Embodiment of the Rubber Hand Across Different Somatosensory Modalities

by

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Abstract

The Rubber Hand Illusion (RHI) can be induced by synchronous brushing of a seen rubber hand and the subject’s real hidden hand. We sought to determine whether the RHI could be induced using one somatosensory modality and maintained using another. In 75 subjects, one of three modalities was used to induce the RHI: touch (brush), vibration (128Hz), or temperature (cooling). We then tested whether the illusion was maintained when only the rubber hand received stimuli from all modalities including kinesthesia (passive movement of arm). The RHI was successfully induced with touch, vibration and cooling modalities in 35 of 75 subjects. When only the seen rubber hand received a stimulus and not the hidden real hand, ownership persisted in 24 of 35 subjects who were successfully induced before. Our results may contribute to the understanding of the RHI and to the development of somatosensory neuroprosthetics.
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<td>BOLD</td>
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<td>DBS</td>
<td>Deep brain stimulating</td>
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<td>EDA</td>
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<td>M</td>
<td>Mean</td>
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<td>M1</td>
<td>Primary motor cortex</td>
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<td>MANOVA</td>
<td>Multivariate analysis of variance</td>
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<td>VP</td>
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Chapter One: Review of Literature

1.1 Introduction

Neurological disability is a significant public health problem in Canada with estimated costs of $2.8 billion per year from strokes and spinal cord injuries alone (Canadian Institute for Health Information, 2013). While rehabilitation improves recovery in some patients, others fail to regain ambulatory or useful limb function despite optimal treatment. Recent advances in neural prostheses have the potential to restore neurological function. For example, cochlear implants have developed to the point of standard of care, novel retinal prostheses to restore vision have been approved for human use, and brain computer interfaces for motor control are being tested in humans (Schwartz, Cui, Weber, & Moran, 2006). Yet development of neural prostheses to restore somatic sensation remains in its infancy. The ideal neural prosthesis is one which effectively restores full function and allows for accurate and instantaneous control by the operator. Integration of finely controlled motor output with intuitive somatosensory feedback is critical in this regard, and with respect to limb use and walking, enables the generation of smooth movements, manipulation of objects and walking on uneven ground (Schwartz et al., 2006).

Our research group is one of only a few investigating whether electrical stimulation (ES) can restore natural somatic perceptions in humans. A previous graduate student in our lab examined the effects of ES on the thalamus, a sensory relay nucleus, in patients undergoing surgery to implant deep brain stimulating (DBS) electrodes (Heming, Sanden, & Kiss, 2010; Heming, Choo, Davies, & Kiss, 2011). We found that different patterns of ES evoked different sensations and could modulate the duration of each percept. However, all patterns felt ‘unnatural’ to the subjects, and naturalness is important to trust and accept the prosthetic as one’s own limb.
(Biddiss, Beaton, & Chau, 2006). Moreover, no one described a feeling of limb movement, or kinesthesia. Kinesthesia is a critical somatosensory percept which is necessary for motor control (Schwartz et al., 2006). A possible reason why subjects described the percepts evoked as ‘unnatural’ is that ES was applied without a behavioural context, in contrast to how a real neural prosthesis would be used in carrying out a task. The Rubber Hand Illusion (RHI) which links somatosensory perception with embodiment is an excellent platform to study how behavioural context can modulate somatosensory perception. Thus, my thesis is focused on adapting the RHI to provide a behavioural context behind the electrical stimulation without providing a confounding physical stimulus.

An artificial limb can be induced to feel as one’s own body in neurologically normal subjects during the RHI (Botvinick & Cohen, 1998). The RHI can be induced in most people by synchronous brushing of a seen rubber hand and the subject’s hidden real hand. The integration of both tactile feedback from the hidden real hand and visual feedback of rubber hand being touched results in a feeling of ownership of the rubber hand (Botvinick & Cohen, 1998). In addition to an embodiment of the rubber hand, RHI also elicits another phenomenon known as a proprioceptive drift. One’s sense of body position in space gets distorted under RHI such that the position of the hidden real hand is biased towards the position of the viewed rubber hand (Botvinick & Cohen, 1998). Thus, the RHI is achieved through visuo-tactile-proprioceptive multisensory integration to affect overall somatosensory perception.

Being able to adapt the RHI across different somatosensory modalities would be helpful in pairing corresponding behaviour context to electrical stimulation which is aimed to restore
various types of senses, not just touch. Following the introduction of the classic RHI, others have described inducing the RHI with multiple somatosensory modalities besides brushing. However, it is unknown whether induction with one modality carries over to testing with other modalities, or even if modalities other than touch with a brush can evoke illusions better. Moreover, while there is a physiologic basis for the RHI being maintained with only visual feedback without a physical stimulus with demonstration of single and multunit firing in monkeys (Shokur et al., 2013), it is unknown whether a similar illusion exists in humans. For example, monkeys’ cortical cells maintained their response when only virtual hand was touched. Thus, would applying a somatosensory stimulus to the rubber hand alone, after inducing the RHI, continue to result in ownership of the rubber hand in humans? The maintenance of ownership when only rubber hand is receiving a stimulus could provide a behavioural context by which electrical stimulation could be applied to the nervous system without a confounding physical stimulus. The present research aimed to determine whether the RHI could be used in this context. In the following sections, I will review the literature on the RHI, including its physiologic basis, maintenance of ownership after induction, and the constraints for measurement and entrainment of the RHI.

1.2 Physiological basis of RHI

1.2.1 Somatosensory perception

The RHI is achieved through somatosensory perception which encompasses tactile, thermal, nociceptive, proprioceptive, and kinesthetic senses. Tactile sense includes both touch and pressure senses. Proprioception encompasses both the sense of our body position and balance in space and the sense of body movement (kinesthesia). Somatosensation begins with receptor organs such as mechanoreceptors in skin, muscles, tendons, and joints. These receptors convey
tactile, thermal, nociceptive, and proprioceptive information to primary afferent neurons. The primary afferent neurons located in the dorsal root ganglion of the spinal nerve carry somatosensory information into the CNS through neurons in the spinal cord gray matter and brainstem. Tactile and proprioceptive information is carried from the cuneate and gracilis nuclei of the medulla to the ventral posterior (VP) nucleus of the thalamus by the dorsal column-medial lemniscal system. The thalamus acts as a sensory relay nucleus and transmits inputs from the ascending fibre tracts into the primary somatosensory cortex (S1) in a somatotopic manner. Further information processing occurs from S1 to the secondary somatosensory cortex (S2) and parietal cortex. S1 outputs also reach the primary motor cortex (M1) directly or indirectly through the posterior parietal cortex.

1.2.2 Multisensory integration and body representation

The RHI is produced through integration between visual, tactile and proprioceptive inputs and two levels of multisensory matching processes. The matching of visual and tactile stimulations in temporal and spatial domains leads to a sense of ownership towards the rubber hand through a bottom-up matching process (Costantini & Haggard, 2007). Subsequently, the perceived location of the hidden real hand adapts to the location of viewed rubber hand through proprioceptive drift and a top-down matching process. The rubber hand is matched against both types of internal body representations, body schema and body image, which are not mutually exclusive to one another. Head’s (1920) classical description of body schema is a standard internal body representation from which one’s changes in postures and movements are derived. In contrast, body image is a mental representation of one’s own body, which includes beliefs, attitudes and emotions (Schilder, 1935; Cash & Brown, 1987). Thus, RHI involves matching of both
stimulations and body representations between the real hand and the rubber hand. Similarly, Tsakiris and Haggard (2005) found a synergistic interaction in the matching of stimulation and body representations between the real hand and the rubber hand for the RHI. Both bottom-up matching of visuo-tactile stimulation and top-down matching of body representation with the rubber hand are necessary but not individually sufficient for the sense of ownership. For example, proprioceptive drift was induced by Rohde, Di Luca, and Ernst (2011) with just an observation of the rubber hand while the real hand was hidden. However, this vision only condition involving top-down modulation was not sufficient for sense of ownership. The ownership was induced only under synchronous stroking of both the seen rubber hand and the hidden real hand, while proprioceptive drift also remained (Rohde et al., 2011).

Brodmann area 5 in the superior parietal lobe and premotor cortex which receive inputs from S1 have been areas of interest for body representation. Area 5 provides outputs to M1, premotor cortex, and supplementary motor cortex (Johnson, Ferraina, Bianchi, & Caminiti, 1996; Jones, Coulter, & Hendry, 1978; Jones & Powell, 1970; Strick & Kim, 1978). Thus, area 5 neurons have both sensory and motor properties. Most area 5 neurons in awake monkeys respond to joint angle and muscle stretch in a complex manner; some have combined joint rotation response with a tactile receptive field on the skin while others responded to multiple joint rotations (Duffy & Burchfiel, 1971). Likewise, Sakata, Takoka, Kawarasaki, and Shibutani (1973) found some area 5 neurons that responded to touch only in a specific arm joint position. Another subset of area 5 neurons in monkeys responded only during finger grasping and object manipulation while others responded only during goal-directed reaches (Mountcastle, Lynch, Georgopoulos, Sakata, & Acuna, 1975). Moreover, Mountcastle et al. (1975) showed additional area 5 neurons whose
responses increased with voluntary movement of the monkey’s arm. By manipulating the position of seen fake monkey arm while the real arm remained hidden, tonic firing rate of area 5 neurons were significantly higher when both the seen fake arm and the hidden real arm were on the left of the fixation point than when the position of the arms were mismatched (Graziano, Cooke, & Taylor, 2000). The convergence of visual and proprioceptive signals modulated the tonic firing rates of 25% of area 5 neurons that were tested; however, seeing the fake arm position did not modulate firing rates of S1 neurons (Graziano et al., 2000). Thus, this study suggests that area 5 is the first site of integration between visual input of the seen rubber arm’s position and proprioceptive feedback from the hidden real arm.

Similarly, premotor cortex and M1 neurons also have multimodal properties. Most M1 neurons respond to both tactile and joint rotation (Gentilucci, Fogassi, Luppino, Matelli, Camarda & Rizzolatti, 1988) similar to area 5 neurons. However, Kalaska, Cohen, Prud’homme, and Hyde (1990) suggest that M1 may play a greater role in initiating and guiding movements while area 5 keeps track of limb positions and movements. By making the monkeys move an externally loaded handle, they showed greater activation in M1 for the muscular force component and in area 5 for selectivity of hand movement. In addition, there are bimodal, visual-tactile neurons in the caudal premotor cortex where the tactile receptive field is paired with visual receptive field that extends 20cm outwards from the responsive skin area; cell response was only seen when the monkey saw or felt an object in a specific body region (Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981). Both visual and tactile receptive fields are arranged somatotopically in the premotor cortex. Thus, these bimodal, visual-tactile neurons may contribute to body
representation by integrating visual space around the body with tactile inputs from the body (Graziano & Botvinick, 2002).

With neuronal recordings implicating parietal and premotor cortex as multisensory integration site (Graziano & Botvinick, 2002), multimodal brain areas have been studied further in humans using functional magnetic resonance imaging (fMRI). Bremmer et al. (2001) found common active regions in separate presentations of visual, tactile, and auditory stimuli. These areas were the intraparietal sulcus, premotor cortex, and the upper bank of the lateral fissure.

