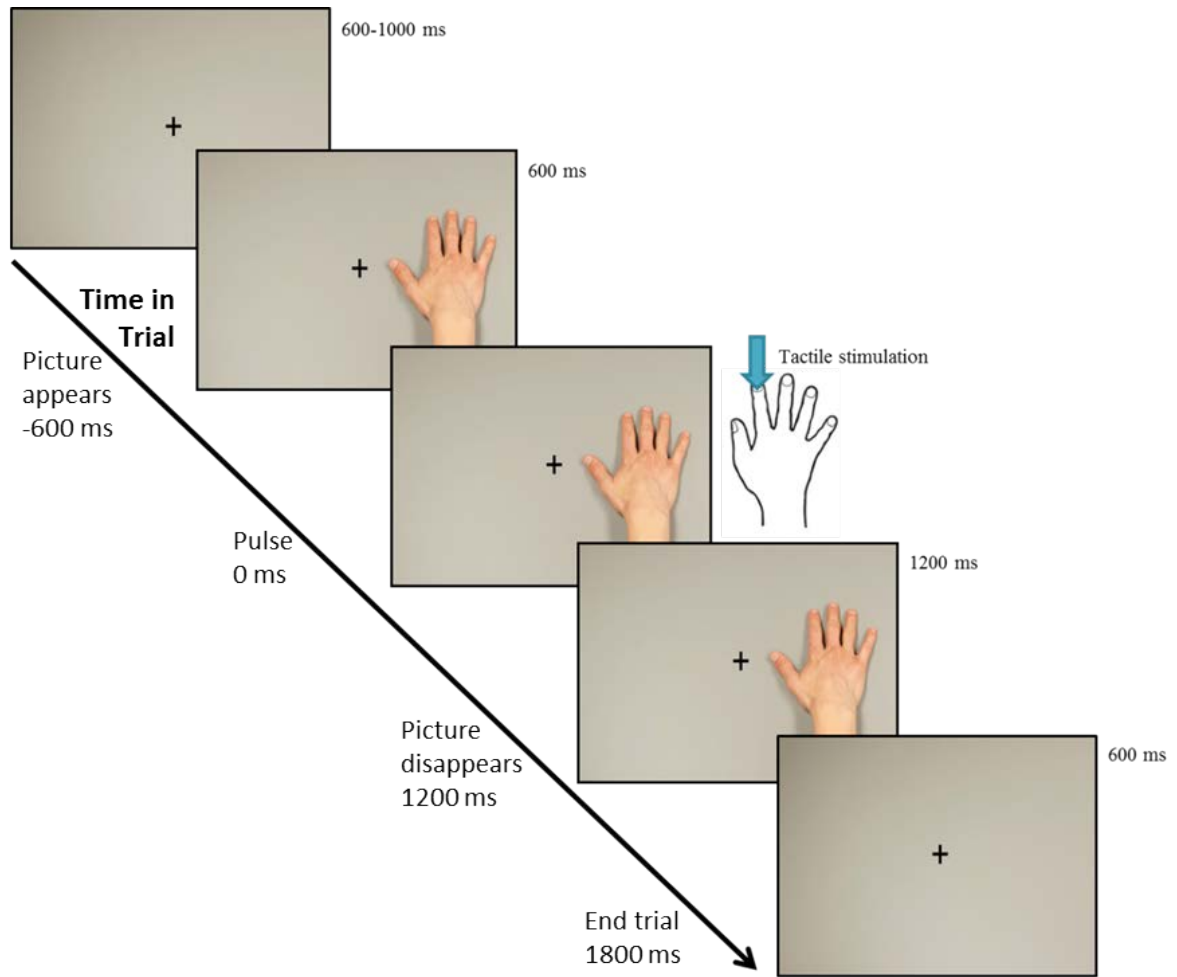


Figure 5. Trial Schematic for Study 1. Each trial lasted 3000-3400 ms with the length of the first fixation screen varying. The time values on the left display the time in trial relative to the tactile stimulation. The time values on the right display the amount of time each screen portion of the trial lasted. After 600 ms of viewing the hand or bar, participants received tactile stimulation. If the stimulation occurred on the back of their hand, they would verbally respond before the end of the trial.

these infrequent trials. The experimenter was blind to whether the participant was receiving stimulation to the back of the hand or the finger. Before each block, the experimenter instructed the participant to move his or her right hand to either a right or left external position (resting on their right or left leg). Participants rested their left hand on the chair's armrest throughout the experiment. A white noise machine was used (62

dB) in order to cover any sound produced by expansion and contraction of the membranes.

***EEG Apparatus and Methods.*** The EEG signal was recorded using a mesh stretch cap (ANT Neuro) with 32 electrodes arranged according to the International 10-20 format. Vertical electro-oculogram (EOG) activity from above and below the left eye was used to monitor eye blinks. Scalp electrode impedances were accepted if they were at or below 25 kilohms. The signal from each electrode was amplified using optically isolated, custom bioamplifiers with high input impedance ( $> 1 \text{ G}\Omega$ : SA Instrumentation) and digitized using a 16-bit A/D converter ( $\pm 5 \text{ V}$  input range). Bioamplifier gain was set at 4000 for EEG channels and 1000 for EOG channels. Hardware filters (12 dB/octave rolloff) were set at .1 Hz (highpass) and 100 Hz (lowpass). During collection, the signal was referenced to the vertex (Cz) with an AFz ground.

The EEG Analysis System (James Long Company) and the EEGLab toolbox for MATLAB (Delorme & Makeig, 2004) were used for data processing. The EEG signals were re-referenced to an average of the left and right mastoids. The signal was then low-pass filtered at 30 Hz and segmented into 2700 ms epochs. Independent component analysis (ICA) was used to clear the EEG data of ocular artifacts (Hoffmann & Falkenstein, 2008). Poor quality channels were corrected on an individual basis using linear interpolation. Epochs with remaining artifacts were removed from further analysis. Participants with 25% or more rejected epochs were not included in analyses. A repeated-measures ANOVA revealed that the mean number of trials ( $M = 42.72$ ;  $SD = 2.90$ ) did not statistically differ between the condition factors of object, participant hand posture, or congruency ( $p$ 's  $> .05$ ). SEPs were computed for each participant relative to a 100 ms

prestimulus baseline. Based on the computation described by Delorme and Makeig (2004), event-related spectral perturbation (ERSP) was calculated for the frequency range of 5 to 30 Hz using 100 overlapping windows starting with a 4-cycle wavelet at the lowest frequency relative to a prestimulus baseline of -500 ms to 0 ms. Analyses of the ERSP focused on the alpha/mu frequency range (8-13 Hz). Extreme values (1.5 x Interquartile Range) of the SEP components and mu rhythm for each condition, window, and electrode were not included in analyses.

*Ownership Questionnaire.* Immediately following the experimental protocol, participants completed a body ownership questionnaire for each of the eight conditions that had been experienced. Participants were first instructed on their hand positioning and then viewed one of the experimental images on the monitor. For each condition, an experimenter verbally read three statements pertaining to ownership of the object on the monitor. The statements were adapted from Longo and Haggard (2009) and were as follows: 1) While viewing this picture, it feels like I am looking at my own hand; 2) While viewing this picture, it feels like I am not looking at my own hand; 3) While viewing this picture, it feels like I am looking at somebody else's hand. After each statement, the participant said a number from a 7-point scale that corresponded to their agreement or disagreement with the statement (-3 to 3; strongly disagree to strongly agree). The experimenter recorded the responses of the participants. The order of the eight conditions was randomized for each participant. An ownership score was calculated for each condition by reverse scoring responses to the second statement then averaging the responses of the first two statements only. In the analyses involving these data, a repeated-measures ANOVA that included 2 (participants' hand posture) x 2 (visual

congruency of space) x 2 (observed object) factors was carried out to examine the differences in ownership scores across conditions for each electrode, for each SEP component or mu rhythm window and frequency band. The Greenhouse-Geisser correction factor was applied.

*Statistical Analyses.* Analyses were time-locked to the onset of the tactile stimulation and included the period from 0 ms to 650 ms, during which participants were viewing the image on the tablet monitor screen. The analysis of EEG data focused on a central ROI overlying sensorimotor regions, specifically electrodes C3 and C4. SEP analyses examined the following components: P50 (20-60 ms), N80 (60-86 ms), P100 (86-115 ms), N140 (115-160 ms), P200 (160-250 ms) and a late positivity (250-650 ms). Analysis of the mu rhythm was carried out by selecting two time window (0-250 ms; 250-650 ms) in which effects were apparent on time–frequency plots (Drew, Quandt & Marshall, 2015; Quandt & Marshall, 2014). Although the mu band was taken as 8-13 Hz, separate analyses were carried out for the lower (8-10 Hz) and upper (10-13 Hz) mu bands. Finally, repeated-measures ANOVAs were carried out for each electrode for each either SEP component or mu rhythm window and band. These ANOVAs included 2 (participants' hand posture) X 2 (visual congruency of space) X 2 (observed object) factors in order to examine a body-specific, visuospatial congruency effect in the neural response to the touch. The Greenhouse-Geisser correction factor was employed where appropriate.

## Results

***Contralateral SEPs (C3).*** Tactile stimulation to the right hand evoked a clear SEP response at the contralateral central site C3 that included the expected components P50, N80, P100, N140, and P200 (Fig. 6). Repeated-measures ANOVAs as specified above did not reveal any significant main effects or interactions for these components ( $p$ 's > .05). In addition to the typical components, visual inspection of the SEPs revealed a late positivity emerging around 250 ms, peaking at 300 ms and gradually declining. The mean amplitude of this long latency component (250-650 ms) was computed and subjected to further analysis.

*Late Positivity (250-650 ms).* The repeated-measures ANOVA for the late positivity revealed an interaction effect between congruency and the participants' hand posture in space ( $F_{(1, 33)} = 9.095, p = .005$ ). When participant's hands were in a right posture, the mean amplitude of this positivity was larger ( $p = .005$ ) for the congruent condition ( $M = 6.711; SE = 0.672$ ) compared with the incongruent condition ( $M = 5.448; SE = 0.697$ ). However, when participants' hands were in a left posture, the mean amplitude of this positivity for the incongruent condition ( $M = 6.132; SE = 0.713$ ) was larger than for the congruent condition ( $M = 5.433; SE = 0.786$ ), a difference that was approaching significance ( $p = .069$ ). Figure 7 shows a graph of the average mean amplitudes of the late positivity for each condition. No other main effects or interactions were significant.

***Ipsilateral SEPs (C4).*** Tactile stimulation to the right hand also evoked an SEP response at the ipsilateral central site C4 (Fig. 8). The ipsilateral SEPs showed a similar pattern of

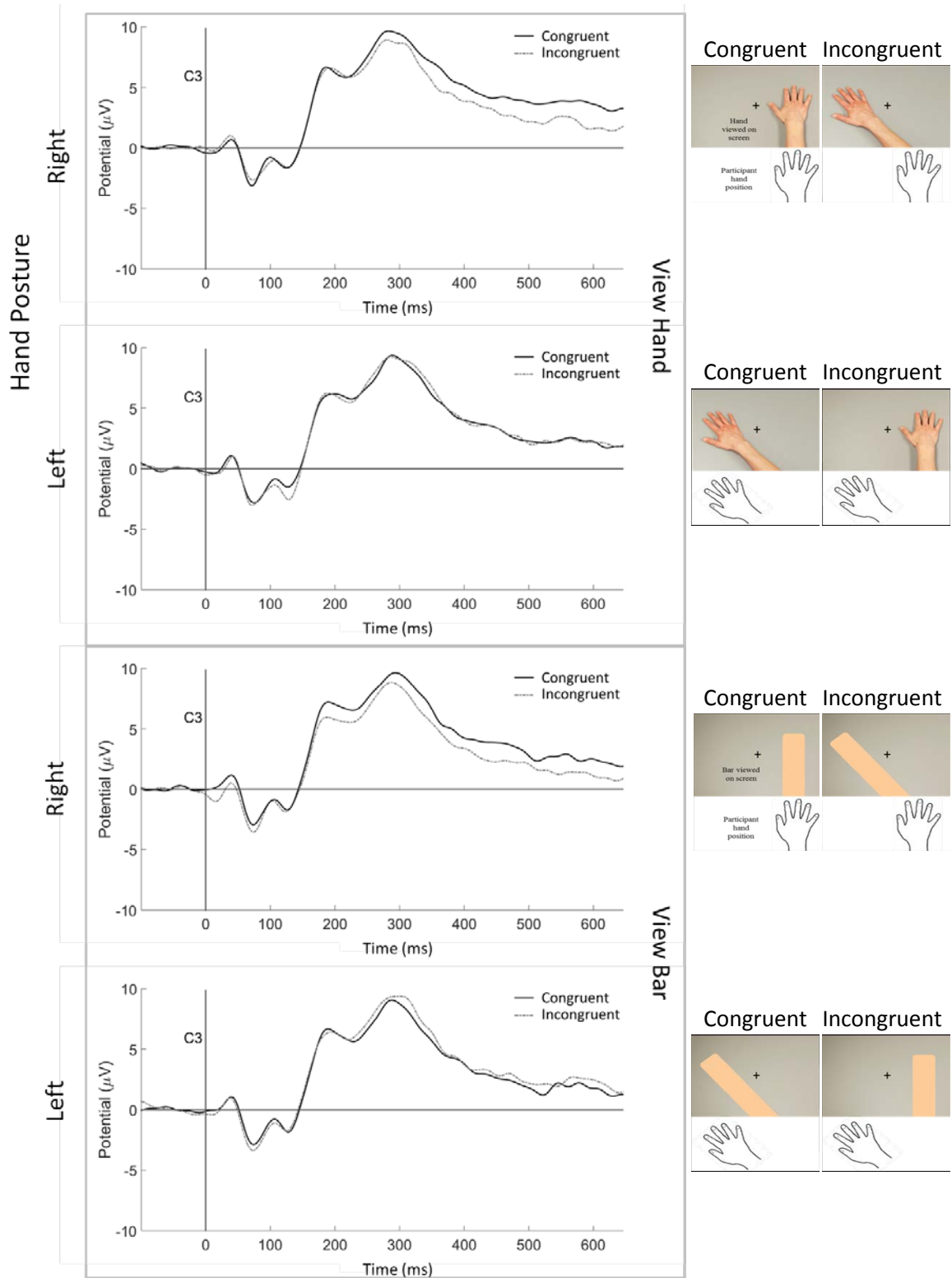


Figure 6. Study 1 Contralateral SEPs. SEPs recorded from contralateral electrode C3.