1.2.3 Neuropsychological basis of the RHI

Various imaging studies using Positron Emission Tomography (PET) and functional Magnetic Resonance Imaging (fMRI) scans have identified a very likely involvement of multisensory integration in forming our sense of ownership. The areas of the brain involved in multisensory integration such as premotor cortex, frontal operculum, posterior insular cortex, intraparietal cortex, and cerebellum are significantly more active under the RHI compared to its absence. The amount of activation in the bilateral ventral premotor cortex correlated positively with the onset of the RHI and also the strength of the illusion (Ehrsson, Spence, & Passingham, 2004; Ehrsson, Holmes, & Passingham, 2005). In contrast, Tsakiris, Hesse, Boy, Haggard, and Fink (2007) found increased activity in the frontal operculum and a lack of increase in the ventral premotor cortex with stronger illusory experience. Ehrsson (2012) explained that the difference between the two studies may be due to identifying areas involved in different time points of the illusion, the onset (Ehrsson et al., 2004) and the maintenance of the illusion (Tsakiris et al., 2007). Tsakiris et al. (2007) also found a positive correlation between the activity of posterior insular
cortex and the magnitude of the proprioceptive drift. This area receives inputs signalling
temperature, pain, muscle fatigue, pleasant touch, and has also shown to be strongly activated
when owned real hand is threatened (Tsakiris, 2010; Ehrsson, 2012). Activity in the left
intraparietal cortex and the bilateral cerebellum was significantly greater with synchronous
touches and congruent position conditions than asynchronous touches and incongruent position
conditions (Ehrsson et al., 2004, 2005).

1.3 Maintenance of illusion after induction
Shokur et al. (2013) examined the cellular basis of the RHI in two monkeys using a modified
version of the RHI. Neural activity of non-mirror neurons in S1 and M1 were recorded during
synchronous physical and virtual touches applied to the monkey’s hand and a virtual monkey
hand, asynchronous physical and virtual touches, and virtual touch only applied to the virtual
hand. The virtual stroking only condition entailed monkeys observing their virtual hand being
touched while their real hand was not touched. S1 and M1 neurons continued to respond to just
virtual touch and were similar to cell responses during synchronous physical and virtual touches
(Shokur et al., 2013). The maintenance of cell response when just the virtual avatar hand was
touched occurred only following a period of synchronous physical and virtual touches. This
phenomenon was absent when virtual touch occurred without a previous session of synchronous
physical and virtual touches; cell firing was significantly higher when both physical and virtual
hands were touched than when only the virtual hand was touched without a prior period of
synchronous physical and virtual touches. These authors suggested that the maintenance of cell
response during only virtual touches may have been due to those cells being primed to respond
from a previous period of synchronous physical and virtual touches. There is no knowledge
about whether an illusory experience can occur in humans with just virtual touches applied to the rubber hand only, after a RHI is induced.

1.3.1 Maintenance of ownership in humans

The maintenance of illusory experience following induction of RHI in humans should be investigated in depth. Thus far, maintenance of illusory experience during asynchronous stroking between real hand and rubber hand following synchronous stroking of real and rubber hands has been studied. RHIs were successfully induced and maintained during a consecutive train of synchronous, asynchronous, and another synchronous stroking periods (Lewis & Lloyd, 2010). Valenzuela-Moguillansky, O’Regan, and Petitmengin (2013) went further to compare these two conditions. Out of 10 participants who were tested under synchronous, asynchronous, and non-stroking conditions in a randomized order, the illusion was experienced in 8, 7 and 3 participants, respectively. The non-stroking condition entailed stroking of only the hidden real hand but not the seen rubber hand. Furthermore, 2 of 3 participants with illusory experience under non-stroking condition were tested with synchronous stroking condition first. In contrast to studies in primates, these maintenance studies in humans did not involve a condition where only visual input was provided through only the rubber hand being touched. Moreover, the maintenance of illusory experience under different sensory modalities than what was used to induce the RHI has yet to be studied.
1.4 RHI measurements

1.4.1 Subjective measures

The original RHI’s subjective ownership experience was captured using 3 target questions and 6 control questions (Botvinick & Cohen, 1998). These authors reported that the responders of the RHI using synchronous stroking of both rubber and real hands showed significantly higher mean scores of the target questions than the control questions. There was 42% prevalence rate of the illusion during 30 min viewing period among synchronously stroked group compared to 7% prevalence rate from asynchronously stroked group. Each averages of the three target questions which refer to ownership were scored significantly greater than 4 on a 7-point Likert scale (from strongly disagree to strongly agree) than the averages of the other 6 control questions by the RHI responders. Thus, the RHI’s subjective ownership experience was captured by the averages of target questions being greater than 4 (an affirmative score) and differing significantly from the averages of control questions across subjects. However, in current literature, there are many different adaptations of the original questionnaire and various methods of analysis and interpretation.

Subsequent experiments that studied classical stroking conditions either shortened the original RHI questionnaire (Botvinick & Cohen, 1998) or used a different definition of a successful RHI. Bekrater-Bodmann, Foell, Diers, and Flor (2012) defined a successful RHI induction as having all 3 embodiment items being rated significantly higher than 6 distracter items. Others (Ehrsson et al., 2004) compared only 2 target illusion questions with 3 control questions to study the effect of rubber arm orientation compared to the hidden real arm (congruent versus incongruent arm positions) under both asynchronous and synchronous stroking conditions. Using paired t-tests
within each condition group, they found significantly higher ratings of illusion questions than control questions under synchronous congruent condition. They then compared ratings for the 2 illusion questions across 4 different conditions using two-way analysis of variance (ANOVA) and found a significant interaction between arm position and timing of brushstrokes during synchronous congruent condition. In a different study involving upper limb amputees, Ehrsson et al. (2008) adapted the original questionnaire (Botvinick & Cohen, 1998) and compared the means of the 9 questions from 18 participants using ANOVA. Moreover, a paired one-tailed t-test was used to compare the mean scores of the 3 illusion questions with the mean scores of the 6 control questions. In addition, they analyzed the illusion on an individual basis and defined the participants as having a strong illusion when all 3 illusion questions had confirmative scores (≥+1, on -3 to +3 Likert scale). In contrast, David, Fiori, and Aglioti (2013) examined overall scores on the standard questionnaire (Botvinick & Cohen, 1998) for each participant. They then compared the mean overall scores between synchronous and asynchronous stroking conditions. A higher mean overall score was reported under synchronous stroking condition than asynchronous stroking condition.

In the original study (Botvinick & Cohen, 1998), the means of each target question were significantly higher than the means for each control question within synchronous stroking condition group, but not within the asynchronous stroking control group. However, the maintenance of illusory experience observed by Valenzuela-Moguillansky et al. (2013) strongly suggests that subsequent testing conditions may interact with each other; 2 of 3 participants who showed embodiment when only the hidden real hand was touched and not the seen rubber hand were previously exposed to synchronous stroking of both real and rubber hands. Thus,
asynchronous condition which was originally used as a between-subjects factor may not act as an ideal control against synchronous condition within an individual.

Additional modification in the RHI questionnaire was made by Longo, Schuur, Kammers, Tsakiris, and Haggard (2008) in hopes to capture more information from the illusion. The group made a new 27-item questionnaire from detailed interviews with five volunteers who experienced the RHI and administered it to 130 subjects. Through principal components analysis (PCA) with orthogonal rotation, the following four major components of the illusion were identified: embodiment of the rubber hand, loss of own hand, movement and affect (Longo et al., 2008). The subcomponents of embodiment which are manipulated in the rubber hand illusion were the sense of ownership and perceived location of the rubber hand. The questions for these subcomponents included target questions from the original study by Botvinick and Cohen (1998). Thus, the original three target questions are sufficient in capturing embodiment that is induced by the RHI.

In summary, the RHI has been scored in multiple ways, and no consensus appears in the literature. An additional score used to analyse the illusion is the vividness score, which is the difference between the average score of target ownership questions and the average score of control suggestibility and task compliance questions (Bekrater-Bodmann et al., 2012). This score shows how vivid the illusory ownership experience is independent of baseline suggestibility. Nevertheless, the vividness score which measures magnitude is only useful after a successful ownership has been confirmed. In another words, it is useful to measure how strong the ownership is felt after it has been achieved. Unfortunately, two subjects can share the same
vividness score of two, and yet one subject can confirm ownership with higher baseline suggestibility while the other can deny ownership with lower baseline suggestibility. Even though David et al. (2013) found higher mean overall score under synchronous stroking condition than asynchronous stroking condition, merging the baseline score for task compliance and suggestibility with target ownership score is another weak indicator of ownership. Mean overall score does not account for variability of baseline control score among responders who may be eager to please the researcher and thus can have higher overall scores. Therefore, the most conservative way to define a successful induction of the RHI within an individual is to have an affirmative average of target questions (>4 on a 7-point Likert scale from strongly disagree = 1 to strongly agree = 7) that differ significantly from the average of control questions (Botvinick & Cohen, 2008; Ehrsson et al., 2008). These two criteria together can identify true responders whose illusory ownership experience is not due to greater suggestibility.

1.4.2 Objective measures

Proprioceptive drift measurement, skin temperature and galvanic skin conductance have been proposed as more objective measures of the RHI (Botvinick & Cohen, 1998; Moseley et al., 2008; Gueterstam, Petkova, & Ehrsson, 2011). During the RHI, the participant’s perceived location of the hidden real hand becomes biased towards the location of the seen rubber hand (Botvinick & Cohen, 1998). While the original study by Botvinick and Cohen (1998) showed more reach displacement with stronger prevalence of the RHI, subsequent literature describes a more complicated relationship between proprioceptive drift and embodiment. Longo et al. (2008) found independent strong correlations for proprioceptive drift with either ownership or location subcomponents of embodiment of the rubber hand. Meanwhile, Holmes, Snijders, and Spence
(2006) found a weak correlation between proprioceptive biases and questionnaire items relating to ownership. They reported a significant reaching bias from a mere passive visual exposure to the rubber hand, independent of occurrence of an embodiment. Similarly, just a visual observation of the rubber hand with a hidden real hand was sufficient to induce a proprioceptive bias, but this vision-only condition was insufficient to induce a sense of ownership (Rohde et al., 2011). The ownership was induced only under synchronous stroking of both the seen rubber hand and the hidden real hand, and the proprioceptive drift also remained under synchronous touches (Rohde et al., 2011). Thus, as the proprioceptive drift accompanies ownership under the RHI, proprioceptive drift measurement may be used in a complementary manner to the RHI Questionnaire. However, it is not a sufficient indicator of ownership by itself.

Another objective measure for the RHI is skin temperature. A decrease of 0.27°C in skin temperature of the real hand was observed under synchronous stroking of both real and rubber hands. The magnitude of skin temperature reduction was correlated with higher subjective vividness of the illusion (Moseley et al., 2008). These authors suggested that a disruption in our sense of body ownership by adapting a new rubber hand can lead to a homeostatic deregulation and a subsequent decrease in skin temperature of the real hand. However, temperature was also lowered during asynchronous stroking condition. Thus, while skin temperature may capture disruption in ownership of the real hand, it may not be a sensitive measure for ownership of the rubber hand.

Electrodermal activity (EDA) is a third objective measure related to the RHI. EDA is also known as skin conductance response and galvanic skin response historically. EDA can measure
changes in skin conductance from arousal and sympathetic responses such as increased sweating (Boucsein, 2012). Guterstam et al. (2011) placed two small electrodes on the index and middle fingers to measure EDA changes when the rubber hand or the real hand is physically threatened with a knife. If one obtains a sense of ownership towards the rubber hand, there should be no significant difference in EDAs when the rubber hand is threatened compared to a threat against the real hand. On the other hand, there should be a significantly smaller EDA from a threat towards a rubber hand towards which one does not feel ownership. There was a significantly stronger EDA when the rubber hand was physically threatened, such as a finger being harmed by a knife (Guterstam et al., 2011) or a needle (Ehrsson, 2012; Newport & Preston, 2011; Ocklenburg, Ruther, Peterburs, Pinnow, & Gunturkun, 2011) or bent backwards (Armel & Ramachandran, 2003) after synchronous stroking of real and rubber hands compared to asynchronous stroking condition. However, Ocklenburg et al. (2011) failed to see a significant correlation between mean EDA amplitude and mean scores for the subjective three target questions pertaining to the ownership of the rubber hand. Thus, EDA may be too sensitive and is able to capture subconscious ownership of the rubber hand which will not be reported on the subjective ownership ratings. Therefore, these objective measures should be used as a secondary measure to compliment subjective ownership measure.

1.5 Different types of RHI induction

Since the original RHI was described by Botvinick and Cohen (1998), others have tested this multisensory integration further by modifying the methods used to induce the RHI. Similar ownership ratings to the classical visuo-tactile condition were induced using synchronous active voluntary and passive imposed movements of both the seen rubber hand and the hidden real hand
Furthermore, while all three conditions have led to similar ownership ratings within responders, there were a significantly smaller number of successful responders using passive movement versus visuo-tactile stimuli (Kalckert & Ehrsson, 2014). On the other hand, Dummer et al. (2009) reported greater ownership mean score for active voluntary movement compared to passive movement imposed by the experimenter (0.63 difference in mean scores on 7-point Likert scale ranging from 1 to 7). Thus, current literature supports achieving RHI using visuo-proprioceptive integration, but it remains unclear on how using a different combination of sensory inputs compares to ownership induced by visuo-tactile inputs.

1.6 RHI apparatus and entrainment constraints

1.6.1 Temporal and anatomical constraints

Several studies have shown that synchronous stroking of both real hand and rubber hand is necessary to induce a sense of ownership towards the rubber hand since this ownership does not occur following asynchronous stroking (Botvinick & Cohen, 1998; Armel & Ramachandran, 2003; Ehrsson et al., 2004; Longo et al., 2008; David et al., 2013; Tsakiris & Haggard, 2005). While intermodal matching between visual and tactile cues is necessary for the RHI, the majority of the literature indicates that it is not sufficient as there are also anatomical constraints. The anatomical constraints include shape (“hand” likeness) and postural matching. Armel and Ramachandran (2003) found using a fake hand was significantly better at inducing the RHI than using the surface of a table; the average intensity rating measuring how much the fake hand felt like one’s own ranging from 1 to 10 was 7.35 ± .44 under stroking a fake hand compared to 4.38 ± .56 under stroking the table. They also reported a marginal difference in EDA between the two
conditions, \( t(23) = 2.07, p = .05 \). Moreover, Haans, Ijsselsteijn, and de Kort (2008) compared the effects of naturalness of hand shape, naturalness of skin texture, and synchrony of stroking. Based on subjective ownership ratings, hand shaped objects induced stronger RHI compared to non-hand like objects, and there was a significant interaction between shape and skin texture for hand shaped objects (Haans et al., 2008). In contrast, Haans et al. (2008) reported no significant effect of skin texture on the induction of RHI. Lastly, the effects of postural matching of the hands and the direction of stroking on the induction of the illusion were studied by Costantini and Haggard (2007). They changed either the angle of the real or rubber hand’s position or the angle of stroking on the real or rubber hand. When the rubber hand served as a spatial reference frame, mismatches in both position and stroking angle reduced the magnitude of proprioceptive drift the most than each factor by itself (Costantini & Haggard, 2007).

### 1.6.2 Spatial constraints

The strength of the RHI is also affected by the distance between between the rubber hand and the real hand (Armel & Ramachandran, 2003; Lloyd, 2007). Armel and Ramachandran (2003) compared the strength of the RHI between the rubber hand being placed in a realistic location versus 0.91m away from the real hand using intensity ratings and EDA. The rubber hand in a realistic location had significantly higher mean intensity rating \( (M = 7.69, SE = .30) \) than when the rubber hand was very distant \( (M = 5.75, SE = .49) \), \( t(23) = 4.22, p < .001 \); however, EDAs showed no significant difference, \( t(23) = 1.31 \). In addition, Lloyd (2007) examined the effect of distance between the real and rubber hands in the horizontal plane using six different displacements ranging from 17.5 to 67.5 cm. The illusion ratings were the strongest at the closest distance of 17.5 cm and significantly decreased at 27.5 cm, but other positions did not show a
significant difference in the strength of the RHI (Lloyd, 2007). Moreover, Bekrater-Bodmann et al. (2012) found significantly higher ownership ratings when the rubber hand was placed above the real hand (vertical set-up) compared to when it was placed beside the real hand (horizontal set-up). They suggested this may be due to less discordance in the visuo-spatial spaces of the seen rubber hand and the hidden real hand in a vertical set-up compared to in a horizontal set-up.

1.7 Remaining questions

Based on these gaps in knowledge and to determine the usefulness of the RHI to provide a behavioural context behind the electrical stimulation, I asked the following specific questions:

(A) Can other modalities of somatosensory stimulation evoke the RHI in addition to simultaneous stroking of rubber hand and real hand with a brush?

(B) After the RHI is induced, can applying a stimulus on the seen rubber hand alone evoke a percept without touching the real hidden hand?

(C) If so, is there transfer between modalities for the illusion? In other words, can the illusion be maintained if a different modality of sensation is applied to the rubber hand than what was applied simultaneously to both the seen rubber hand and hidden real hand for induction?

I HYPOTHESIZE that the RHI can be induced by other sensory modalities such as temperature, and vibration in a similar manner to brushing and that ownership can be maintained across different sensory modalities including kinesthesia (passive movement) than what was used for induction of the RHI.
Chapter Two: Pilot Study

2.1 Rationale for pilot study

As discussed in Chapter 1, my long term aim with this project was to use the RHI to provide an illusory ownership experience and a behavioural context behind electrical stimulation applied in intact subjects without a confounding physical somatic stimulation. Percepts to be elicited by the electrical stimulation span beyond the sensation of touch, but the studies on the RHI have primarily been focusing on touch. Therefore, I needed to first determine induction of the RHI using other somatosensory modalities and then examine whether these can be maintained when only the rubber hand is exposed to a modality of interest.

A pilot study was conducted to troubleshoot the RHI apparatus and test the study protocol. Since the somatosensory modalities of interest were touch, vibration, cold, and passive movement, all four were investigated for both induction and maintenance phases of the pilot study. Passive movement was a concern due to the limitation of movement of the rubber hand across the RHI apparatus being confined to the length of the table over the trial period.

2.2 Method

2.2.1 Subjects and recruitment

Pilot experiments were performed in 25 naïve healthy volunteers (11 males and 14 females, all university students). They were recruited from University of Calgary Foothills campus without a preference for sex, age, or handedness.
2.2.2 Materials

2.2.2.1 RHI apparatus

A left rubber hand was presented vertically 17.5 cm above the hidden left hand (Bekrater-Bodmann et al., 2012; Ockelenburg et al, 2010; Lloyd, 2007). The dimensions of the wooden apparatus were: 65 cm length x 50 cm width x 22.5 cm (experimenter’s side) or 12 cm (subject’s side) height. Both surfaces for placements of the rubber hand (above) and the real hand (below) were covered with dark brown fabric. Dark brown fabric was used to cover the real hand from the subject’s wrist to elbow and the rubber hand from its wrist to the subject’s shoulder.

2.2.2.2 RHI Questionnaire

The original RHI Questionnaire (Botvinick & Cohen, 1998) was used. It consists of three target questions for ownership and six control questions for task compliance and suggestibility (see Figure 2.1 for questionnaire items) which were measured on a seven point Likert scale from strongly disagree to strongly agree. Since the original RHI questionnaire was based on a stroking sensation (Botvinick & Cohen, 1998), it was modified to accompany the different somatosensory modalities being tested in my research, such as cooling, vibration, and passive movement (see Appendix A-D for questionnaire items for each modality). The modality of interest and the means to provide that stimulus replaced the touch sense. For example, the statement “it seemed as though the touch I felt was caused by the paintbrush touching the rubber hand” was replaced with “it seemed as though the vibration I felt was caused by the tuning fork touching the rubber hand.” The order of questionnaire items was randomized for each trial. The subjects were instructed to indicate their extent on agreeing with the statements anywhere on the Likert scale.
For the modified versions of the questionnaire, the subjects were instructed to concentrate on the modality of interest which was indicated with bolded and underlined words in the statements.

- **Target questions (ownership)**
  - Q1: It seemed as if I were feeling the touch in the location where I saw the paintbrush touch the rubber hand.
  - Q2: I felt as if the rubber hand were my hand.
  - Q3: It seemed as though the touch I felt was caused by the paintbrush touching the rubber hand.

- **Control questions (task compliance and suggestibility)**
  - Q4: It felt as if my real hand was drifting towards the rubber hand.
  - Q5: It felt as if I might have more than one left hand or arm.
  - Q6: The rubber hand began to resemble my own (real) hand, in terms of shape, skin tone, freckles or some other visual feature.
  - Q7: It seemed as if the touch I was feeling came from somewhere between my own hand and the rubber hand.
  - Q8: It felt as if my real hand were turning ‘rubbery’.
  - Q9: It appeared (visually) as if the rubber hand were drifting towards my hand.

**Figure 2.1.** The original RHI Questionnaire items (Botvinick & Cohen, 1998). Target questions relate to ownership, and control questions that pertain to task compliance and suggestibility. These questions are presented on a seven point Likert scale in a randomized order.

### 2.2.3 Pilot study set up

The experiment was conducted in a quiet room at University of Calgary. Figure 2.2 shows the placements of the rubber hand on the top surface of the RHI apparatus and the real hand on the bottom surface, which are both covered by dark brown fabric. Upon arrival, subjects were asked to sit across from the experimenter’s end of the RHI apparatus on the table. They were exposed to the following sensations: cooling of a frozen reusable ice cube, a reusable ice cube at room temperature, vibration from an activated 125 Hz tuning fork, and brushing using paint brush. Subjects were requested to take any jewellery or watch off of their left hand prior to placing their arms into the RHI apparatus at 45 degrees from their torso. The rubber hand was placed on the
top surface of the apparatus such that it lay directly above the hidden real hand. The proximal end of the rubber hand was affixed to subject’s elbow using tape. A dark brown fabric was put on the subject’s real arm from wrist to elbow and another dark brown fabric covered the rubber arm from its wrist to subject’s shoulder. This procedure was adapted from the vertical RHI set-up used by Bekrater-Bodmann et al. (2012). Participants were videotaped for post-hoc speed of movement measurements.