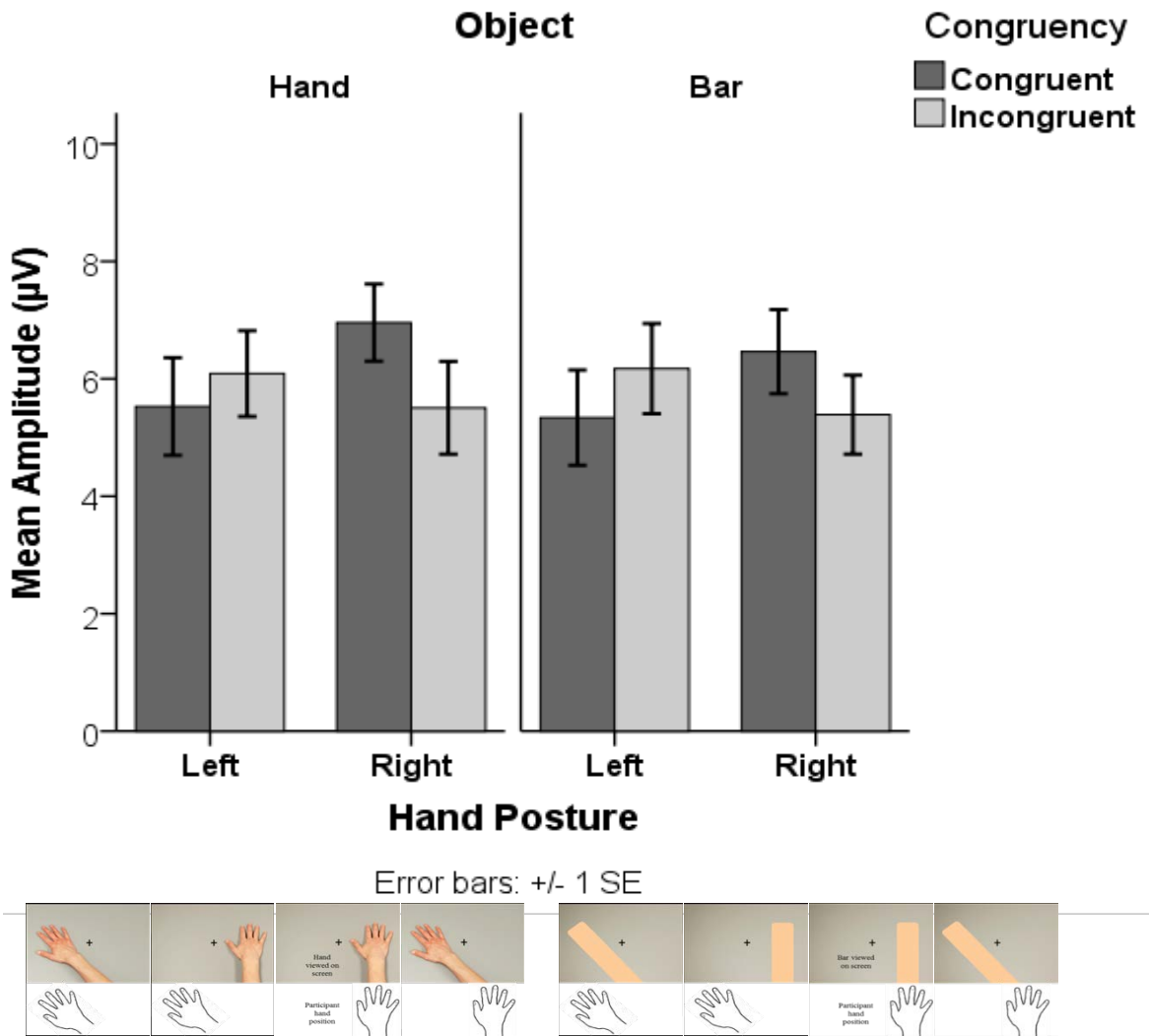


Figure 7. Contralateral Late Positivity. The average mean amplitudes of the late positivity in the SEP response recorded at contralateral electrode C3. There was an interaction effect between the hand posture of the participants and the congruency to the hand posture in the viewed picture.

components as the contralateral SEPs starting around 90 ms with the appearance of the components P100, N140, P200, and a late positivity. There were no ipsilateral P50 and N80 components as expected. The results of the repeated-measures ANOVAs on the P100 and N140 components are presented below. The repeated-measures ANOVA for the P200 and late positivity components did not reveal any significant main effects or interactions.

*P100.* Figure 9 shows average mean amplitudes of the P100 for each condition. The repeated-measures ANOVA for the P100 component revealed a significant main effect of participants' hand posture in space ( $F_{(1, 33)} = 4.527, p = .041$ ). The mean amplitude was greater when the participants' hands were positioned in a right space ( $M = 0.800; SE = 0.339$ ) compared to when they were positioned in a left space ( $M = 0.350; SE = 0.358$ ). No other main effects or interactions were significant.

*N140.* Figure 10 shows average mean amplitudes of the N140 for each condition. The repeated-measures ANOVA for the N140 component revealed a significant three-way interaction of congruency, hand posture in space, and object ( $F_{(1, 33)} = 4.177, p = .049$ ). When participants were viewing a hand and their hands were positioned in left space, mean N140 amplitude for the incongruent condition ( $M = -2.463; SE = 0.518$ ) was more negative ( $p = .013$ ) compared to the congruent condition ( $M = -1.405; SE = 0.477$ ). No other main effects, simple main effects, or interactions were significant.

***Contralateral Mu Rhythm ERS/ERD (C3).*** The mu rhythm response to tactile stimulation was first examined at the contralateral central site (C3). Figure 11 shows time-frequency plots of mu rhythm activity in each condition at C3. Analyses were then conducted separately for the lower (8-10 Hz) and upper (10-13 Hz) mu bands.

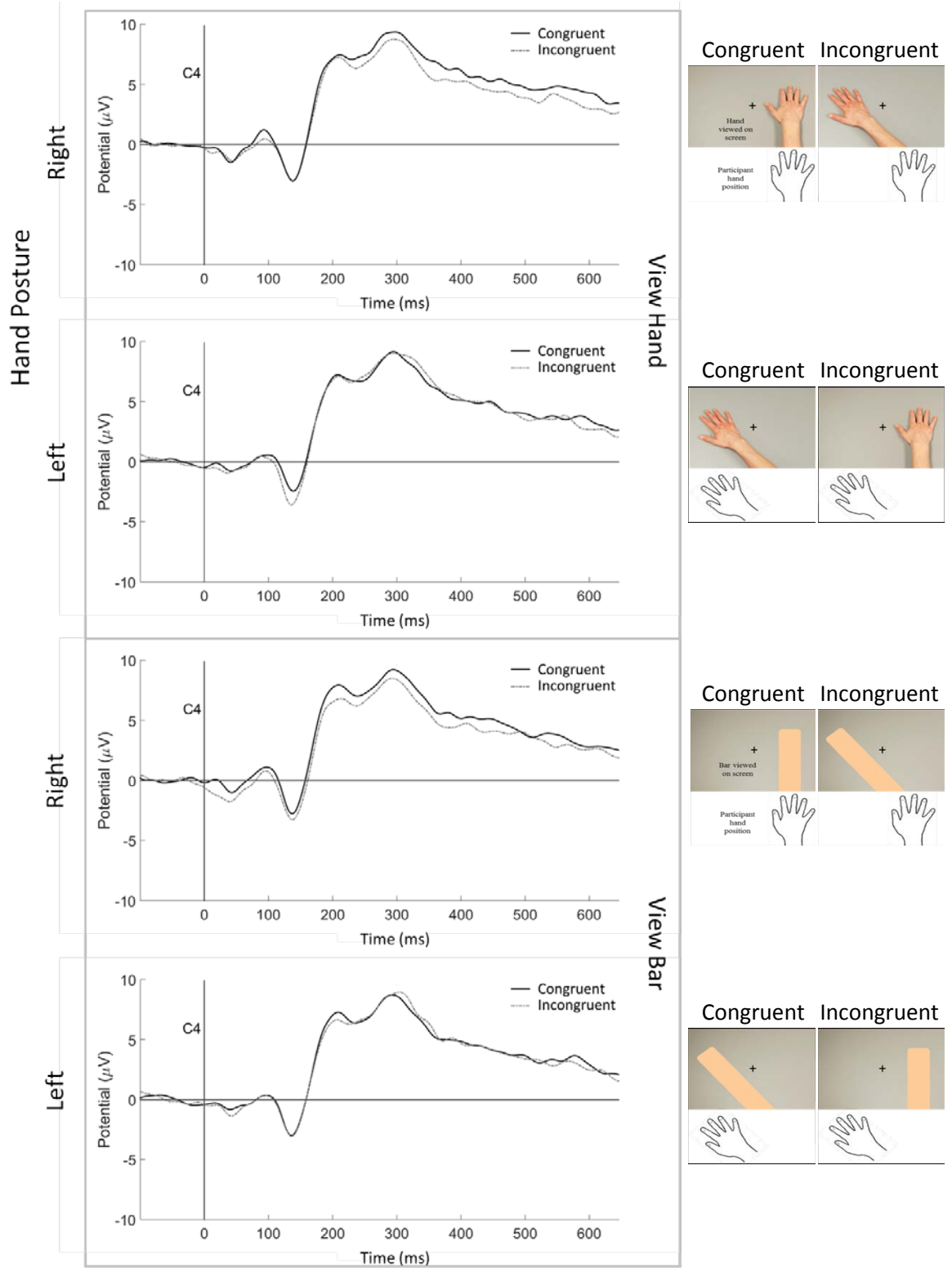


Figure 8. Study 1 Ipsilateral SEPs. SEPs recorded from ipsilateral electrode C4.

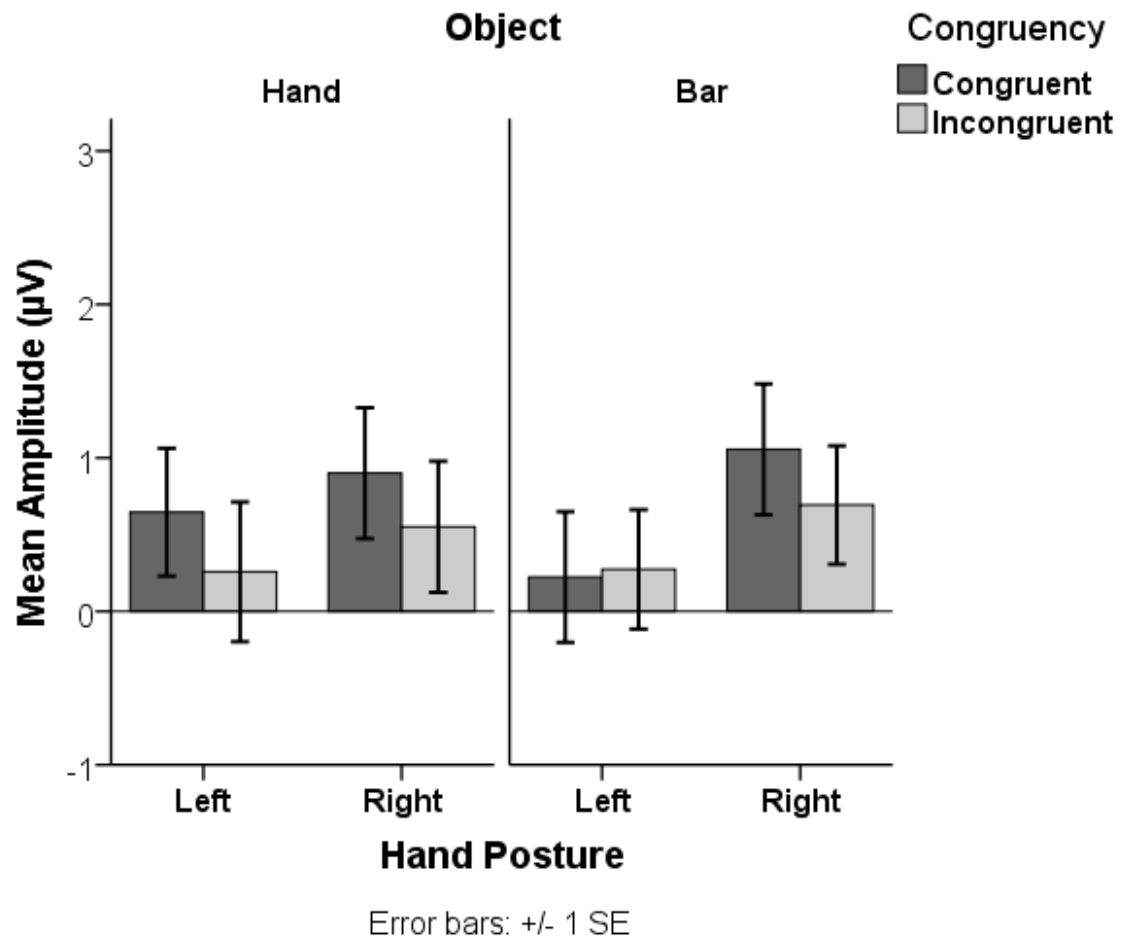


Figure 9. Ipsilateral P100. The average mean amplitudes of the P100 component in the SEP response recorded at ipsilateral electrode C4. There was a main effect of hand posture.