Figure 2.2. Induction phase set-up where stimuli are applied to both real and rubber hands. The real hand is hidden on the lower part of the RHI apparatus whereas the rubber hand is placed on top of the apparatus and is seen. The participant (shown) is placed across from the experimenter (not shown). Red arrows indicate the testing somatosensory modalities.
The participants were instructed to keep their hands relaxed and still while focusing their attention on the rubber hand where it was being exposed to different stimuli. Each participant was induced with the RHI using only one of the four modalities that was randomly assigned (stroking, vibration, cooling, or passive movement). All stimuli were synchronously applied to both the hidden real hand and the seen rubber hand in congruent locations (dorsum of the left index fingers) for 3 minutes. Stroking involved brushing downward strokes with paint brushes every other second. Vibration was applied through 125 Hz tuning forks. The vibration lasted up to five seconds after the forks were hit to vibrate, therefore this stimulus was re-applied repeatedly every four seconds for the duration of induction. Frozen reusable ice cubes were used for cooling and applied every other second. Passive movement was achieved by experimenter continuously pulling the fabric that was placed below both real and rubber hands 20 cm over the three minute period at around 0.1 cm per second. Participants then answered the corresponding RHI Questionnaire without moving their left hands. Subsequently, each of the 4 sensory modality stimuli was pseudo-randomly applied to the rubber hand only for 10 seconds (see Figure 2.3). The first modality to be tested under the maintenance phase was always the same modality which was used for induction, while the rest of the modalities were randomized for the remaining three maintenance phase trials. Since the illusory ownership experience is intended to be paired with electrical stimulation, the maintenance exposure period is limited by the exposure time to electrical stimulation. Our previous findings demonstrated that most percepts elicited by electrical stimulation are felt within 3 seconds (Heming et al., 2010, 2011). Thus, the stimulation period for maintenance phase was selected for 10 seconds to leave room for human error during pairing. The modalities were applied in similar fashion to the induction phase with the following exceptions. Only the rubber hand was brushed for stroking. Tuning forks were applied on both
real and rubber hands; however, only the tuning fork applied on the rubber hand was left to vibrate while the tuning fork for the real hand was prevented from vibrating prior to exposure to the real hand. A frozen ice cube was applied on to the rubber hand while a reusable ice cube at room temperature was applied to the real hand. For passive movement, the fabric underneath both real and rubber hands was pulled in a manner where only the rubber hand was moved while the real hand remained stationary. After each 10 s stimulus application, the participants answered the corresponding RHI Questionnaire (see Figure 2.4 for study protocol).

Figure 2.3. Maintenance phase set-up where stimulus of interest is only applied to the rubber hand. The real hand is hidden on the under the RHI apparatus whereas the rubber hand is placed on top to be seen. The participant (shown) is placed across from the experimenter (not shown). Red arrow indicates the testing somatosensory modalities on only the rubber hand.
Figure 2.4. Study protocol for the pilot study. Induction phase involved exposing one of four testing modalities to both real and rubber hands. The induction modality was randomly assigned. Maintenance phase involved exposing all four modalities to just the rubber hand and not the real hand. Maintenance modality was tested in pseudo-randomized order such that first testing modality was always the same modality which was used for induction, while the rest of the modalities were randomized for the remaining three maintenance phase trials. Corresponding questionnaires were answered after each trial.

2.2.4 Data analysis

2.2.4.1 RHI Questionnaire

Based on the lack of consensus about how to define successful RHI induction, I chose to use the most conservative method to define successful induction. This required an average >4 (on a 7-
point Likert scale from 1 strongly disagree to 7 strongly agree) for target questions and this had to differ significantly from the average of control questions (Botvinick & Cohen, 2008; Ehrsson et al., 2008). A two-sample one-tailed t-test was used to test significance for each trial with an adjustment for unequal variances when appropriate following Levene’s Test of Equality of Variances. A priori hypothesis was that the mean of target questions is greater than the mean of control questions. In most literature, the scores for each question were averaged between subjects and/or within a specific condition group. However, since I am interested in induction and subsequent maintenance of RHI when only the rubber hand is stimulated within an individual, the RHI questions were analyzed within each subject.

2.2.4.2 Speed of passive movement

The speed of passive movement was measured using free, open source Kinovea software (http://www.kinovea.org/). Distances and times can be measured directly from the video footage of the experiment. Average speed of passive movement was determined for induction and maintenance phases.

2.3 Results

2.3.1 RHI induction (real and rubber hands)

Of the 25 participants randomly assigned to one of four induction modalities, 7 subjects were assigned to stroking induction, 6 were assigned to vibration induction, 6 were assigned to cooling induction, and 6 were assigned to passive movement induction. The average speed of movement was 0.120 cm/s ($SD = .027$ cm/s). In total, 5 of 25 subjects were successfully induced with the RHI; individual two-sample one-tailed t-tests for the trials with ownership yielded $p$-values <
.05. Of these 5 subjects, 2 subjects received induction using stroking condition while the other 3 subjects were induced by vibration (see Table 2.1).

**Table 2.1**

*RHI induction using one of four sensory modalities: stroking, vibration, cooling, and passive movement.*

<table>
<thead>
<tr>
<th>Induction Modality</th>
<th>Successful RHI</th>
<th>Unsuccessful RHI</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stroking</td>
<td>2</td>
<td>5</td>
<td>7</td>
</tr>
<tr>
<td>Vibration</td>
<td>3</td>
<td>3</td>
<td>6</td>
</tr>
<tr>
<td>Cooling</td>
<td>0</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>Passive movement</td>
<td>0</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>5</strong></td>
<td><strong>20</strong></td>
<td><strong>25</strong></td>
</tr>
</tbody>
</table>

**2.3.2 RHI maintenance (rubber hand only)**

All 5 subjects, who were successfully induced with RHI, also maintained the ownership when only the rubber hand was exposed to one of four sensory stimuli. The average speed of passive movement of only the rubber hand was 0.166 cm/s ($SD = .068$ cm/s). These 5 subjects were all able to maintain the illusion under a different sensory modality than what was used for the induction of RHI (see Table 2.2).
Table 2.2

Maintenance of the ownership towards the rubber hand after successful induction across all four sensory modalities: stroking, vibration, cooling, and passive movement.

<table>
<thead>
<tr>
<th>Modality used for successful induction</th>
<th>Successful maintenance modality</th>
<th>Total ownership under maintenance (in any one modality)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Vibration</td>
<td>Stroking</td>
</tr>
<tr>
<td>Stroking</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Vibration</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>3</strong></td>
<td><strong>1</strong></td>
</tr>
</tbody>
</table>

2.4 Discussion

The RHI was successfully induced through stroking (2/7 subjects) and vibration (3/6 subjects), and the ownership of the rubber hand was maintained in these 5 successfully induced subjects when only the rubber hand received the same and/or different stimulus. All 5 of the successfully induced subjects maintained the ownership of the rubber hand when a different stimulus was used than what was used previously used for induction. Thus, a transfer of ownership is possible between modalities as the subjects were able to maintain the ownership in a different modality than what was used to induce the illusion. Since there were more subjects who maintained the ownership using a different modality, this phenomenon also suggests that successful maintenance under one modality is not necessarily dependent on successful induction of the same modality. Hence, in my subsequent experiment, the first modality to test under maintenance phase will not be the same modality used for induction, and the RHI questionnaire should be answered after each illusion trial to confirm ownership of the rubber hand.
Unfortunately, the induction rate using brushing (29%) was lower than the induction rates reported in the literature, which ranged from 32.5% to 78% (Kalckert & Ehrsson, 2014; Lloyd, 2007; Ehrsson et al., 2004, 2005; Ehrsson, Wiech, Weiskopf, Dolan, & Passignham, 2007). This may be due to the data being analysed on an individual basis with most conservative definition of truly achieving illusory ownership of the rubber hand beyond having a greater suggestibility. Since Botvinick and Cohen (1998) showed that synchronous stroking led to target questions being answered more affirmatively (>4 on 7 point Likert scale) while the control questions were not, others have compared the mean ratings of the questionnaire items between different conditions such as synchronous stroking versus asynchronous stroking or congruent position versus incongruent position. Nonetheless, the illusory ownership experience must be confirmed on an individual basis for the purpose of my future experiment to use the illusory ownership to provide a behavioural context behind the electrical stimulation. A fairer comparison to the literature would be to compare how the responders and/or the modality types as a group have answered each questionnaire item versus the non-responders and also observe the tendency to score higher than 4 on the target questions within the responders. Thus, a two-way multivariate ANOVA (MANOVA) should also be conducted to compare the main effects of modality type used and the presence of ownership (independent variables) on the mean ratings from nine questionnaire items (dependent variables) in the definitive experiment.

One possible reason that passive movement did not induce RHI in any of the subjects could be the speed at which we moved the real hand ($M = .120$ cm/s, $SD = .027$ cm/s) being too slow for the subjects’ muscle spindles to be activated (Hall & McCloskey, 1983). The speed was limited by total length of the RHI apparatus and duration of the induction (three minutes). Nevertheless,
the ownership of the rubber hand was present in 4 subjects when only the rubber hand was passively moved for 10 seconds at an average of 0.166 cm/s ($SD = .068$ cm/s). As a result of these pilot data, for my definitive experiment, I decided to test passive movement condition only during the maintenance phase when it is being used to test whether the illusion is transferable to another modality. Because the maintenance stimulus is applied for 10 seconds, the speed of movement will be increased in the larger experiment.

In addition to the RHI Questionnaires, ownership during passive movement of the rubber hand will be verified by proprioceptive drift measurements. Due to the vertical set-up, proprioceptive drift along the horizontal plane will only occur during the passive movement of the maintenance phase when only the rubber hand is moved towards the left side while the real hand remains stationary. Thus, proprioceptive drift measurements will be made prior to induction, post induction, and following each of the 3 different maintenance phases of cooling, stroking, and vibration. These will serve as controls to compare against horizontal bias with ownership following passive movement under maintenance phase.