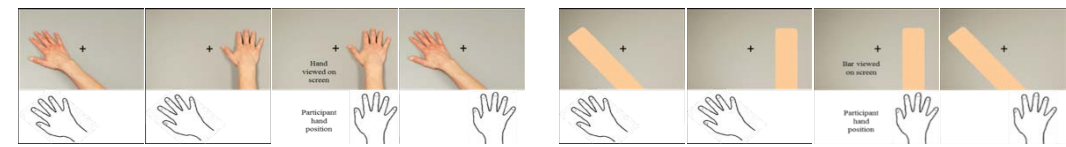
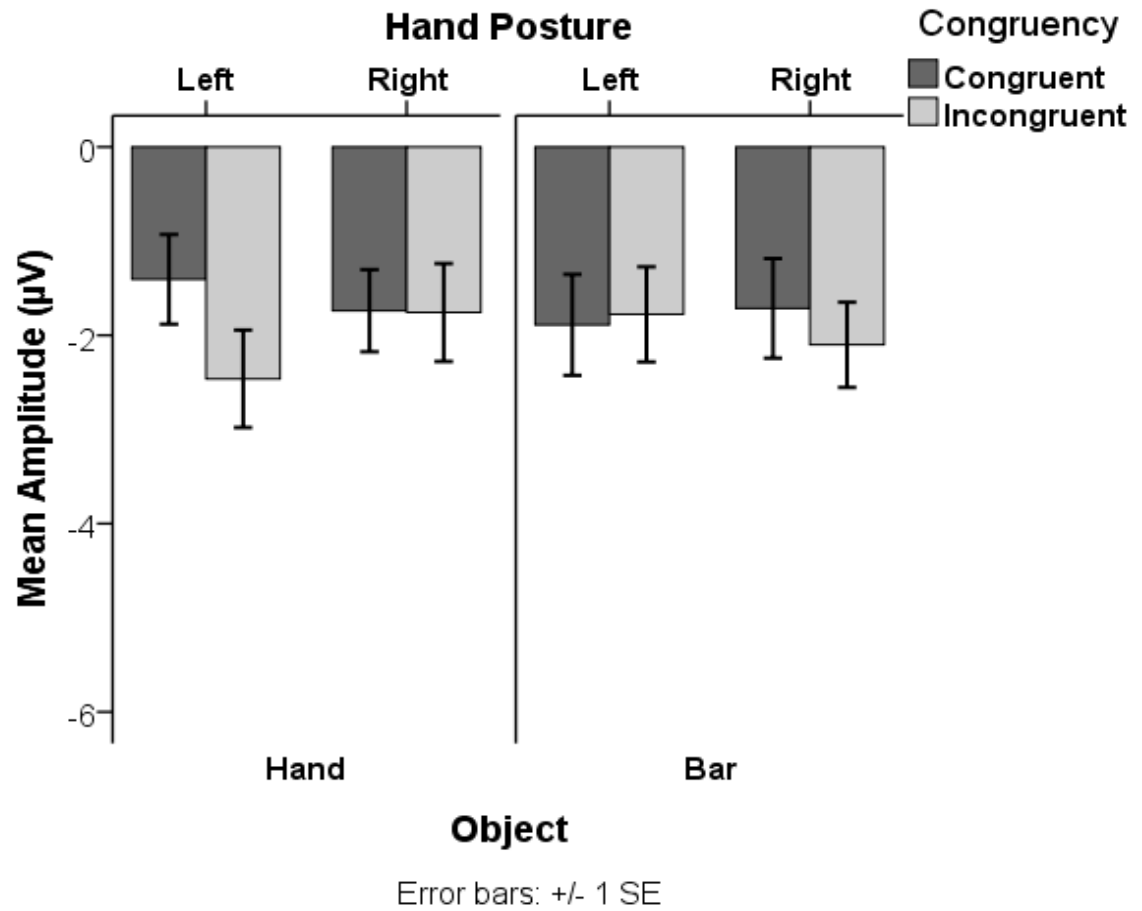


Figure 10. Ipsilateral N140. The average mean amplitudes of the N140 component in the SEP response recorded at ipsilateral electrode C4. There was a three-way interaction between the hand posture of the participants, the congruency to the hand posture in the viewed picture, and the object viewed in the picture.

### ***Lower Mu Rhythm (8-10 Hz)***

*Early Mu ERS/ERD (0-250 ms).* The repeated-measures ANOVA revealed a main effect of object ( $F_{(1, 33)} = 5.310, p = .028$ ). Overall, there was greater mu synchronization in the lower band while participants viewed bars ( $M = 0.656; SE = 0.156$ ) compared to viewing hands ( $M = 0.444; SE = 0.180$ ). No other main effects or interactions were significant.

*Late Mu ERS/ERD (250-650 ms).* As with the early window, the repeated-measures ANOVA revealed a main effect of object ( $F_{(1, 33)} = 19.840, p < .001$ ). Similarly, there was greater mu synchronization in the lower band while participants viewed bars ( $M = 0.461; SE = 0.169$ ) compared to viewing hands ( $M = 0.026; SE = 0.174$ ). No other main effects or interactions were significant.

### ***Upper Mu Rhythm (10-13 Hz)***

*Early Mu ERS/ERD (0-250 ms).* The repeated-measures revealed a main effect of participants' hand posture in space ( $F_{(1, 33)} = 11.647, p = .002$ ). Overall, there was greater desynchronization of upper mu when participants' hands were positioned in a right spatial posture ( $M = -0.360; SE = 0.243$ ) compared to a left spatial posture ( $M = -0.069; SE = 0.226$ ). No other main effects or interactions were significant.

*Late Mu ERS/ERD (250-650 ms).* The repeated-measures ANOVA revealed a main effect of object ( $F_{(1, 33)} = 5.091, p = .031$ ). There was greater upper mu desynchronization when participants viewed hands ( $M = -0.544; SE = 0.280$ ) compared to bars ( $M = -0.306; SE = 0.280$ ). In addition, a main effect of participants' hand posture in space was approaching significance ( $F_{(1, 33)} = 3.993, p = .054$ ). There was greater upper

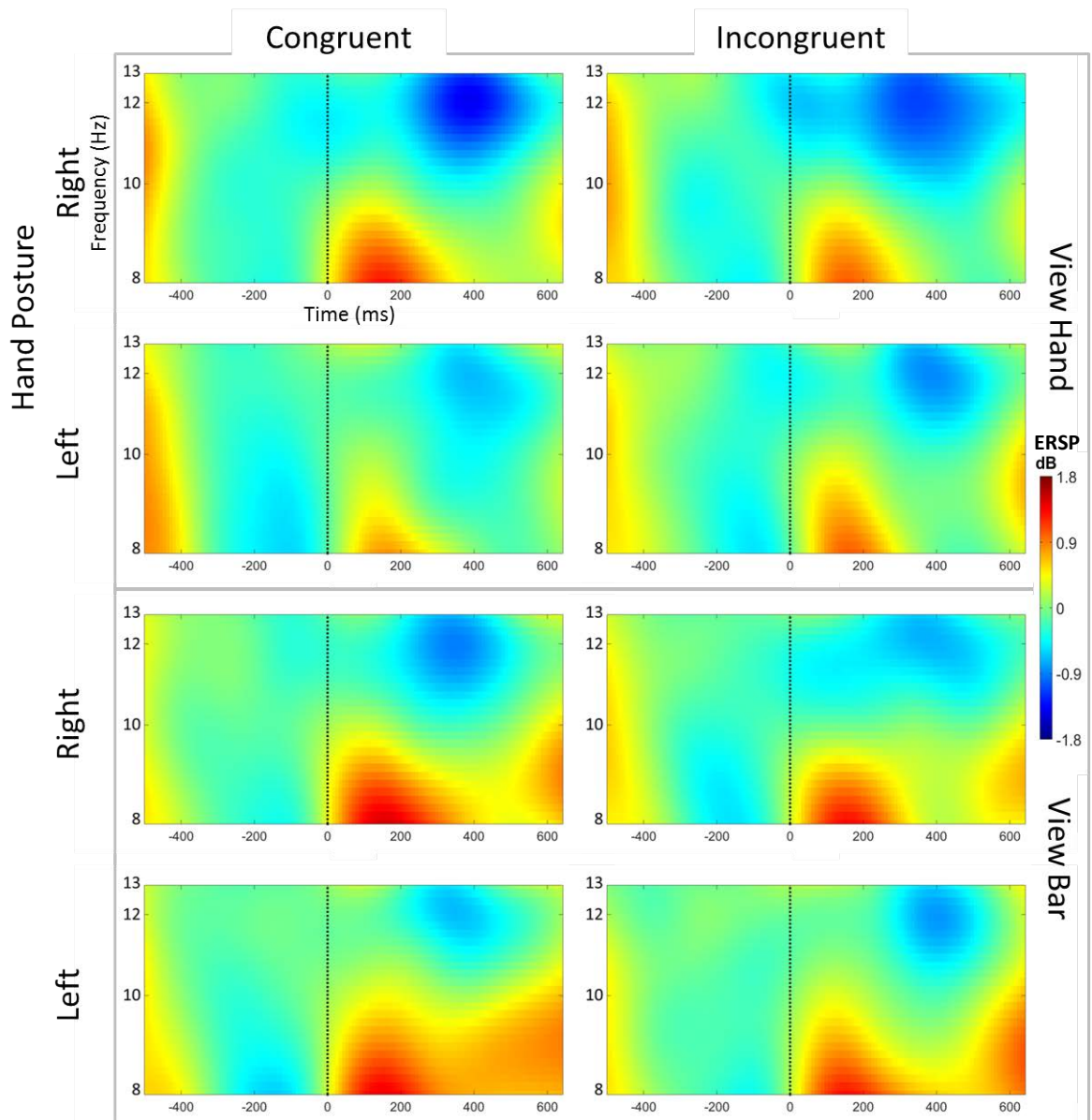


Figure 11. Contralateral Mu Rhythm. Time-frequency plots showing mu rhythm (8-13 Hz) synchronization (red) and desynchronization (blue) across the trial at contralateral electrode C3. The top four plots show responses to viewing hands and the bottom four plots show responses to viewing bars each separated by the hand posture of the participant (right or left) and congruency of the object in space in the viewed picture (congruent or incongruent).

mu desynchronization when participants' hands were positioned in a right spatial posture ( $M = -0.540$ ;  $SE = 0.297$ ) compared to a left spatial posture ( $M = -0.310$ ;  $SE = 0.263$ ). No other main effects or interactions were significant.

***Ipsilateral Mu Rhythm ERS/ERD (C4).*** The mu rhythm response to tactile stimulation was then examined at the ipsilateral central site (C4). Figure 12 shows time-frequency plots of mu rhythm activity in each condition at C4. Analyses were then conducted separately for the lower (8-10 Hz) and upper (10-13 Hz) mu bands.

***Lower Mu Rhythm.***

*Early Mu ERS/ERD (0-250 ms).* The repeated-measures ANOVA revealed a main effect of object ( $F_{(1, 33)} = 6.242$ ,  $p = .018$ ). There was greater mu synchronization in the lower band when participants viewed bars ( $M = 0.734$ ;  $SE = 0.177$ ) compared to viewing hands ( $M = 0.488$ ;  $SE = 0.182$ ). No other main effects or interactions were significant.

*Late Mu ERS/ERD (250-650 ms).* Again, the repeated-measures ANOVA revealed a main effect of object ( $F_{(1, 33)} = 11.630$ ,  $p = .002$ ). Similarly, there was greater lower mu synchronization when participants viewed bars ( $M = 0.265$ ,  $SE = 0.181$ ) compared to viewing hands ( $M = -0.134$ ,  $SE = 0.166$ ). No other main effects or interactions were significant.

***Upper Mu Rhythm.***

*Early Mu ERS/ERD (0-250 ms).* The repeated-measures ANOVA revealed no significant main effects or interactions.

*Late Mu ERS/ERD (250-650 ms).* The repeated-measures ANOVA revealed no significant main effects or interactions.