For the subsequent experiment, only three modalities will be used for induction phase: vibration, stroking and cold. The vibration modality will be used as it was the most successful modality for both induction and maintenance. The stroking modality will serve as a comparison to the RHI literature, and the cooling modality will be included as an example of a less successful induction modality. Twenty-five further subjects will be studied for each induction modality. This was a sample size of convenience that meets the minimum published Cohen’s $d$ effect sizes which ranged from $.63$ to $.69$ (Guterstam et al., 2011; Asai et al., 2011). Given these effect sizes, a
minimum of 60 participants with one-tailed hypothesis could achieve a statistical power of 0.8. After responders have been identified using t-tests, a two-way MANOVA will be conducted to compare the main effects of modality type used and the presence of ownership (independent variables) on the mean ratings from nine questionnaire items (dependent variables). All 75 subjects will experience four different sensory modalities (stroking, vibration, cooling, and passive movement) in a pseudo-randomized order during the maintenance phase. The assignment will be pseudo-randomized such that the first modality being tested during maintenance phase is not the same modality which was used to induce the RHI. The speed of passive movement will also be increased to match the speed that activates muscle spindles. For the distal joints of the fingers, threshold to detect movements ranges from 8° at a movement velocity of 1.25°/s to 1° at a velocity of 10°/s (Hall & McCloskey, 1983). At a faster movement velocity at 10 - 80°/s, the threshold of movement detection is maintained at 1°.
Chapter Three: RHI Experiment

As discussed in chapter 2, my pilot study demonstrated that the RHI can be successfully induced using stroking or vibration modalities in 5 of 25 subjects. When only the rubber hand received the same and/or different stimulus, all 5 of the successfully induced subjects maintained the ownership of the rubber hand. More subjects maintained the ownership using a different modality than what was used for induction. Thus, a successful maintenance under one modality seemed to not depend on a successful induction of the same modality. The pilot study provided adjustments for my definitive experiment such as exclusion of passive movement modality for induction due to limitation of the apparatus, an order of presentation for maintenance modalities, an addition of proprioceptive drift measurements, and additional statistical analysis of the questionnaire items to compare with the existing literature. To determine the usefulness of the RHI to provide a behavioural context behind electrical stimulation, the following experiment explored the induction of the RHI using other somatosensory modalities and the maintenance of the achieved ownership when only the rubber hand is exposed to a stimulus of interest. Here I tested my hypothesis in a definitive manner that the RHI can induced by other sensory modalities such as temperature and vibration in a similar manner to brushing and that ownership can be maintained even across different sensory modalities than what was used for induction of the RHI, including kinesthesia (passive movement).

3.1 Method

3.1.1 Subjects and recruitment

All participants were recruited from the University of Calgary Foothills campus through posters and associates of the researcher (see Appendix E for recruitment materials). The study (REB14-
... was approved by the Conjoint Health Research Ethics Board of University of Calgary. All 75 naïve healthy volunteers (29 males and 46 females, age range: 20 – 76 years, Median = 27 years, Mean = 31.6 years, SD = 11.6 years) were asked to sign a consent form prior to the study (See Appendix F for consent form).

### 3.1.2 Power calculations

Twenty-five participants were recruited for each of the three induction modalities which made a total of 75 participants. This was a sample size of convenience that meets the minimum published Cohen’s $d$ effect sizes which ranged from .63 to .69 (Guterstam et al., 2011; Asai et al., 2011). A minimum of 60 participants could achieve a statistical power of .8 with one-tailed hypothesis for these effect sizes.

### 3.1.3 Materials

The RHI apparatus and the RHI Questionnaires were the same as in the pilot study. The only addition was a 30 cm ruler on the hidden researcher side of the RHI apparatus to measure proprioceptive drift.

### 3.1.4 Experimental set-up

The participants were informed to relax and keep their hands still while focusing on the rubber hand where it was being exposed to different stimuli. The experiment was videotaped to calculate post-hoc speed of passive movement. After the true position of the participant’s third digit was noted by the experimenter, the participant made estimates of where he thought his third digit was while the experimenter moved a pen from both right to left and left to right directions...
in a random order (see Figure 3.1 for initial position estimation and subsequent section for details). Each participant was randomly assigned to one of the three modalities (stroking, vibration, and cooling) for inducing the RHI. Both the hidden real hand and the seen rubber hand were synchronously exposed to stimuli of interest in congruent locations (dorsum of the left index fingers) for 3 minutes, as described in the pilot study. Participants then made estimates of their third digit position before answering the corresponding RHI Questionnaire without moving their left hands (see Figure 3.2 for final position estimation). Subsequently, each of the 4 sensory modality stimuli were pseudo-randomly applied to the rubber hand only for 10 seconds. First modality to be tested under the maintenance phase could not be the same modality which was used for the induction, and the rest of the modalities were randomized for the remaining three maintenance phase trials. The modalities were applied in a similar fashion to the induction phase with the same exceptions discussed in the pilot study which ensured only the rubber hand was exposed to the stimulus of interest. For passive movement, the fabric underneath both real and rubber hands was pulled continuously to move only the rubber hand at approximately 2 cm/s for 10 seconds. After each 10 s stimulus application, the participants made their estimates of third digit positions and answered the corresponding RHI Questionnaire.
Figure 3.1. The participant’s true position and initial estimation of where his third digit is on the apparatus. The real hand is placed on the bottom, and the rubber hand is placed on top. The subject’s estimation of his real hand position across the horizontal plane is shown by a hand drawn in a dotted line. The black arrow shows where the participant has instructed the experimenter’s pen to be stopped to align with the participant’s estimation of his real hand position. The experimenter’s pen is presented on the edge of the apparatus from the experimenter’s side from both left to right and right to left directions in a randomized order. The angles indicated above are 90 degrees.
Figure 3.2. The participant’s final estimation of where his third digit is on the apparatus. The real hand is placed on the bottom, and the rubber hand is placed on top. The subject’s estimation of his real hand position across the horizontal plane is shown by a hand drawn with a dotted line. The black arrow illustrates where the participant has instructed the experimenter’s pen to stop in congruence with the participant’s estimation of his real hand position. The experiment’s pen is presented on the edge of the apparatus from the experimenter’s side from either left to right or right to left directions in a randomized order. The angles indicated above are 90 degrees.

3.1.4.1 Proprioceptive drift measurement

The proprioceptive drift measurement was included for the current study as a secondary measure to confirm ownership of the rubber hand following a passive movement of only the rubber hand during the maintenance phase. Since the passive movement occurs along the horizontal plane, the proprioceptive drift was also measured horizontally. Thus, proprioceptive drift measurements made prior to induction, post induction, post cooling maintenance, post touch maintenance, and
post vibration maintenance served as controls against horizontal proprioceptive bias following a passive movement of only the rubber hand.

The proprioceptive drift was determined by subtracting the subject’s mean estimates made from both directions (left to right and right to left directions in a random order) at the end of each trial from the true position of the subject’s third digit. Thus, a negative value indicated a bias towards the rubber hand’s position. The true position of the subject’s third digit was measured by the researcher prior to RHI induction using a 30 cm ruler attached to the RHI apparatus. Subjects reported their estimates by vocal indications of where they thought the tip of their third digit were when the researcher’s pen going across the visible surface of the apparatus reached the same position on the horizontal plane. Their estimates were made prior to induction, post induction, and post maintenance trials from both left to right and right to left directions in a randomized order.

3.1.5 Data analysis

3.1.5.1 RHI Questionnaires

A two-sample one-tailed t-test was used to test significant difference between the mean of target questions and the mean of control questions and confirm individual RHI inductions and maintenances. An adjustment was made for unequal variances when appropriate following Levene’s Test of Equality of Variances. As described in the pilot study, a successful induction or maintenance of ownership was defined as having an average of >4 for target questions which also differed significantly from the average of control questions (Botvinick & Cohen, 2008; Ehrsson et al., 2008).
Subsequently, a two-way MANOVA was conducted to compare the main effects of modality type used and the presence of ownership (independent variables) on the mean ratings from nine questionnaire items (dependent variables) for the RHI induction. The questionnaire items which were randomized during trials were classified as Q1 to Q9 as is numbered in Figure 2.1 for data analysis.

For the maintenance of the RHI, a three-way mixed MANOVA was performed to compare the multivariate effects of maintenance modality type used (within-subjects factor), the type of subjects (between-subjects factor), and the type of induction modality used (between-subjects factor) on the mean ratings of the questionnaire items (dependent variables). There were two types of subjects: those who were successfully induced and maintained the ownership in at least one modality (achievers) and those who were successfully induced but failed to maintain the ownership in any modalities (failures).

To examine the multivariate effects of time (within-subjects factor), the type of subjects (between-subjects factor), and the type of induction modality used (between-subjects factor) on the mean ratings of the questionnaire items (dependent variables) with subsequent trials, a three-way mixed MANOVA was performed with the mean ratings obtained from both induction and maintenance phases. The subjects were categorized as those who maintained ownership in at least one modality (achievers) and those who did not maintain ownership in any modalities (failures). The time factor was five consecutive trials: one induction modality trial and four maintenance modality trials, respectively.
3.1.5.2 Proprioceptive drift measurements

A two-way mixed ANOVA was conducted to compare the main effects of the rubber hand’s movement (within-subjects factor) and the presence of ownership (between-subjects factor) on the average proprioceptive drift (dependent variable). The control measurement was made prior to induction, post induction, post cooling maintenance, post touch maintenance, and post vibration maintenance, where the real hand was placed directly underneath the rubber hand which remained still under the vertical set-up. The experimental measurement was made following the rubber hand being moved horizontally away from the participants while the hidden real hand remained stationary.

3.1.5.3 Speed of passive movement

The average speeds of passive movement measured post-hoc with KINOVEA software were compared between responders and non-responders of passive movement during maintenance phase. Participants who were successfully induced and maintained the ownership when only the rubber hand was moved were identified as responders. Those who were successfully induced but did not maintain the ownership were identified as non-responders. A two sample t-test was conducted for these two conditions to test whether different speeds were administered by experimenter error.

3.2 Results

3.2.1 RHI induction

A total of 35 of 75 subjects were successfully induced with the RHI using stroking, vibration, and cooling (individual two-sample t-tests, one-tailed, \( ps < .05 \)). Ten of 25 subjects were induced
with stroking. Twelve of 25 subjects were induced with vibration. Lastly, 13 of 25 subjects were induced with cooling (see Table 3.1).