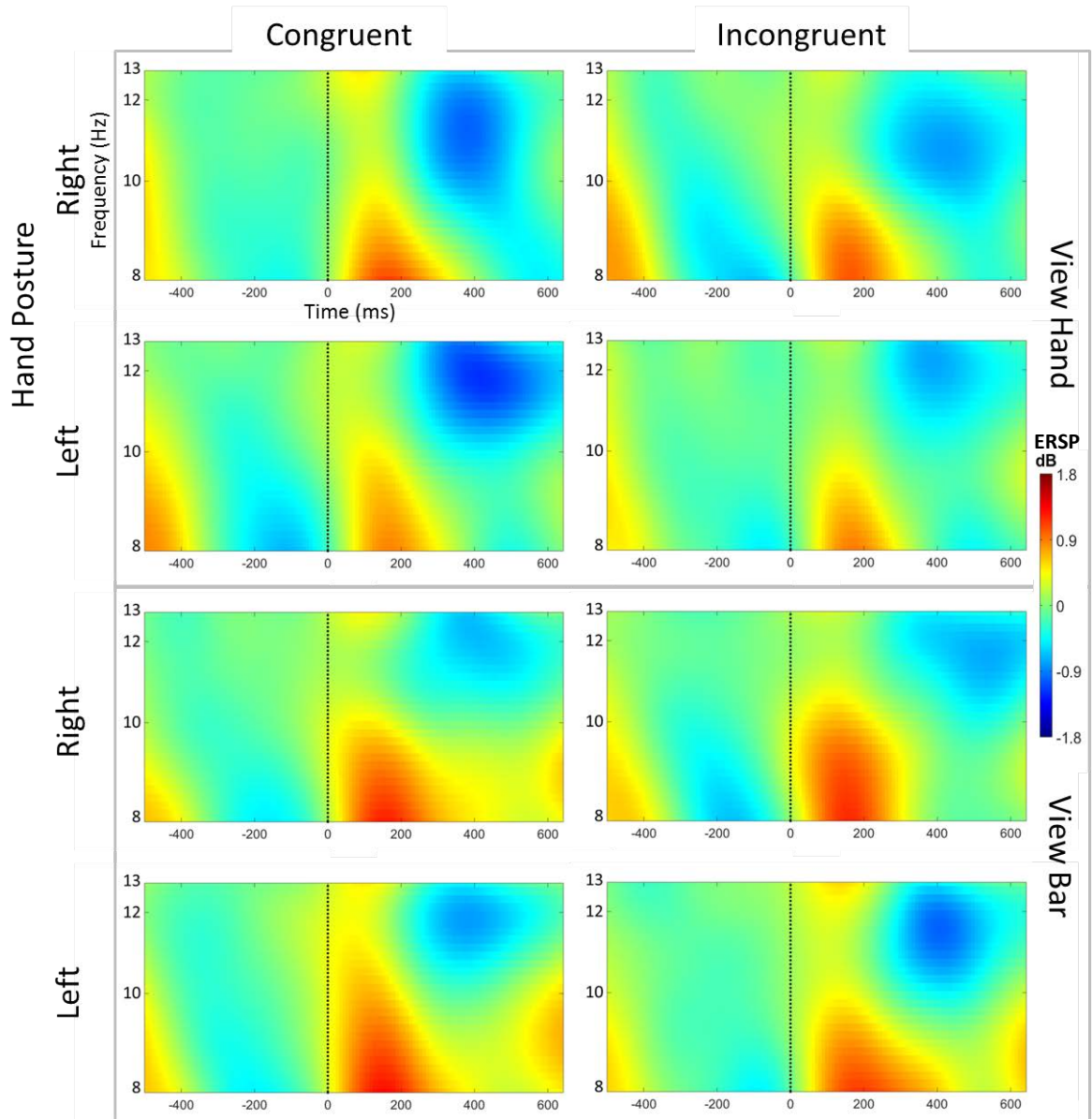
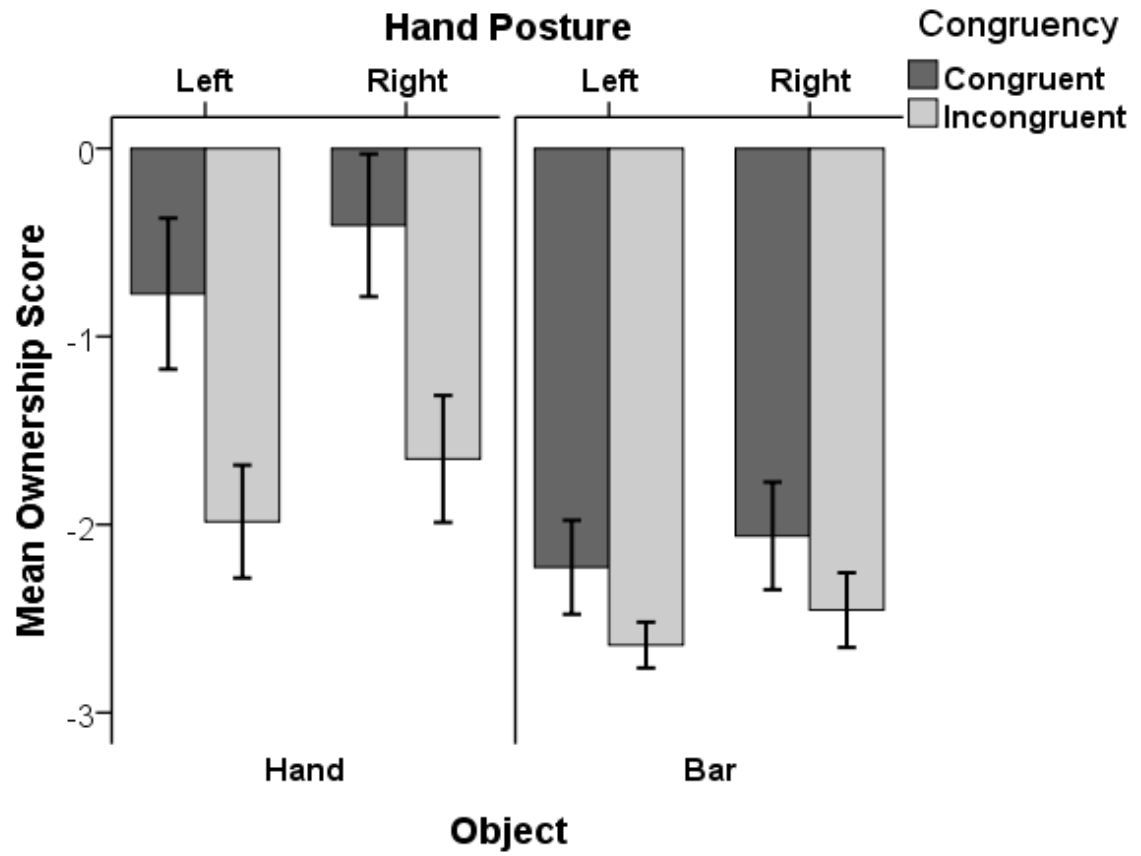


Figure 12. Ipsilateral Mu Rhythm. Time-frequency plots showing mu rhythm (8-13 Hz) synchronization (red) and desynchronization (blue) across the trial at ipsilateral electrode C4. The top four plots show responses to viewing hands and the bottom four plots show responses to viewing bars each separated by the hand posture of the participant (right or left) and congruency of the object in space in the viewed picture (congruent or incongruent).

**Ownership Scores.** For each condition, the average feelings of ownership were negative indicating low levels of ownership reported by the participants (Fig. 13). Only 18% of the ownership scores calculated for each condition and participant were greater than zero. The repeated-measures ANOVA on the mean ownership scores revealed significant main effects of congruency ( $F_{(1, 31)} = 16.651, p < .001$ ), hand posture ( $F_{(1, 31)} = 7.847, p = .009$ ), and object ( $F_{(1, 31)} = 16.971, p < .001$ ). There was also a significant interaction between congruency and object ( $F_{(1, 31)} = 8.569, p = .006$ ). Overall, participants reported feeling more ownership over the object on the monitor when their hand was in a right posture ( $M = -1.602; SE = 0.239$ ) compared to a left posture ( $M = -1.883; SE = 0.199$ ). Participants reported feeling greater ownership over congruent conditions ( $M = -1.316; SE = 0.281$ ) compared to incongruent conditions ( $M = -2.168; SE = 0.185$ ). Furthermore, participants reported feeling greater ownership over pictures of the hand ( $M = -1.156; SE = 0.304$ ) compared to the bar ( $M = -2.328; SE = 0.199$ ). The difference between congruent and incongruent feelings of ownership was greater when participants viewed the hand (Congruent:  $M = -0.516, SE = 0.385$ ; Incongruent:  $M = -1.797, SE = 0.298; p < .001$ ) compared to when they viewed the bar (Congruent:  $M = -2.117, SE = 0.236$ ; Incongruent:  $M = -2.539, SE = 0.151; p = .014$ ).

## **Discussion of Study 1**

In the current study, participants received tactile stimulation to their right index finger while viewing pictures of another person's right hand in either a right or left (across the midline of the body) spatial posture. The position of the participants' right hand also alternated between a right and left spatial posture. This created two conditions of congruent and two conditions of incongruent visuotactile events. In addition, four



Error bars: +/- 1 SE

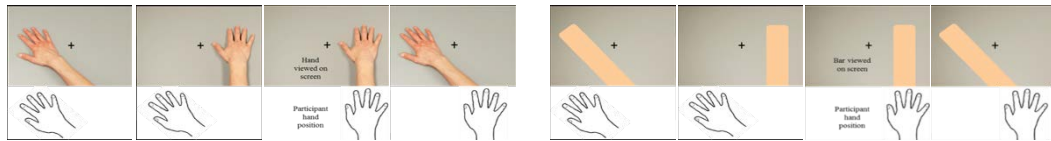


Figure 13. Ownership Scores. The mean ownership scores reported by the participants for each condition.

more conditions were created by replacing the pictures of hands with pictures of bars to test whether an effect of spatial congruency was body-specific. SEP and mu rhythm responses recorded from central electrodes C3 and C4 were computed from the EEG signal for each of the eight combinations of conditions. Lastly, participants reported feelings of ownership of the viewed hand or bar for each condition. An ownership score of each condition was calculated.

SEP responses recorded from electrode C3, located over the contralateral hemisphere to the tactile stimulation, were expected to show mean amplitude differences for the viewed object (hand vs. bar) in the earliest somatosensory components (P50, N80). Additionally, differences between the participants' hand position in space (right vs. left) were expected for the succeeding SEP components (P100, N140). However, neither of these effects was readily observed in our sample at electrodes contralateral to the touch on the finger. For all components of the contralateral and ipsilateral SEP responses, there was a surprising lack of differences between viewing the hand compared to the object (with one exception of an interaction effect for the N140, discussed below). This lack of findings is somewhat surprising given that a visual modulation of viewing the hand on the SEP response has been reported in several studies (Cardini et al., 2012; Deschrijver et al., 2015; Longo et al., 2011; Sambo et al., 2009; Taylor-Clarke et al., 2002). It is possible that the experimental design of the current study was not optimal for finding a body-specific visual modulation on the SEP response, perhaps due to the pictures of the hands and bars being randomly intermixed across a block, meaning the system was responding generally to visual information. Another explanation may be that visual modulations are more likely to occur when participants are viewing their own limb

compared to an picture of another's limb. If this were the case, interpersonal body mappings may not be registered during early stages of somatosensory processing.

In line with expectations, P100 and N140 components were observed bilaterally in the SEP at both C3 and C4 electrodes. The P100 component at the scalp site ipsilateral to the tactile stimulation showed differences in mean amplitude between participant hand positions in space. The appearance of this effect of hand posture in the P100 component matches the timing (P100 & N140) of the effect reported in studies using a crossed hands manipulation (Heed & Röder, 2010; Ley et al., 2015; Rigato et al., 2013). In studies examining the SEP response using crossed hands, it has been suggested that the difference in the SEP response reflects the timing of a spatial remapping for accurate tactile localization. Although Heed and Roder (2010) reported differences due to crossed hands at contralateral electrodes to the tactile stimulation, they also reported that the effect was largest over ipsilateral regions. Greater positivity was found between the 100-140 ms time interval for an anatomical matching of attended body space and stimulated hand. Comparably, in the current study, mean amplitude of the ipsilateral P100 was greater when the participant's hand was located in their right space compared to their left space (i.e., a "match" of the anatomical and external location of the stimuli).

Furthermore, Rigato and colleagues (2013) found hand posture effects at ipsilateral regions (for the N140 component) when participants could not view their own hand, just as the participants in the current study could not view their hands. As the authors discuss (Rigato et al., 2013), the differences at ipsilateral sites may be due to a preferential processing toward an external frame of reference when only proprioceptive information of posture is available (Lloyd, Shore, Spence, & Calvert, 2003). Thus, a possible reason

for greater differences between right and left hand posture in the ipsilateral SEP response to tactile stimulation of the right hand could be that while the hand is located in the left space, the hand is being represented externally to the left while tactile stimulation is being represented to the right anatomical space. Therefore, activity would occur contralateral to the left space and the right anatomical space, and this activity would be registered at both left (C3) and right (C4) central electrodes. In contrast, when the hand is located in the right space, the hand is being represented externally and anatomically to the right space. Therefore, activity in the ipsilateral region to the touch may be significantly reduced (as nothing is occurring in the left space) which would account for the differences observed at electrode C4. Future work would benefit from further explorations of modulations of ipsilateral SEP components.