**Table 3.1.**

*RHI induction using one of three sensory modalities: stroking, vibration, and cooling.*

<table>
<thead>
<tr>
<th>Induction Modality</th>
<th>Successful RHI</th>
<th>Unsuccessful RHI</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stroking</td>
<td>10</td>
<td>15</td>
<td>25</td>
</tr>
<tr>
<td>Vibration</td>
<td>12</td>
<td>13</td>
<td>25</td>
</tr>
<tr>
<td>Cooling</td>
<td>13</td>
<td>12</td>
<td>25</td>
</tr>
<tr>
<td>Total</td>
<td>35</td>
<td>40</td>
<td>75</td>
</tr>
</tbody>
</table>

A two way MANOVA was conducted for multivariate effects of the modality type used and the presence of ownership on the mean ratings of the questionnaire items. There was no significant multivariate effect of modality type on the combined dependent variables of Q1 to Q9, $V = .301, F(18, 124) = 1.219, p = .256$; and no significant interaction between the modality type and the presence of ownership, $V = .141, F(18, 124) = .524, p = .924$. There was a significant multivariate effect for the combined dependent variables of Q1 to Q9 in respect of the presence of ownership, $V = .660, F(9, 61) = 13.170, p < .001$. Post-hoc 2-tailed t-tests with adjustments for unequal variances showed significant difference between how Q1,2 and 3 were answered with induced versus not induced: $t(53.595) = 2.267, p = .027$ for Q1, $t(68.485) = 7.109, p < .001$ for Q2, and $t(64.220) = 6.511, p < .001$ for Q3 (see Figure 3.3). Target questions 1 to 3 all had mean ratings which were greater than 4 while control questions 4 to 9 had mean ratings of less than 4.
Figure 3.3. A comparison of mean ratings for each questionnaire item with and without ownership answered following RHI induction. Error bars show standard errors. Each target questions were scored greater than 4 on a 7 point Likert scale by those subjects who were induced in the RHI. Mean ratings of target questions within the responders differed significantly than the non-responders, $t(53.595) = 2.267, p = .027$ for Q1, $t(68.485) = 7.109, p < .001$ for Q2, and $t(64.220) = 6.511, p < .001$ for Q3. Mean ratings of control questions did not differ significantly between the two groups and were less than 4.
3.2.2 RHI maintenance

Of the 35 subjects who were successfully induced, 24 subjects maintained the ownership under at least one modality when only the rubber hand was exposed to the modality stimulus of interest (individual two-sample t-tests, one-tailed, $p < .05$, see Table 3.2). Eleven subjects did not report ownership under all four tested modalities when only the rubber hand was exposed to the modality stimulus (individual two-sample t-tests, one-tailed, $p > .05$). Subjects who were successfully induced using vibration modality demonstrated the highest rate of maintenance in any one modality (92%). Successful induction by stroking resulted in only 50% maintenance of ownership in any one modality when only the rubber hand was stimulated. Successful induction by cooling led to 62% maintenance rate.

Table 3.2.

Maintenance of the ownership towards the rubber hand after successful induction ($n=35$).

<table>
<thead>
<tr>
<th>Induction Modality</th>
<th>Maintenance – Ownership</th>
<th>Maintenance - No ownership</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stroking</td>
<td>5</td>
<td>5</td>
<td>10</td>
</tr>
<tr>
<td>Vibration</td>
<td>11</td>
<td>1</td>
<td>12</td>
</tr>
<tr>
<td>Cooling</td>
<td>8</td>
<td>5</td>
<td>13</td>
</tr>
<tr>
<td>Total</td>
<td>24 (in any one modality) achievers</td>
<td>11 (in all four modalities) failures</td>
<td>35</td>
</tr>
</tbody>
</table>

A three-way mixed MANOVA was performed to examine the main effects of the maintenance modality type (within-subjects factor), the type of induction modality used (between-subjects factor), and the type of successfully induced subjects (between-subjects factor) on the mean ratings of each questionnaire items (dependent variables). No significant multivariate effect of induction modality type was found, $V = .684$, $F(18, 44) = 1.270$, $p = .253$. There was no
significant multivariate effect of maintenance modality types, $V = .938, F(27, 3) = 1.677, p = .377$. There was a significant multivariate effect of subject type, $V = .552, F(9, 21) = .552, p = .022$, on the combined dependent variables of Q1 to Q9. No significant interactions were found between: subject type and induction modality type, $V = .579, F(18, 44) = .996, p = .482$; maintenance modality type and induction modality type, $V = 1.617, F(54, 8) = .625, p = .853$; maintenance modality type and subject type, $V = .976, F(27, 3) = 4.569, p = .118$; and all 3 factors, $V = 1.771, F(54, 8) = 1.143, p = .456$. Post hoc tests using the Bonferroni corrections yielded significant differences between the achievers and the failures for the mean ratings of: Q1, $p = .039$; Q2, $p = .004$, and Q3, $p = .004$ (see Figure 3.4). The achievers rated Q1 to 3 all greater than 4 on a 7 point Likert scale while the control questions Q4 to 9 were rated less than 4. The failures scored all the questions less than 4.
Figure 3.4. A comparison of mean ratings for each questionnaire item between those who were able to maintain ownership under at least one modality (achievers) versus those who were unable to maintain ownership under any modality (failures) following a successful RHI induction. Error bars show standard errors. There was a significant multivariate effect of subject type, $V = .552$, $F(9, 21) = .552$, $p = .022$, on the combined dependent variables of Q1 to 9. Post hoc tests using the Bonferroni corrections revealed significant differences in the mean ratings of target questions between the achievers and the failures, $p = .039$ for Q1, $p = .004$ for Q2, and $p = .004$ for Q3. Mean ratings of control questions did not differ significantly between two groups, $p > .05$. The achievers rated the target questions greater than 4 on a 7 point Likert scale and rated the control questions lower than 4. The failures rated all the questions lower than 4 on average.
A three-way mixed MANOVA examined the multivariate effects of time (within-subjects factor), the type of induction modality used (between-subjects factor), and the type of successfully induced subjects (between-subjects factor) on the mean ratings of questionnaire items (dependent variables). Achievers were able to maintain ownership in at least one modality while failures were successfully induced but could not maintain ownership in any modalities. There were significant multivariate effects of time, $V = .470$, $F(36, 444) = 1.643$, $p = .013$, and the type of subjects, $V = .566$, $F(9, 21) = 3.041$, $p = .017$, on the combined dependent variables of Q1 to Q9. The induction modality type did not have a significant multivariate effect on the questionnaire items, $V = .682$, $F(18, 44) = 1.266$, $p = .256$. There was also no significant multivariate effects across the interactions between: time and induction type, $V = .511$, $F(72, 920) = .871$, $p = .768$; time and subject type, $V = .394$, $F(36, 444) = 1.348$, $p = .090$; time, induction type, and subject type, $V = .471$, $F(72, 920)$, $p = .886$; and induction type and subject type, $V = .548$, $F(18, 44) = .922$, $p = .559$.

Univariate between-group analyses showed that Q1, Q2, Q3, Q4, and Q9 were rated significantly higher by the achievers than the failures, regardless of induction type or time: $F(1, 29) = 6.861$, $p = .014$ for Q1; $F(1, 29) = 11.321$, $p = .002$ for Q2; $F(1, 29) = 10.961$, $p = .002$ for Q3; $F(1, 29) = 4.543$, $p = .042$ for Q4, and $F(1, 29) = .180$, $p = .902$ for Q9. Within the achievers, Q1 to 3 were rated greater than 4 while Q4 to 9 were rated lower than 4 (see Figure 3.5). The subject type did not have a significant univariate effect on the mean ratings of Q5, Q6, Q7, and Q8: $F(1, 29) = 1.888$, $p = .180$ for Q1; $F(1, 29) = .616$, $p = .439$ for Q6; $F(1, 29) = 1.847$, $p = .185$ for Q7; and $F(1, 29) = .072$, $p = .790$ for Q8. Within the failures, all the questions had a mean rating of lower than 4.
Figure 3.5. The effect of subject type on the mean ratings of questions 1 to 9. Error bars show standard errors. There was a significant multivariate effect of the type of subjects, $V = .566, F(9, 21) = 3.041, p = .017$, on the combined dependent variables of Q1 to Q9. Univariate between-group analyses showed that Q1, Q2, Q3, Q4, and Q9 were rated significantly higher by the achievers than the failures, regardless of induction type or time: $F(1, 29) = 6.861, p = .014$ for Q1; $F(1, 29) = 11.321, p = .002$ for Q2; $F(1, 29) = 10.961, p = .002$ for Q3; $F(1, 29) = 4.543, p = .042$ for Q4, and $F(1, 29) = .180, p = .043$. The achievers rated Q1 to 3 (target questions) greater than 4 while Q4 to 9 (control questions) were rated lower than 4. All the questions were scored lower than 4 by the failures.
Additional univariate within-group analyses showed that Q1, Q2, and Q3 were rated significantly different across time (regardless of induction type or subject type): $F(2.968, 101.895) = 7.624, p < .001$ for Q1 with Greenhouse-Geisser correction, $F(4, 132) = 6.539, p < .001$ for Q2, and $F(3.084, 108.443) = 23.679, p = .001$ for Q3, see Figure 3.6. Time did not have a significant univariate effect on Q4 to Q9: $F(4, 132) = .619, p = .650$ for Q4; $F(2.589, 87.241) = .483, p = .667$ for Q5 with Greenhouse-Geisser correction; $F(4, 132) = .1.238, p = .299$ for Q6; $F(1.628, 55.954) = .612, p = .514$ for Q7 with Greenhouse-Geisser correction; $F(4, 132) = .678, p = .608$ for Q8; and $F(4, 132) = .356, p = .840$ for Q9. Post-hoc pairwise t-tests showed the mean rating of Q1 from the first trial (induction trial) being rated significantly higher than from the rest of the trials (maintenance trials): $p = .017, p < .001, p = .005$, and $p < .001$, respectively. Likewise, the mean rating of Q2 from the first trial was significantly greater than from the second, the third, and the fifth trials: $p = .048, p < .001$, and $p = .001$, respectively. The mean rating of Q3 from the first trial also differed significantly from the rest of the trials: $p = .003, p < .001, p = .038$, and $p < .001$, respectively. The rest of pairwise comparisons (including among maintenance trials) did not show significant differences, $ps > .05$. 
Figure 3.6. The effect of time on the mean ratings of questions 1 to 9. Error bars show standard errors. There was a significant multivariate effect of time on the mean ratings of Q1-9, $V = .470$, $F(36, 444) = 1.643$, $p = .013$. Univariate within-group (time) analyses showed that Q1 to 3 were rated differently across time regardless of induction type or subject type: $F(2.968, 101.895) = 7.624$, $p < .001$ for Q1 with Greenhouse-Geisser correction, $F(4, 132) = 6.539$, $p < .001$ for Q2, and $F(3.084, 108.443) = 23.679$, $p = .001$ for Q3. The mean ratings of first (induction) trials from Q1, Q2, and Q3 were rated significantly higher from subsequent (maintenance) trials; post-hoc pairwise t-tests yielded $ps < 0.05$ for these trials. Asterisks indicate a significant difference from the first trial within each questionnaire item.
3.2.3 Transfer across modalities

Upon further analysis of the 24 subjects who were induced and had maintained the ownership with at least one modality, 23 of 24 subjects maintained ownership in a different modality than what was used for induction (see Table 3.4). Six of these 23 subjects were also able to maintain the ownership under same modality that was used for induction. Lastly, one subject of the 24 subjects who had been induced and maintained the ownership could only maintain the ownership using the same modality (vibration) as the one used for induction.

Table 3.3.

Transfer of ownership across different modalities during maintenance of the ownership towards the rubber hand following a successful induction under a different modality.