An interesting result was also present in the N140 component of the SEP response at the electrode ipsilateral to the stimulated hand (C4). A three-way interaction was observed between the position of the participant's hand, the congruency between the position of their hand and that of the observed hand, and the type of object being viewed (hand or bar). When participants were viewing a hand and their hands were positioned in left space, the mean amplitude for the N140 for the incongruent condition was more negative compared to the congruent condition. While a difference in the N140 mean amplitudes was expected for participants' hand position in either right or left space, an interaction with the congruency or object of the viewed pictures was not expected. One explanation for this finding could be related to the idea presented above for ipsilateral P100 differences. For instance, while the right hand is located in the left space, the hand is contralateral to electrode C4 (which we still call the ipsilateral electrode due to it being

on the same side of the body as the anatomical location of tactile stimulation). Without visual input of the hand, the brain shifts towards an external frame of reference, which may be reflected by the increased response at C4 (Lloyd et al., 2003; Rigato et al., 2013). Therefore, while a hand is located to the left of the body's midline, a difference between a spatially congruent and incongruent hand is detectable ipsilateral to the tactile stimulation. One study reported that when participants viewed uncrossed rubber hands while their hands were in a crossed position, the detrimental effect of the crossed hands on tactile localization was reduced (Azañón & Soto-Faraco, 2007). The reduction of a crossed hands effect by the observation of uncrossed hands may be analogous to the observation of the hand in right space while participants' hands were located in left space in the current study. This may help explain why a congruency difference between the N140 amplitude is constrained to when the participants' hands are in the left space. When participants have their hand located in a left space, neural processing may be shifting between an external frame of reference (observing a hand in left space) and an anatomical frame of reference (observing a hand in right space) depending on the congruency of the trial. In contrast, when participants' have their hand in the right space, the observation of the hand may not modulate the N140 response because a shift between references frames is not necessary. The hand is therefore represented in an anatomical reference frame, regardless of the congruency. However, this explanation is somewhat speculative and should be tested further in future studies.

Contrary to the findings observed at C4, the only significant finding in the SEP response to tactile stimulation at the contralateral site (C3) was observed in the late positivity. Here, there was an interaction between the posture of the participants' hands

and the spatial congruency of the viewed object. The interaction was not dependent upon the object being viewed (hand or bar). This is contradictory to our expectations of an interaction between the spatial congruency and the object viewed. Specifically, effects of congruency were expected while participants viewed a hand, but not while they viewed a bar, as visuotactile responses were thought to be body-specific. The lack of the expected modulation of the SEP by the viewed object may be due to the pictures of the hands and bars being too similar, as noted above. In terms of the observed interaction between hand posture and congruency, the average mean amplitude of the late positivity contralateral to the touch was found to be greater when participants were viewing a spatially congruent object (hand or bar) compared to a spatially incongruent object when participants' hands were located in their right space. In an opposite manner, the average mean amplitude of the late positivity was slightly greater when participants were viewing a spatially incongruent object compared to a spatially congruent object when participants' hand were located in their left space. A greater difference between spatial congruent and incongruent conditions may have occurred only while participants' hands are located in the right space due to a matching of anatomical and external frames of reference of the tactile stimulation. In comparison, when participants hands are in the left space, the tactile stimulation is still occurring anatomically on the right hand regardless of the spatial congruency of the viewed object. The matching of the anatomical and external frames of reference may have elicited a stronger response of the SEP due to corresponding visuotactile input.

The influence of spatial attention on the SEP late positivity cannot be ruled out, in part because the congruent and incongruent conditions are confounded by the visual field

of the picture. In the current study, when participants' hands were in right space, the late positivity was greater for pictures appearing in the right space (spatially congruent pictures) compared to pictures appearing in the left space (spatially incongruent pictures). Moreover, when participants' hands were in left space, the positivity was slightly greater for pictures appearing in the right space (spatially incongruent pictures) compared to pictures appearing in the left space (spatially congruent pictures). Therefore, the interaction observed in the late positivity of the contralateral SEP may be related to the spatial attention (greater positivity for the space contralateral to the SEP response). Prior studies have also provided evidence of spatial attention modulating the late window of the SEP (Sambo et al., 2009) as well as components within 100-200 ms (P100 & N140) (Cardini et al., 2012; Ohara et al., 2006).

The mu rhythm response to the tactile stimulation was also analyzed for the current study. Based on different patterns of activity viewed in the time-frequency plots, two separate bands of the mu rhythm were analyzed including a lower mu band (8-10 Hz) and an upper mu band (10-13 Hz). Prior studies of the sensorimotor mu rhythm have reported functional differences between lower and upper bands (Drew et al., 2015; Neuper, Scherer, Wriessnegger, & Pfurtscheller, 2009; Pfurtscheller, Neuper, & Krausz, 2000; R  ther, Brown, Klepp, & Bellebaum, 2014). For instance, Pfurtscheller and colleagues (2000) tested differences between lower and upper mu bands by participants performing voluntary foot and finger movements. The lower mu band was associated with in a more widespread ERD pattern across the scalp whereas the upper mu band showed a more effector-specific, somatotopic pattern of ERD response.

In the current study, a broad response pattern was observed in the lower mu band. At both electrodes C3 and C4 and in both early and late time intervals, there was a modulation of the response of the lower mu band according to the object being viewed. Surprisingly, an increase in power (synchronization) of the lower mu response was observed instead of desynchronization following tactile stimulation. This ERS response was significantly greater when participants were viewing bars compared to viewing hands, suggesting that the lower mu band responds differently to a picture of a body part, specifically of a hand, than a non-body object when receiving tactile stimulation to the hand. While only a handful of studies have reported on the mu response following tactile stimulation, the current study is the first to report visuotactile influences on this sensorimotor rhythm. It is conceivable that the ERS observed instead of ERD may be due to the chosen baseline in the current analyses (-500 to 0 ms). During the baseline period, the picture of the trial was already displayed, and anticipation of the upcoming tactile stimulus may have been occurring. Previous studies have shown that desynchronization of the mu rhythm occurs during the anticipatory period just before tactile stimulation in the hemisphere contralateral to the touch (Haegens et al., 2011; Jones et al., 2010; van Ede et al., 2011). A desynchronization of the rhythm in the baseline period may make the response following the tactile stimulation more positive, producing an ERS response instead of an ERD response. If this were the case, the direction of the difference between viewing bars and hands would still be observed. While a synchronization of the mu rhythm has been reported during the anticipatory period in the ipsilateral hemisphere of an impending touch, ipsilateral synchronization may only be present when distracter stimuli are present. The direction of the difference would then follow an expected pattern

of greater desynchronization for hands compared to bars. Notably, an effect of the observed object was present in the mu rhythm response, but not across SEP response components. It is important to remember that the two EEG measures reflect different cortical activity. While oscillations reflect responses of neuronal networks, ERPs reflect momentary post-synaptic responses of cortical neurons (Pfurtscheller & Lopes da Silva, 1999).

The response of the upper mu band in the current study also follows the idea that this band shows a more effector-specific response than the lower mu band (Pfurtscheller et al., 2000). While effects were observed at the contralateral electrode (C3) to the tactile stimulation, no significant findings were observed in the upper mu band at the ipsilateral electrode (C4). Regardless of the spatial congruency of the viewed picture, greater desynchronization of the upper mu band was found when participants' hands were placed in the right hand posture compared to the left hand posture. The hand posture effect was observed in the early time interval and approaching significance in the late time interval. The current study is the first to report a modulation to the mu rhythm response to touch by a change in the space of the touch. Greater ERD for the hand in a right space may be due to a "match" of the anatomical and external reference frames of the tactile location in the contralateral hemisphere. Moreover, a "mismatch" of the two reference frames when participants' hands are located in the left space of the tactile stimulation (right anatomical/left external) may have resulted in a less powerful suppression of the upper mu band. Future work examining the influence of external body positions on sensorimotor measures should report on mu rhythm response to the tactile stimulation as

it may provide new insights into the process of remapping the body for accurate tactile localization.

Participants' self-reported ownership of the viewed picture differed between conditions. Specifically, participants reported greater feelings of ownership when their hand posture was congruent with the space of the viewed object especially when viewing the hand. The effect of spatial congruency on body ownership scores was expected, as the pictures of the hand were directly overlying their own hand. In addition, greater feelings of ownership were reported when the participant's own hand was located in the right space compared to the left space, regardless of the viewed image. The effect of hand posture on body ownership of the image is surprising and somewhat difficult to explain. One possibility is that placing the right hand on the left leg is a rather unnatural position and participants may feel less ownership even over their own arm when it is in this crossed configuration. Lastly, a significant difference in ownership between the observed object (hand or bar) was found. Overall, strong feelings of ownership over the observed pictures were not observed in the current sample (average ownership scores were negative for each condition). Therefore, the ownership scores were not analyzed further with respect to the EEG measures.

## CHAPTER 3

### STUDY 2

#### **Method**

***Participants.*** Seventy-four infants were recruited for this study from a diverse urban environment using commercially available mailing lists. All participating infants were born within three weeks of their due date and had not experienced serious developmental delays or illness. Infants taking long-term medication or who had two left-handed parents were excluded from the study. The final sample used in statistical analyses comprised 47 infants (mean age = 6 mos., 21 days;  $SD = 16$  days). Within the final sample, 23 infants received stimulation to the hand (16 females) and 24 infants received stimulation to the foot (11 females).

***Tactile Stimulation.*** Tactile stimulation was delivered to infants' hands or feet using an inflatable membrane mounted in a plastic casing as described in Study 1 (10 mm diameter; MEG International Services; see Fig. 14). For each tactile stimulus, a keypress by an experimenter triggered the solenoid to be opened on the pneumatic stimulator for 10 ms. This elicited an expansion of the membrane beginning 15 ms after trigger onset, peaking at 2 N about 35 ms after trigger onset. The total duration of the membrane movement was around 100 ms. The 15 ms delay between trigger and membrane movement was corrected for in the timing of the events so that the time of 0 ms was the beginning of the membrane movement. The experimenter and pneumatic stimulator were located in an adjacent room behind a closed door to minimize audible solenoid operation.

***Procedure.*** The infant's head was measured and the infant was then fitted with an appropriately sized EEG cap while seated on their caregiver's lap. Two tactile stimulators



Figure 14. Study 2 Tactile Stimulation. An inflatable membrane mounted in a plastic casing (10 mm diameter; MEG International Services) taped to the top of the right hand and right foot of an infant for Study 2.

were attached at the midpoint of the dorsal surface of the right hand and right foot of the infant. The stimulators were attached using double-sided adhesive electrode collars in combination with medical tape, and then covered with a tubular bandage to hold them firmly in place, following the procedure used by Saby et al. (2015). A between groups design was used to maximize the number of trials per condition. Infants were randomly assigned to one of two conditions: to receive stimulation to their hand or to receive stimulation to their foot.

While infants sat on their caregiver's lap, the caregivers were given instructions to prevent infants from putting objects in their mouth and to minimize extra movements. The protocol involved the coordinated work of three experimenters. Sitting behind a curtain, Experimenter 1 began by reaching beyond the curtain to display a spinning toy to attract the infant's attention (~56 cm away from the infant). Once the infant's attention was obtained, Experimenter 1 retracted the toy and held out either her hand or foot.

Experimenter 2 (who was out of sight to the infant) touched the hand or foot with a feather duster (see Figure 15) for approximately 3-4 seconds. While the feather duster was touching the hand or foot of Experimenter 1, Experimenter 3 (sitting in an adjacent room) triggered the opening of the solenoid twice, allowing the infant to receive two successive tactile stimulations (~2 seconds apart). This process was repeated four more times for a total of 10 tactile stimulations in one block. The blocks alternated between the display of the hand and foot of experimenter 1 to the infants. The protocol contained a maximum total of 160 tactile stimuli within 16 blocks, although the procedure was terminated if the infant could no longer maintain attention to the visual stimuli or became overly fussy.

The experimental session was recorded on video for the purpose of coding infant attention and movement. During the recording, a vertical interval time code (VITC) was placed on the video signal that was aligned with EEG collection at the level of one video frame. For each tactile stimulus, the epoch -250 ms to 250 ms before and after the onset of the stimuli was coded for infant attention toward the experimenter's hand or foot, and large movements of the infant. Attention was coded if the infant maintained looking toward the hand or foot for the entirety of the epoch. Epochs were coded as containing large movements if they included gross body movements or large, repetitive movement of a limb (e.g., kicking a leg or batting a hand). Only trials coded as attended to were included in the final EEG analyses. In addition, trials containing large movements were excluded from the analyses.

***EEG Collection & Processing.*** The EEG signal was recorded using a lycra stretch cap (Electro-Cap International) or a mesh stretch cap (ANT Neuro) with 21

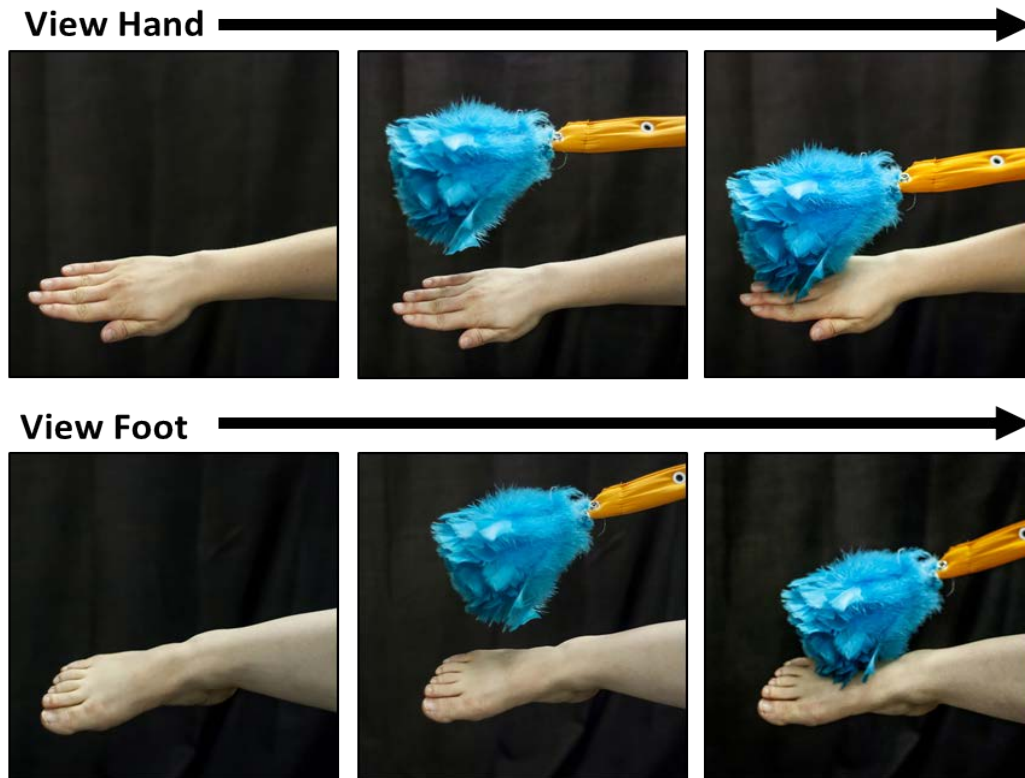


Figure 15. Experimenter Hand and Foot Presentation. The view of the hand or the foot presented to infants during trials for Study 2. A feather duster comes in and touches the experimenter's hand or foot for the duration of two tactile stimulations to the infant.

electrodes (Fp1, Fp2, F3, F4, Fz, F7, F8, C3, C4, Cz, T7, T8, P3, P4, Pz, P7, P8, O1, O2, M1, M2) placed according to the 10-20 system. Scalp electrode impedances were accepted if they were at or below 35 kilohms. The signal from each electrode was amplified using optically isolated, custom bioamplifiers with high input impedance ( $> 10^9 \Omega$ ; SA Instrumentation) and digitized using a 16-bit A/D converter ( $\pm 5$  V input range). Bioamplifier gain was set at 4000 with hardware filter (12 dB/octave rolloff) settings at .1 Hz (highpass) and 100 Hz (lowpass). During collection, the signal was referenced to the vertex (Cz) with an AFz ground.

The EEG Analysis System (James Long Company) and the EEGLab toolbox for MATLAB (Delorme & Makeig, 2004) were used for data processing. EEG signals were re-referenced to an average of the left and right mastoids. The signal was then low-pass filtered at 30 Hz and segmented into 750 ms epochs. Epochs containing ocular or muscle artifact or amplitudes exceeding  $\pm 250 \mu\text{V}$  at central sites (C3, Cz, C4) were excluded. After trial rejection, participants with less than nine trials within a condition were excluded from further analyses. The average number of trials were not statistically different ( $ps > .05$ ) for either congruent/incongruent limb-visual pair within groups (hand-hand = 14.57 & hand-foot = 16.35; foot-foot = 17.58 & foot-hand = 20.79). SEPs were computed for each participant relative to a prestimulus baseline of -100 ms to 0 ms, with time zero corresponding to the onset of membrane expansion at the skin surface. Extreme outliers visually present by participants' averaged SEPs were also excluded from further analyses. Three participants from each group were excluded due to outliers.

***Statistical Analyses.*** Analyses were time-locked to the onset of the tactile stimulation (i.e., 0 ms corresponded to the onset of the tactile stimulation to the skin). The analyses included the period from 0 ms to 600 ms. During this time, the participants received the tactile stimulation and viewed the hand or foot of the experimenter being touched by a feather duster. The EEG analyses focused on a central ROI overlying sensorimotor regions, specifically electrodes Cz, C3, C4 (Saby et al., 2013, 2015). SEP analyses examined the early positivity peaking between 100–300 ms and a late potential peaking within the window of 400–600 ms after the onset of tactile stimulation. A repeated-measures ANOVA was carried out for each SEP time window that included

factors of 2 (limb-visual congruency) x 3 (electrodes) with a between-subjects factor 2 (stimulation). The Greenhouse-Geisser correct factor was applied as appropriate.

## Results

Tactile stimulation of the right hand and right foot elicited SEP responses (Fig. 16 & 17) that were examined at the central sites C3, Cz, and C4. The SEP responses consisted of an early response at 100-300 ms and a later response at 400-600 ms.

**Early SEP Positivity (100-300 ms).** The repeated-measures ANOVA for the early positivity revealed a significant main effect of electrode ( $F_{(1.890, 85.071)} = 12.059, p < .001$ ). Pairwise comparisons revealed the mean amplitude at Cz ( $M = 6.924; SE = 0.726$ ) was statistically greater than the mean amplitude at C3 ( $M = 4.163; SE = 0.938; p < .001$ ) and C4 ( $M = 4.541; SE = 0.796; p < .001$ ). There was also a significant interaction between electrode and stimulated limb ( $F_{(1.890, 85.071)} = 11.939, p < .001$ ). Specifically in the group receiving foot stimulation, the mean amplitude at electrode Cz ( $M = 10.081; SE = 1.038$ ) was significantly greater than the mean amplitude at C3 ( $M = 4.388; SE = 1.341; p < .001$ ) and C4 ( $M = 5.779; SE = 1.138; p < .001$ ). No other effects or interactions were significant. Figure 18 shows bar graphs for the average mean amplitudes of the early positivity for each condition.

**Late SEP Potential (400-600 ms).** The repeated-measures ANOVA for the late potential revealed a main effect of electrode ( $F_{(1.899, 85.468)} = 5.256, p = .008$ ). Pairwise comparisons revealed that the mean amplitude at C3 ( $M = -0.035; SE = 1.295$ ) was significantly lower than electrodes Cz ( $M = 2.606; SE = 1.094; p = .002$ ) and C4 ( $M = 1.993; SE = 1.163; p = .037$ ). There was a significant interaction between the limb-visual congruency and the stimulated limb ( $F_{(1.000, 45.000)} = 7.962, p = .007$ ). Pairwise

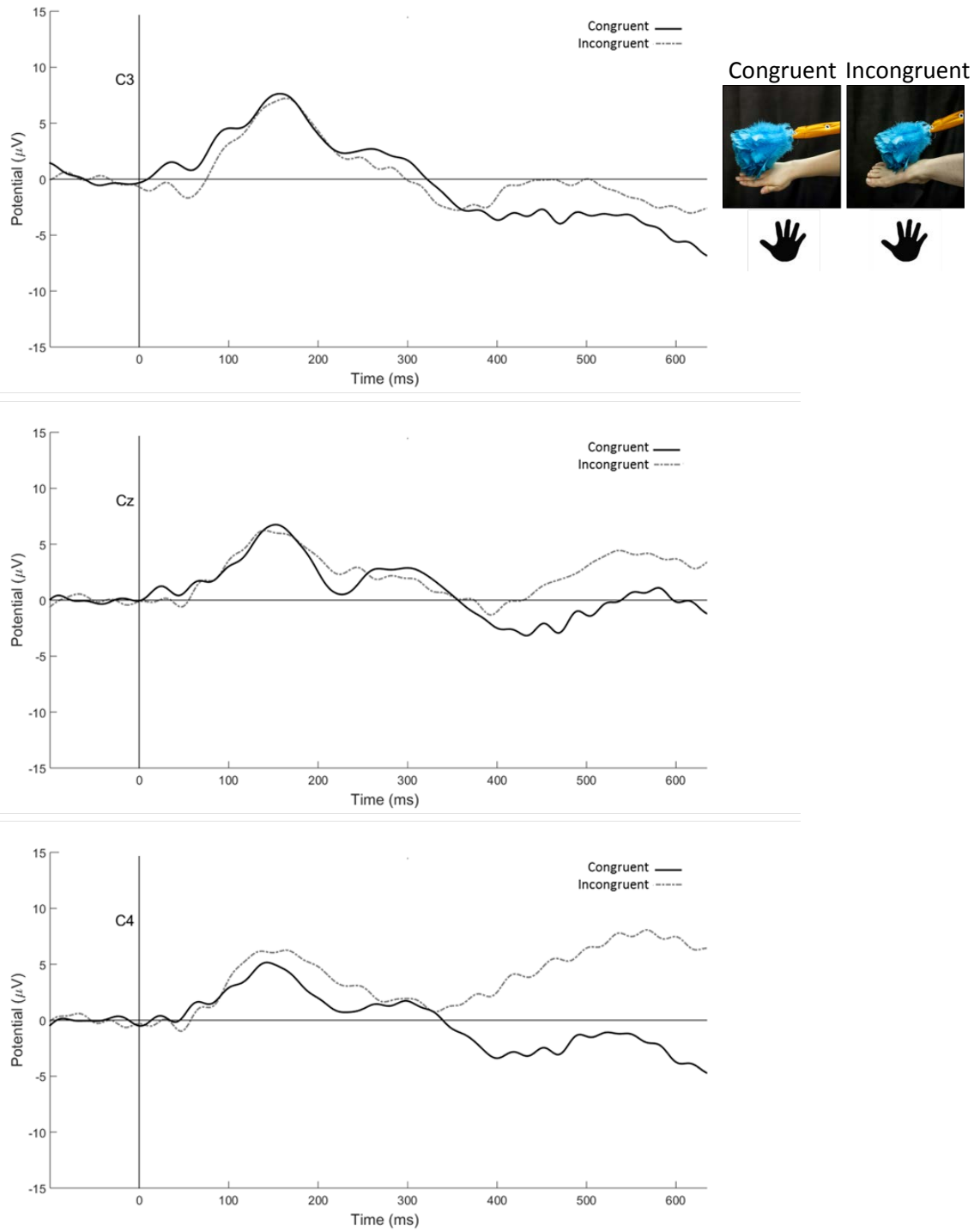


Figure 16. Hand SEPs. SEP responses to tactile stimulation of the right hand in 7-month-old infants. The plots display responses at central electrodes C3, Cz and C4.

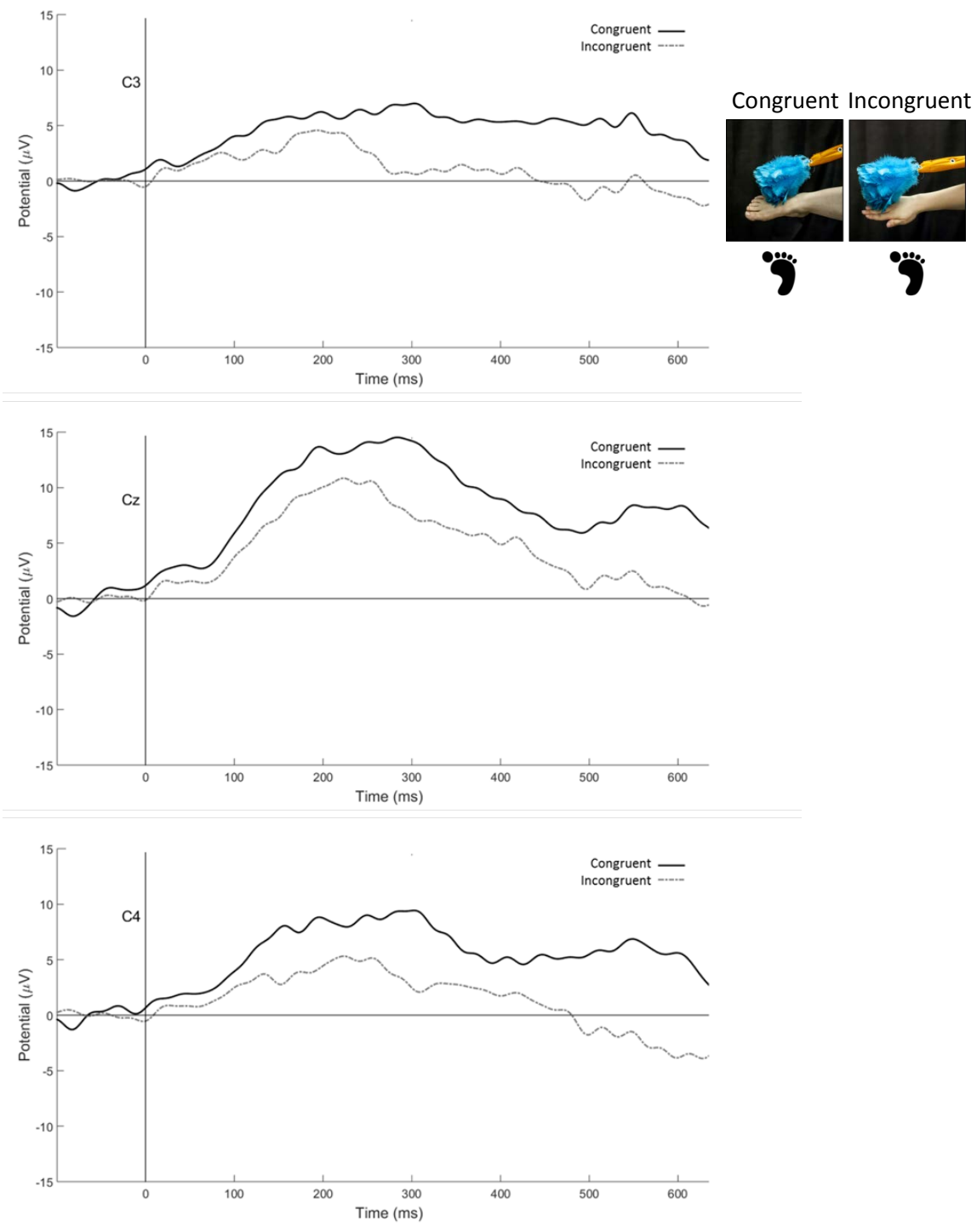


Figure 17. Foot SEPs. SEP responses to tactile stimulation of the right foot in 7-month-old infants. The plots display responses at central electrodes C3, Cz and C4.