<table>
<thead>
<tr>
<th>Successful Induction Modality</th>
<th>Successful Maintenance Modality</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Vibration</td>
<td>Stroking</td>
</tr>
<tr>
<td>Stroking</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Vibration</td>
<td>2</td>
<td>6</td>
</tr>
<tr>
<td>Cooling</td>
<td>7</td>
<td>1</td>
</tr>
<tr>
<td>Total</td>
<td>12</td>
<td>8</td>
</tr>
</tbody>
</table>

To test whether different speeds of passive movement were administered by the experimenter in responders and non-responders, the average speed of passive movement was checked using KINOVEA software. The average speed of passive movement did not differ significantly between the responders ($M = 2.38$, $SD = .404$) and the non-responders ($M = 2.55$, $SD = .480$) of the passive movement modality under maintenance phase ($t(22) = -0.826$, $p = .417$, two-tailed) confirming that it was not error that was responsible for differences in response.
3.2.3.1 Proprioceptive drift during passive movement of the rubber hand

Proprioceptive drift from only the rubber hand being moved across the horizontal plane by the experimenter was measured as a secondary and an objective measure to confirm ownership of the rubber hand. Due to a vertical set-up, the measurements made prior to induction, post induction, post cooling maintenance, post touch maintenance, and post vibration maintenance served as controls against any horizontal bias following a passive movement of only the rubber hand. A two-way mixed ANOVA yielded a significant main effect of conditions (rubber hand not moved versus moved), $V = .363, F(1, 73) = 41.650, p < .001$. The main effect of ownership was not significant, $F(1, 73) = 2.438, p = .123$; and there was no significant interaction, $V = .022, F(1, 73) = 1.653, p = .203$ (see Figure 3.7 below).
Figure 3.7. Proprioceptive drift (horizontal) measurements as a secondary measure of ownership. Error bars show standard errors. There was a significant main effect of visual passive movement of the rubber hand on the mean proprioceptive drifts, $V = .363$, $F(1, 73) = 41.650$, $p < .001$. However, there was no significant effect of presence of ownership on the mean proprioceptive drifts; and there was no significant interaction effect on the proprioceptive drifts by the presence of ownership with visual passive movement of the rubber hand.

3.3 Discussion

The RHI illusion was successfully induced in 35 out of 75 subjects using the touch, vibration, and cooling modalities. The induction rates ranged from 40% for stroking, 48% for vibration, and 52% for cooling. However, a two-way MANOVA analysis showed that there was no significant multivariate effect of modality type on the mean ratings of questionnaire items.
Moreover, there was no significant interaction between the modality type used and the presence of ownership. Only the presence of ownership had a significant multivariate effect on the mean ratings of the questionnaire items or more specifically the target questions 1 to 3 which pertain to ownership. Each of the target questions were rated greater than 4 on a 7 point Likert scale while the control questions were all rated less than 4.

Of these 35 subjects who were successfully induced with the RHI, 24 subjects maintained the ownership of the rubber hand with only the rubber hand receiving a somatosensory stimulus of interest. There was no significant difference in the average speed of passive movement performed by the experimenter between the responders and non-responders during the maintenance trial using passive movement. Similar to RHI induction results, a three-way mixed MANOVA analysis showed no significant multivariate effects of induction or maintenance modality type on the mean ratings of questionnaire items for maintenance; and again, there were no significant interactions between the induction modality type, the maintenance modality type, and the subject type. However, there were significant multivariate effects of time and the type of subjects on the mean ratings of the questionnaire items. Univariate between-group analyses showed that Q1, Q2, Q3, Q4, and Q9 were rated significantly higher by the achievers than the failures, regardless of induction type or time. Target Q1 to 3 were rated greater than 4 on a 7 point Likert scale while control Q4 to 9 were rated lower than 4. This finding is in alignment with the observed effect of ownership of the rubber hand on the RHI questionnaire by Botvinick and Cohen (1998). In addition, univariate within-group analyses showed that Q1, Q2, and Q3 were rated significantly different over time. Post-hoc pairwise t-tests showed that the mean ratings of first (induction) trials from Q1, Q2, and Q3 were rated significantly higher from
subsequent (maintenance) trials. In contrast, pairwise comparisons of the ownership ratings among the maintenance trials did not show significant differences. This indicates that the degree of ownership felt may have been less vivid during maintenance trials compared to initial induction trial. Regardless, the achievers still rated target ownership questions greater than 4, and they were significantly higher than the control questions. Thus, the achievers do not need to be re-induced with the RHI in between the maintenance trials.

Finally, a transfer of ownership across different somatosensory modalities was observed in 23 of 24 subjects who were successfully induced. They retained ownership using a different modality of testing than what was used for induction. These included 7 subjects who also maintained ownership using the same modality used for induction. One subject could only maintain his ownership of the rubber hand using the same modality as the one used for induction. Interestingly, observing the rubber hand being moved had a significant main effect on proprioceptive drift while there was no significant effect of the ownership being maintained.

Similarly, proprioceptive drift was induced by Rohde, Di Luca & Ernst (2011) with just an observation of the rubber hand placed beside the hidden real hand. However, this was not sufficient for sense of ownership. Holmes et al. (2006) also reported a significant reaching bias from a mere passive visual exposure to the rubber hand, independent of occurrence of an embodiment. As discussed in the introduction, proprioceptive drift may be used as a secondary measure to confirm ownership, but is not a sufficient indicator of ownership by itself. Even under maintenance of ownership in this study, proprioceptive drift was more sensitive to visual exposure to the rubber hand than the presence of ownership.
Individual differences could explain why some naïve participants failed to be induced and why some responders could not maintain or transfer ownership to a different modality despite being “primed.” During the RHI, a person must activate certain cognitive and sensorimotor processes while inhibiting others to embody the rubber hand. This creates different cognitive demands which develop different susceptibility and experiences related to the RHI. Haans, Kaiser, Bouwhuis, and Ijsselsteijn (2012) suggested that it is these fluctuations in cognitive demands that are responsible for the variability of RHI experience across individuals. Research into the factors determining susceptibility for the RHI is lacking, and many studies do not report failure rates. Nonetheless, individual differences are known to affect entrainment of the illusion. For example, participants diagnosed with eating disorder experienced stronger proprioceptive drift than healthy controls (Eshkevari, Rieger, Longo, Haggard, & Treasure, 2012). Mussap and Salton (2006) also found a correlation between the strength of the RHI with body-image oriented behaviours such as bingeing, purging and taking diet supplements. Meanwhile, yoga practitioners with greater self-reported body awareness on the Body Perception Questionnaire than yoga-naïve subjects were equally susceptible to the RHI (David et al., 2013). Thus, David et al. (2013) demonstrated that the RHI did not correlate with body awareness. These authors reasoned that their conflicting finding may be due to the fact that while nonvisual body awareness may be related to the disturbance of body image (visual sense of physical appearance), body awareness is ultimately different from body image. Indeed, Mehling et al. (2009) described the body awareness as encompassing both interoceptive (non-visual, internal) and exteroceptive (visual and/ or other external) processes. Thus, research into individual differences for the RHI should focus more on the differences in body image perception and exteroception rather than body awareness levels.
Although different modalities were stimulating different receptors and pathways, the three somatosensory modalities resulted in an overall RHI induction rate of 46.7%. This rate is similar to the induction rates reported in existing literature which ranges from 32.5% to 78% (Kalckert & Ehrsson, 2014; Lloyd, 2007; Ehrsson et al., 2004, 2005, 2007). Although tactile and vibratory stimuli activate all types of cutaneous receptors, Merkel receptors mainly contribute to overall sense of touch while Pacinian corpuscles are most sensitive for vibration from 125 Hz to 160 Hz (Oey & Mellert, 2004). These cutaneous receptors from the hand convey localized information about vibration, fine touch, and proprioception through the medial lemniscal pathway.

Information about non-discriminatory, light, or crude touch is carried by the anterior spinothalamic tract. On the other hand, cold stimulus activates cold-sensitive thermoreceptors in the skin, and the information is transmitted through the lateral spinothalamic tract. Through the different pathways, all these inputs eventually synapse on VP nucleus neurons of thalamus and arrive at a common destination, the SI.

The lack of multivariate effect of induction modality type on the mean ownership ratings emphasizes the idea of RHI being dependent on the quality of congruent multisensory inputs rather than quantity of different input types (Ehrsson et al., 2005; Walsh et al., 2011). Walsh et al. (2011) achieved an illusion of plastic finger ownership through integration of non-cutaneous proprioceptive and visual cues while blocking the finger’s cutaneous inputs through anaesthesia. While they showed that cutaneous inputs are not essential for the illusion of ownership when there are congruent proprioceptive signals with vision, Ehrsson et al. (2005) showed that even visual inputs are not necessary to induce the RHI as long as other available inputs are congruent. Their participants were blindfolded and in place of vision, their left index finger was moved by
the experimenter to touch the fake hand. At the same time, the experimenter touched their real right hand. In their study, tactile and proprioceptive signals were matched together. Within about 10 seconds, the participants reported feeling that the rubber hand they touched was their own hand; and there was significantly greater neural activity indicated by blood oxygen level-dependent contrast (BOLD) signals in the bilateral ventral premotor cortex, the left intraparietal cortex, and the medial and right cerebellum during the illusion condition compared to asynchronous and incongruent conditions, along with significantly greater vividness and continuance scores. Their post-hoc analysis showed that the strength of illusion (vividness score x continuance score) was positively correlated with the BOLD signals in the bilateral ventral premotor cortex and bilateral lateral cerebellum.

Although an induction through passive movement was not tested within this study due to limitations with our RHI apparatus, the importance of cross-modal congruence and the fact that subjects were able to maintain and transfer their obtained ownership over to passive movement modality somatosensory stimulus suggests a high likelihood for at least equally successful induction rates using passive movement. However, one would need to meet the required speed of movement to activate the muscle spindles and achieve the vital congruency of kinesthetic input with a visual feedback.

Alternatively, there was a lack of congruency in visual input and somatosensory input during the maintenance phase when only the rubber hand received a stimulus; and yet, the ownership of the rubber hand remained in 68.6% of previously successfully induced subjects. Aimola Davies and White (2013) also tested whether ownership could be obtained with touching just the seen rubber
hand to study vision-touch synaesthesia. People with vision-touch synaesthesia report synaesthetic feeling of touch on one’s own body from seeing another person being touched. However, in contrast to this study, Aimola Davies and White (2013) tested rubber hand only condition prior to the traditional synchronous brushing of both seen rubber hand and hidden real hand. Their control normal subjects did not report an embodiment of the rubber hand through the questionnaire items when they initially started by touching just the rubber hand. Subsequently, these normal subjects reported ownership when they were exposed to synchronous touch of both real and rubber hands. Thus, merely seeing the rubber hand being touched without touching the hidden real hand is not sufficient for an embodiment of the rubber hand. Instead, timing is critical in achieving the ownership of the rubber hand through stimulation of just the seen rubber hand.