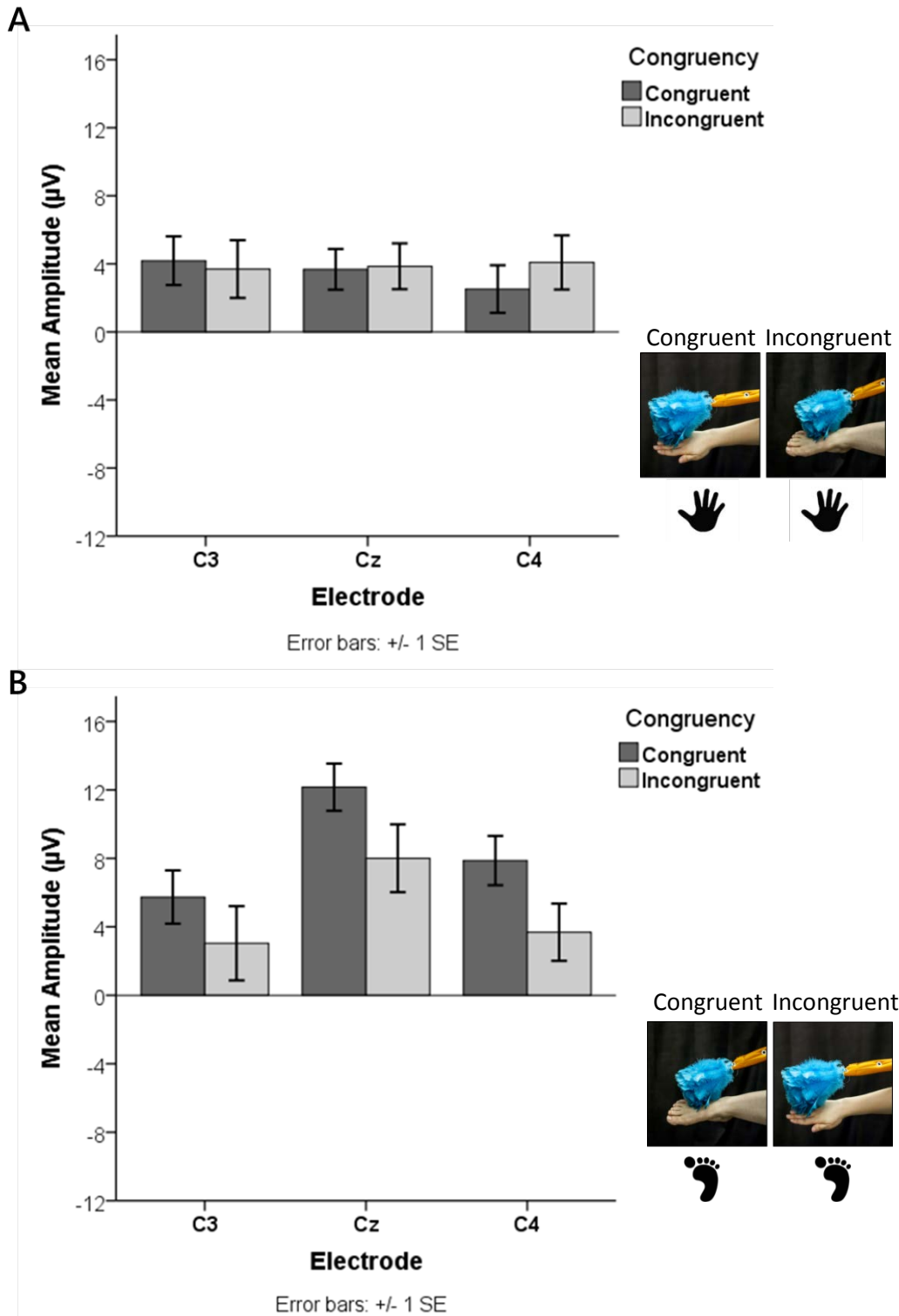


Figure 18. SEP Early Positivity. The average mean amplitudes of the early positivity in the SEP response at each electrode to tactile stimulation of the right hand (A) and the right foot (B) from 7-month-old infants.

comparisons revealed a significant difference ( $p = .037$ ) between the mean amplitudes of the congruent ( $M = 5.926$ ;  $SE = 1.998$ ) and incongruent ( $M = 0.220$ ;  $SE = 2.027$ ) conditions for the group receiving foot stimulation, but not the group receiving hand stimulation (Congruent:  $M = -2.408$ ;  $SE = 1.956$ ; Incongruent:  $M = 2.349$ ;  $SE = 2.027$ ;  $p = .073$ ). There was also a significant interaction between electrode and stimulated limb ( $F_{(1.899, 85.468)} = 3.861$ ,  $p = .027$ ). Specifically in the group receiving hand stimulation, the mean amplitude at electrode C3 ( $M = -2.541$ ;  $SE = 1.812$ ) was significantly lower than electrode Cz ( $M = 0.685$ ;  $SE = 1.530$ ;  $p = .007$ ) and C4 ( $M = 1.768$ ;  $SE = 1.627$ ;  $p = .002$ ). In the group receiving foot stimulation, the mean amplitude at electrode Cz ( $M = 4.527$ ;  $SE = 1.563$ ) was significantly greater ( $p = .047$ ) than the mean amplitude at electrode C4 ( $M = 2.219$ ;  $SE = 1.663$ ).

Lastly, there was a significant three-way interaction between limb-visual congruency, electrode, and stimulated limb ( $F_{(1.792, 80.659)} = 3.960$ ,  $p = .027$ ). Within the group receiving foot stimulation, there was a significant difference ( $p = .048$ ) between congruent ( $M = 7.283$ ;  $SE = 1.940$ ) and incongruent conditions ( $M = 1.772$ ;  $SE = 2.193$ ) at electrode Cz. The mean amplitude difference between congruent ( $M = 5.519$ ;  $SE = 2.137$ ) and incongruent conditions ( $M = -1.081$ ;  $SE = 2.115$ ) was also significant ( $p = .016$ ) at electrode C4. The mean amplitudes were greater for the congruent condition compared to the incongruent condition. Within the group receiving hand stimulation, there was a significant difference ( $p = .003$ ) between congruent ( $M = -2.238$ ;  $SE = 2.092$ ) and incongruent ( $M = 5.773$ ;  $SE = 2.070$ ) conditions at electrode C4. Here, the mean amplitudes were greater for the incongruent condition compared to the congruent

condition. No other effects were significant. Figure 19 shows bar graphs of the average mean amplitudes of the late potential for each condition.

## **Discussion of Study 2**

Two groups of infants received tactile stimulation on either their right hand or right foot while both groups viewed an experimenter's hand or foot being touched. The time-locked SEP response to the tactile stimulation was analyzed for central electrodes C3, Cz, and C4. Analyses focused on an early positivity occurring between 100-300 ms post-stimulus and a late potential between 400-600 ms. An effect of the congruency between the viewed stimulus and body part of the tactile stimulus was expected to be apparent in the early positivity. In addition, mean amplitudes of the early positivity were expected to be greatest overlying regions associated with the particular body part being stimulated. This somatotopic pattern was expected to be apparent in greater potentials medially at electrode Cz for foot stimulation and contralaterally at electrode C3 for right hand stimulation.

Contrary to expectations, an effect of congruency was not observed in the mean amplitudes of the early positive peak between congruent and incongruent conditions regardless of the limb stimulated (hand or foot). A somatotopic pattern of response was only observed for infants receiving foot stimulation such that greater mean amplitudes in response to foot stimulation were recorded at Cz compared to C3 and C4. When examining the late potential, effects of congruency on the mean amplitudes were dependent upon electrode and the limb stimulated. Specifically, more positive mean amplitudes were elicited for congruent trials when the infant was receiving foot stimulation and observing the experimenter's foot at electrode Cz and C4. In contrast,

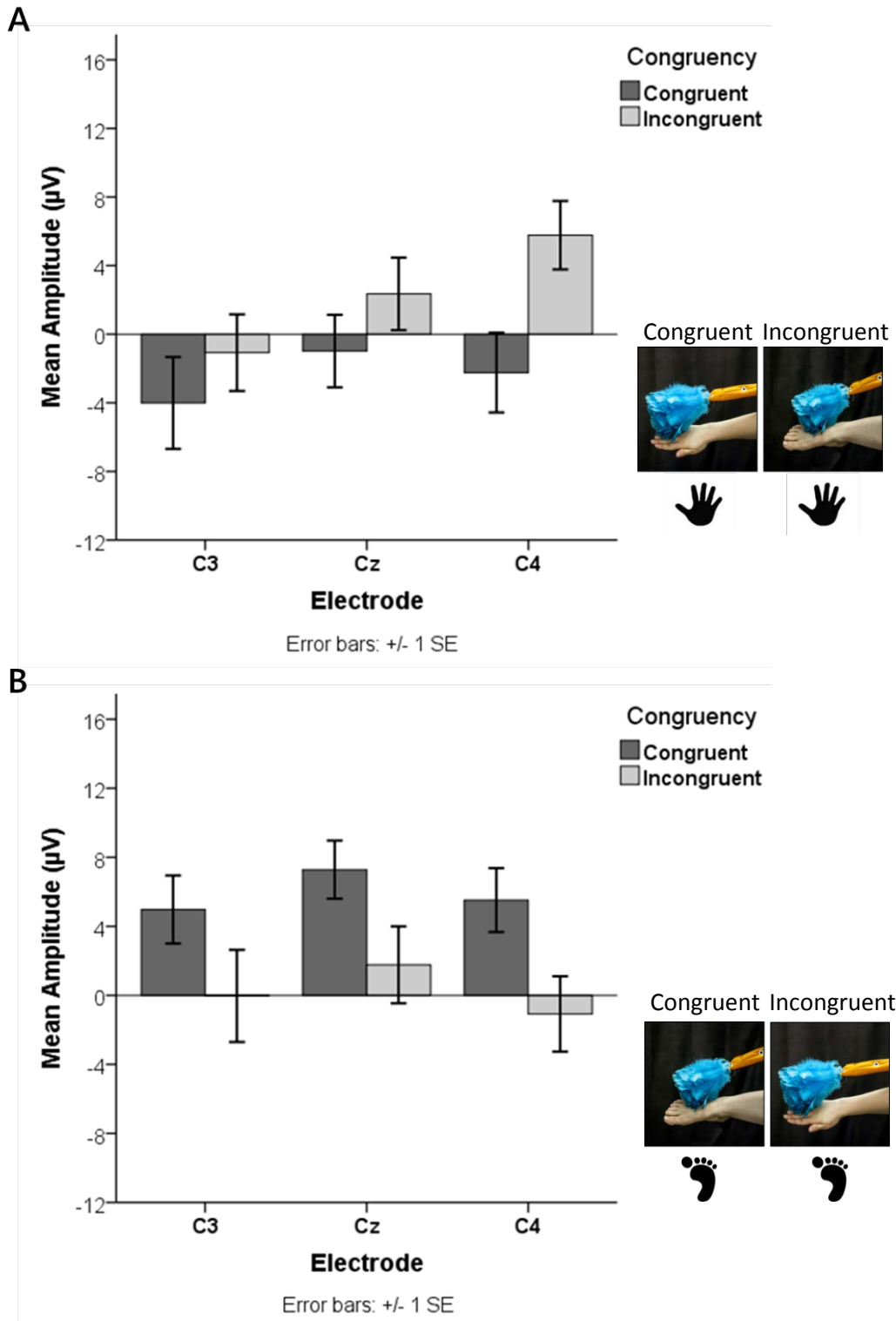


Figure 19. SEP Late Potential. The average mean amplitudes of the late potential in the SEP response at each electrode to tactile stimulation of the right hand (A) and the right foot (B) from 7-month-old infants.

more positive mean amplitudes were elicited for incongruent trials when the infant was receiving hand stimulation and observing the experimenter's foot at, unexpectedly, electrode C4. These results are discussed further below.

The early positive peak generated in the current study was similar to the peak observed in a previous study of 7-month-old infants (Saby et al., 2015; Fig. 3). An early positive peak was also reported in other studies looking at SEP responses to tactile stimulation in infants (Gondo et al., 2001; Nevalainen et al., 2008; Pihko et al., 2011). This peak is likely reflective of activity occurring in the SII region (Nevalainen et al., 2014). In the current study, there was some evidence of a somatotopic pattern of response when infants were being stimulated on the foot. Surprisingly, a somatotopic pattern was not observed during hand stimulation, as differences in mean amplitude of the early positivity were not significant between sites. The somatotopic topography of the SEPs in response to foot stimulation coincides with the response found by Saby et al. (2015). Tactile stimulation to the foot in infants has not been further explored by other studies recording SEPs, but the response, located medially at Cz, corresponds to areas known to respond to foot activity (Nakamura et al., 1998). The lack of an observable somatotopic pattern in response to hand stimulation does not support previous findings on the early positive peak showing greater lateral responses, specifically contralateral to the stimulated hand (Nevalainen et al., 2008; Pihko et al., 2011; Rigato et al., 2014; Saby et al., 2015).

The lack of a readily observable somatotopic pattern in response to hand stimulation may relate to the origin of the activity being reflected in the early positivity. A somatotopic response is expected in the earliest stage of somatosensory processing

beginning within the SI region. In adults, the activity generated by SI occurs prior 100 ms post-stimulus (Allison et al., 1992). The earliest stages of somatosensory processing may be occurring prior 100 ms post-stimulus in infants as well. Indeed, evidence from studies using MEG to explore tactile stimulation to the fingertip in newborns report that early components (M30 & M60) are generated in SI contralateral to the stimulation (Nevalainen et al., 2014). In addition, MEG studies report a later component (M200) reflecting activity in SII. There is evidence that the M200 is a bilateral response as found in sleeping newborns (Nevalainen et al., 2008). The M200 reported in MEG studies may correspond to the early positive peak observed in EEG studies within the 100-300 ms range. In adults, activity presumed to reflect the SII response shows a bilateral pattern (Hari & Forss, 1999). Thus, the early positivity in the SEP response to hand stimulation in infants may be expected to be bilateral or have less somatotopic distinction than the earliest stage of somatosensory processing. Early components corresponding to SI can be harder to observe when using EEG recordings or tactile stimulation compared to median nerve stimulation. As in the study of Saby et al. (2015), clear components prior to 100 ms were not observed in the current study.

Experimental differences in protocol may have further reduced prospective somatotopic SEP responses in the current study. For instance, somatotopy in response to hand stimulation was previously reported in the early positivity using the same tactile stimulation and hand location (Saby et al., 2015). One important difference between the current study and the prior study was the occurrence of tactile stimulation on different limbs. In the current study, only the right hand was stimulated throughout the entire experiment. In the prior study, the right and left hand were stimulated as well as the right

and left foot in each infant. Therefore, somatotopic responses may have been more salient within the context of the variation in the location of tactile stimulation or neural adaptation to hand stimulation may have occurred throughout the course of the experiment.

The early positivity in 7-month-old infants did not show differences between congruent and incongruent conditions in either group receiving hand or foot stimulation. A body-specific correspondence between the observed and stimulated body part was not apparent in the SEP response. It is possible that limb-specific congruency between visuotactile stimuli may be more apparent in later stages of somatosensory processing in 7-month-old infants, or they are not discernible in the neural response at this age. Maturation of the peripheral and central somatosensory pathways develops gradually throughout the first four years of life (Boor & Goebel, 2000). Thus, sensory connections may also be maturing during infancy. While adult work has shown viewing the body modulates SEP responses to tactile stimulation during a similar stage of somatosensory processing in SI and SII, no study to date has directly tested this in infants. Perhaps, the infant SEP is not as influenced by visual information. A beneficial future direction would be to compare SEP responses in infants while viewing a body compared to a non-body object.

Examining a later window of the SEP response in infants showed findings for a potential occurring between 400-600 ms post-stimulus, which was also analyzed at central electrodes (C3, Cz, and C4). To date, only one prior study investigating SEP responses in infancy has reported a response at 400 ms or later after the onset of a tactile stimulus. The response observed in the study by Rigato and colleagues (2014) showed a

positive peak clearly between 400-600 ms, matching the timing of the current study but having a different appearance (as more of a positive peak). The late peak observed in the prior study may be due to the use of long-duration, intense vibrating tactile stimulation lasting for 200 ms on the palms of the infants. Therefore, the late peak may be a response to the completion of the tactile stimulation about 200 ms later. In the current study, a three-way interaction between the congruency, stimulated limb, and electrode was observed in the late potential. While the difference between congruent and incongruent trials was significant at the medial electrode (Cz) and ipsilateral electrode (C4) when infants received foot stimulation, the difference between congruent and incongruent trials when infants received hand stimulation was significant at the ipsilateral electrode (C4). Additionally, when infants received stimulation to the foot, the differences between conditions followed an expected pattern where the congruent trials elicited more positive mean amplitudes compared to the incongruent trials. In contrast, when infants received stimulation to the hand, the mean amplitude for incongruent trials was more positive than the congruent trials. In both groups, greater mean amplitudes of the late potential were found when infants were viewing the experimenters' foot (implications of this are discussed below).

Differences seen in the late potential between observed and stimulated body parts may be similar to the effects of visuotactile limb congruency reported in adult work (Deschrijver et al., 2015; Longo et al., 2012; Sambo et al., 2009). In the adult studies, congruency effects were present in the SEP response after 200 ms post-stimulus bilaterally over central sites. In addition, congruency effects were observed in the late positive component of the SEP in Study 1. It is conceivable that the late potential in

infants (emerging at 400 ms) could be related to or even develop into the late positivity in the adult SEP response (emerging between 200-300 ms), reflecting a late stage of somatosensory processing. While further work should be done to clarify the function of the late potentials in adult and infant SEPs, the current findings are the first to provide electrophysiological evidence for visuotactile aspects of self-other correspondences in preverbal infants. Cross-modal correspondences between vision and somatosensation may be one foundation for a self-other body mapping in early development. This self-other body mapping process likely involves the identification of a body part used by another person and then the selection of one's own corresponding body part. This body mapping may provide a framework for infants to then learn or imitate from others by observing that others are "Like Me" (Meltzoff, 2007a). Thus, self-other body mapping has been proposed to be important for social cognitive learning in infancy (Marshall & Meltzoff, 2015).

Questions remain about the current findings, such as the strong ipsilateral effect of congruency at electrode C4 when infants received stimulation to the right hand or right foot. In Study 1, effects were observed ipsilateral to the stimulated hand, with the effects being elicited by changes in the hand posture of the participant and proposed to be due to the touch occurring on the left side of the body while still on the right hand. More work in infants and adults should investigate and report modulations of ipsilateral SEPs, since studies have generally focused on the more expected contralateral responses.

The results of Study 2 also suggest a discrepancy between foot stimulation and hand stimulation in the direction the late potential was modulated by limb congruency. While the late potential increased in positivity for congruent trials during foot

stimulation, it decreased in positivity for congruent trials during hand stimulation. One factor for this discrepancy between the two groups could be due to the different SEP morphology observed in response to hand and foot tactile stimulation (Fig. 16 & 17). The SEPs in response to foot stimulation show a very strong positivity particularly while infants were also viewing a foot, a pattern that persisted throughout the entirety of the SEP. In a different way, the SEPs in response to the hand stimulation were slightly weaker and appear to return to a baseline prior to the late potential. The reasons behind this different morphology of the SEP responses are uncertain, since it was not observed in Saby et al. (2015). One possible reason is that the mean numbers of trials per condition were lower for the current study compared to the prior work. Other possible explanations may be related to different receptor types on the top of the foot compared to the top of the hand, a novelty effect for tactile stimulation occurring on the top of the foot, or distortion effects occurring as the elicited electrical activity moves through the skull from different underlying sources.

Importantly, a visual difference between the limbs viewed cannot be ruled out of the current results. For instance, the congruent and incongruent conditions were confounded by the viewed limb also differing between those two conditions. In the congruent condition, infants viewed either a hand or foot while in the incongruent condition the opposite was always viewed. The confounding visual difference may account for the discrepancy of the direction of the congruency effect between hand and foot stimulation. When infants were viewing the experimenter's foot, the mean amplitude of the late potential was greater than when they were viewing the experimenter's hand in both stimulation groups. Interestingly, studies examining ERP responses to visual stimuli

in infancy have reported on a component often referred to as the Nc (negative central) which occurs between 400-600 ms post-stimulus (Ackles, 2008; Ackles & Cook, 2007; Nelson & Salapatek, 1986; Reynolds & Richards, 2005; Richards, 2003; Wiebe et al., 2006). Although the morphology of the late potential observed in the current study does not necessarily resemble the large negative peak of the Nc, the onsets of the two potentials bear a resemblance to each other. Studies on the Nc have shown that it is modulated by factors such as frequency (Ackles, 2008; Ackles & Cook, 2007) and familiarity or novelty (Nelson & Salapatek, 1986; Reynolds & Richards, 2005; Wiebe et al., 2006) of the visual stimuli such that the Nc is more negative for infrequent or novel stimuli. Attention toward the visual stimuli has also been shown to facilitate the Nc response in infants 4.5-months- and 7.5-months-old (Richards, 2003). The Nc has been proposed to reflect a top-down mechanism allocating attention (Ackles, 2008) and reflecting activity in the prefrontal cortex and anterior cingulate cortex (Reynolds & Richards, 2005). Similarly, differences observed in the late potential of the current study may be due to attentional differences between infant's viewing the hands compared to viewing the feet. Even though infants were looking at both the hand and foot of the experimenter, the difference observed could draw upon some deeper attentional mechanism. Possibly, at 7 months of age, hands are being used and observed in more functional tasks than feet such as social interactions (e.g., imitation), the beginnings of tool usage, or eating.

## CHAPTER 4

### GENERAL DISCUSSION

In the current studies, electroencephalography was used to investigate the interplay between responses to tactile stimulation and the observation of a body part in both infants and adults. Congruency between visuotactile information may be one aspect of the formation of body representations through multisensory neural processes. SEP and mu rhythm sensorimotor responses were recorded during congruent and incongruent visuotactile events. Two separate studies were carried out to investigate influences of different characteristics of body-specific congruency on the neural response to touch. In Study 1, we explored spatial congruency aspects of visuotactile events in adults. In Study 2, the presence of limb-specific visuotactile body mappings was explored in a group of typically developing, preverbal infants.

Recent work on adult neural body maps showed that congruency between visuotactile events can influence the somatotopic organization of responses to tactile stimulation. The somatotopic pattern of response can be blurred or sharpened on a short timescale by manipulating the congruency of visual and tactile input (Cardini & Longo, 2016). In Study 1, the spatial specificity of congruency between a viewed limb and a tactile stimulation was tested. There was some evidence of the congruency of space modulating the SEP response in adults, specifically for a late positivity occurring at the contralateral electrode to the touch (C3) and the N140 component at the ipsilateral electrode (C4). However, this evidence for spatial congruency effects is complicated by interactions with the spatial location of the participants' hands, and further work is needed to parse apart the possible effects of the viewed image from congruency.

Additionally, there was little evidence that the spatial congruency effect for visuotactile events was body-specific. Mu rhythm ERS and ERD responses were observed differentially for upper and lower mu bands following tactile stimulation, with these responses being modulated by space and visual information.

In Study 2, a limb-specific congruency was tested for in the SEP response in 7-month-old infants. Although not occurring in the expected somatotopic pattern, SEP differences were found between the limbs viewed in both groups receiving hand or foot stimulation. Study 2 is the first study to report modulations of the infant SEP response by visual presentation of another's body, however these modulations do not appear to be specific to the limb congruency. Instead, the visual influence on the SEP responses are postulated to arise from differences in attention toward the hand and foot. The findings of both Study 1 and Study 2 shed light on the seamless integration of sensory information that is necessary for coherent body representations.

An important consideration when reviewing the current findings is that congruency was confounded by the viewed image (Study 1) or limb (Study 2). In Study 1, the effects of congruency in the SEP response interacted with the hand posture of the participants. In Study 2, the direction of the congruency modulation on the SEP was the opposite for the stimulated hand and foot group. In both studies, the visual information changed along with the factor of congruency. Differences in attentional factors may be underlying the observed changes in the SEP responses. A prior study examining modulations of the SEP to visuotactile stimuli reported that effects of eye gaze and spatial attention toward the tactile stimuli are independent of each other and separate mechanisms underlie their corresponding SEP modulations (Gherri & Forster, 2015). In

the current studies, the participants were looking at the visual stimuli in the analyzed trials, but separate top-down attentional factors may be driving the modulations of the SEPs. A follow-up study should be carried out in order to parse apart the effects of congruency and attention to clarify the current findings.

There are several avenues for continuing investigations of neural body maps using visuotactile stimuli with the purpose of learning how multisensory processes in the brain function and how body representations utilize multisensory information. Specifically, responses to visuotactile stimuli could be further explored in the context of interpersonal body representations. Study 1 may not have been optimal for emphasizing the body-specificity of visuotactile SEP responses in adults, and a follow-up study could use other stimuli to either corroborate or challenge the current findings. Furthermore, interpersonal body representations in adults could be tested by having participants observing limbs of an experimenter while receiving tactile stimulation. Additionally, work involving EEG and MEG techniques should report measures of both frequency band oscillations (e.g.,  $\mu$ ) and evoked potentials (i.e., SEP responses). By reporting on both measures, researchers can efficiently investigate sensorimotor processes and better understand functional differences between the two measures. Another interesting avenue of investigation would be to explore individual differences in body representations and their relation to sensorimotor measures. Finally, the current study is the first to explore directly the interaction between somatosensation and vision in an interpersonal context during infancy. Further study of neural body maps using visuotactile stimuli can help form a better understanding of correspondences between the self and other during the earliest stages of life.

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