In this regard, one may suggest either a training effect or a priming effect in which a previous exposure to induction of RHI may be influencing subsequent response during the maintenance phase. Training effect implies the subjects became more compliant with the task and the questionnaire items including the control questions. However, results from three-way mixed MANOVA showed no significant univariate effect of time on the mean ratings of control questions 4 to 9 that account for task compliance and suggestibility. This suggests that a priming effect may be more accurate terminology to describe the ownership observed with a stimulation of only the rubber hand following a previous exposure to induction with synchronous stroking of both real and rubber hands. This maintenance phenomenon was also demonstrated in two monkeys by Shokur et al. (2013). The SI and M1 neurons which continued to respond to a virtual touch without a real touch were similar to cell responses found during synchronous physical and
virtual touches; however, this phenomenon was absent when virtual touch occurred prior to being exposed to synchronous physical and virtual touches (Shokur et al., 2013). Thus, these authors suggested that being primed to respond from the previous period of synchronous physical and virtual touches may be responsible for the observed maintenance of cell response during only virtual touch. The priming effect could explain the maintenance of ownership although there is incongruence with seeing the rubber hand being touched yet missing the physical touch of the hidden hand. Indeed, univariate between-group analyses showed that Q1, Q2, Q3 were rated significantly higher by the participants who maintained the ownership in at least one modality (each $M > 4$ on 7 point Likert scale) than those who failed to maintain the ownership, regardless of induction type or time. Meanwhile, univariate within-group analyses showed that control Q1 to 3 were rated significantly lower in subsequent maintenance trials than from the first induction trial, regardless of subject type or induction modality type. Taken together, this suggests that the participants who maintained the ownership may have individual differences that allowed a priming effect to maintain ownership despite incongruent inputs.

Likewise, the transfer of ownership across different modalities could be due priming effect. Although different somatosensory inputs were transmitted through different pathways, they share common destinations such as the VP nucleus of the thalamus, S1 and S2. This means that the same cells at these common sites which were activated during previous synchronous stimulations of both real and rubber hands under one modality could have been primed to respond to the subsequent visual input of a stimulus on the rubber hand. Thus, the priming effect could also explain why the present study found no significant multivariate effects of either induction or maintenance modality types on the mean ratings of the questionnaire items. It would be
interesting to confirm this effect for the first time in humans either through cell recordings and/or imaging studies.

The current study explored the usefulness of using the illusory ownership achieved through the RHI to provide a behavioural context behind percepts which could be elicited by electrical stimulation without a confounding physical stimulation. The RHI was successfully induced and confirmed by the RHI questionnaire in 35 of 75 subjects using either stroking, cooling or vibration modalities. Finding no significant main effect of modality type used on the mean ratings of the questionnaire items supports the achievement of ownership favouring the quality of congruency in multisensory inputs rather than the quantity of inputs. For the first time in humans, subjects who were successfully induced using one modality were also able to maintain ownership of the rubber hand when only the rubber hand was exposed to a stimulus. This maintenance of ownership in at least one modality was observed in 24 of 35 subjects who were successfully induced with the RHI. Most subjects maintained the ownership under a different modality than what was used for induction. There were no significant multivariate effects of induction or maintenance modality types on the mean ratings of the questionnaire items. In contrast, subjects who maintained the ownership under at least one modality scored each of the three target questions significantly greater while rating them above 4 on a 7 point Likert scale than those who did not maintain the ownership. Both types of subjects, however, rated subsequent (maintenance) trials significantly lower than the first (induction) trials for each of the three target questions. These findings highlight the interplay of individual differences and priming effect on the maintenance of ownership despite incongruent inputs and beg further investigations in future research.
Chapter Four: Future Directions and Final Conclusion

4.1 Future directions

The current findings agree with the existing literature on the importance of the congruency of multisensory inputs for the embodiment of a rubber hand. The illusory ownership was induced using stroking, vibration, and cooling. Interestingly, despite incongruent inputs of seeing the rubber hand being stimulated while missing the stimulus on the real hand, responders were able to maintain the achieved ownership across all sensory modalities including kinaesthesia. Maintenance of ownership in humans in this context has never been studied, but this priming phenomenon has been observed in primates by recording cells in M1 and S1 cortex (Shokur et al., 2013). Further research is required to identify the underlying mechanism for the maintenance phenomenon. In particular, future imaging studies could compare differences in activated brain areas between stimulation of only the rubber hand, synchronous stimulations on both real and rubber hands, and back to stimulation of only the rubber hand. Similar to current findings and those of Shokur et al. (2013), the changes in brain activity responsible for the embodiment of the rubber hand would be present during synchronous stimulations and also when only the rubber hand is stimulated for the second time. However, these changes would not be seen under a mere naïve visualization of the rubber hand being exposed to a stimulus. In other words, the activity of brain areas responsible for the illusory ownership would be sustained only after they have been primed through previous synchronous stimulations of both real and rubber hands.

The current study has established that an illusory ownership of the rubber hand can be achieved without a confounding physical stimulation on the real hand. Hence, the RHI could be used in a future experiment examining the effect of pairing an observable sensorimotor behaviour on the
naturalness and types of percepts that are elicited by an electrical stimulation in the somatosensory system. For example, in patients with thalamic DBS electrodes in place, electrical stimulation can be applied through the DBS system with and without inducing the RHI. From the current study, there were no significant multivariate effects of either induction or maintenance modality types on the mean ratings of the questionnaire items, and no significant interaction between these two factors. In addition, the ownership ratings among the maintenance trials did not show significant differences over time. Thus, there is no need for a re-induction in between the maintenance trials. Subjects who were successfully induced using vibration modality demonstrated the highest rate of maintenance in any one modality (92%). Thus, future experiments with electrical stimulation should use vibration modality for induction and test maintenance across all four sensory modalities to optimize greatest maintenance rate.

After confirming ownership of the rubber hand to ensure uptake of the illusion with the questionnaire, electrical stimulation could be applied at the same time as different somatosensory stimuli are applied only to the rubber hand. The percepts elicited during the illusion paired with the electrical stimulation could then be contrasted to those evoked without pairing (electrical stimulation applied alone). When various patterns of electrical stimulation are applied as our lab did in previous studies (Heming et al., 2010, 2011), I expect that similar to the previous data, these patients will generally describe the percepts evoked by electrical stimulation alone as ‘unnatural’. However, when a behavioural context is introduced by maintenance of the RHI, I hypothesize that the type and quality of percepts evoked by thalamic electrical stimulation can be modulated in a manner dependent on paired observable sensorimotor behaviour or illusions. Kinaesthetic sense has not yet been elicited by electrical stimulation, and perhaps it was simply
prevented by missing a visual feedback of movement. Proprioceptive drift measurements from this current study confirmed that a visual input could bias the subject’s estimate of where his real hand was in space. Even without an individual’s cognitive appraisal of the illusory ownership experience on the questionnaire, a physiological response to the illusion such as proprioceptive drift still provides a behavioural context and may modulate the percepts elicited by the electrical stimulation.

4.2 Final conclusion

This study examined the feasibility of using the RHI and its illusory ownership experience to provide a behavioural context behind percepts elicited by electrical stimulation without a confounding physical stimulation. The RHI was successfully induced by stroking, cooling, and vibration and confirmed by the RHI questionnaire. Type of somatosensory modality did not have a significant effect on the RHI questionnaire ratings. This supports the importance of the congruency of multisensory inputs on achieving embodiment of the rubber hand, rather than their quantity. Subjects who were induced using one modality were able to maintain the achieved ownership of the rubber hand when only the rubber hand was exposed to a stimulus. This is the first study to demonstrate a maintenance of embodiment in humans when only the rubber hand is stimulated, and thus, in the presence of incongruent multisensory inputs. This is consistent with existing research on primates using single cell recordings. The maintenance of the ownership was observed across all modalities, and the majority of subjects who had successfully been induced, maintained the ownership under a different modality than what was used for induction.
This study has demonstrated the usefulness of the RHI to provide a behavioural context to electrical stimulation which can be used to restore somatosenses. The maintenance of ownership when only rubber hand is receiving a stimulus provides a behavioural context by which electrical stimulation could be applied to the nervous system without a confounding physical stimulus. The adaptability of the RHI across different somatosensory modalities will be especially useful in pairing corresponding behavioural contexts to electrical stimulation, aimed to restore various types of somatosenses.
References


Bekrater-Bodmann, R., Foell, J., Diers, M., & Flor, H. (2012). The perceptual and neuronal stability of the rubber hand illusion across contexts and over time. *Brain Research, 1452*(0), 130-139. doi:http://dx.doi.org/10.1016/j.brainres.2012.03.001


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doi:10.1016/j.concog.2014.08.022; 10.1016/j.concog.2014.08.022


doi:http://dx.doi.org/ezproxy.lib.ucalgary.ca/10.1016/j.cognition.2007.12.004

doi:10.1371/journal.pone.0005614

10.1073/pnas.0803768105


APPENDIX A: RHI QUESTIONNAIRE FOR TOUCH

1. The rubber hand began to resemble my own (real) hand, in terms of shape, skin tone, freckles or some other visual feature.

2. It seemed as if I were feeling the touch of the paintbrush in the location where I saw the rubber hand touched.

3. It felt as if my real hand was drifting towards the rubber hand.

4. It appeared (visually) as if the rubber hand were drifting towards my hand.

5. It seemed as if I might have more than one left hand or arm.
6. It seemed as though the touch I felt was caused by the paintbrush touching the rubber hand.

7. It seemed as if the touch I was feeling came from somewhere between my own hand and the rubber hand.

8. I felt as if the rubber hand were my hand.

9. It felt as if my real hand were turning ‘rubbery’.

Comments:
APPENDIX B: RHI QUESTIONNAIRE FOR VIBRATION

1. It seemed as if I were feeling the vibration of the tuning fork in the location where I saw the tuning fork touch the rubber hand.

   - Strongly Disagree
   - Neither/Undecided
   - Strongly Agree

2. I felt as if the rubber hand were my hand.

   - Strongly Disagree
   - Neither/Undecided
   - Strongly Agree

3. It felt as if my real hand was drifting towards the rubber hand.

   - Strongly Disagree
   - Neither/Undecided
   - Strongly Agree

4. It seemed as if I might have more than one left hand or arm.

   - Strongly Disagree
   - Neither/Undecided
   - Strongly Agree

5. The rubber hand began to resemble my own (real) hand, in terms of shape, skin tone, freckles or some other visual feature.

   - Strongly Disagree
   - Neither/Undecided
   - Strongly Agree
6. It seemed as though the **vibration** I felt was caused by the tuning fork touching the rubber hand.

![Rating Scale]

7. It seemed as if the **vibration** I was feeling came from somewhere between my own hand and the rubber hand.

![Rating Scale]

8. It felt as if my real hand were turning 'rubbery'.

![Rating Scale]

9. It appeared (visually) as if the rubber hand were drifting towards my hand.

![Rating Scale]

Comments:
APPENDIX C: RHI QUESTIONNAIRE FOR COOLING

1. It seemed as if I were feeling the **cooling** of the ice cube in the location where I saw the ice cube touch the rubber hand.

<table>
<thead>
<tr>
<th>Strongly Disagree</th>
<th>Neither/Undecided</th>
<th>Strongly Agree</th>
</tr>
</thead>
</table>

2. It seemed as if I might have more than one left hand or arm.

<table>
<thead>
<tr>
<th>Strongly Disagree</th>
<th>Neither/Undecided</th>
<th>Strongly Agree</th>
</tr>
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</table>

3. It felt as if my real hand was drifting towards the rubber hand.

<table>
<thead>
<tr>
<th>Strongly Disagree</th>
<th>Neither/Undecided</th>
<th>Strongly Agree</th>
</tr>
</thead>
</table>

4. It seemed as though the **cooling** I felt was caused by the ice cube touching the rubber hand.

<table>
<thead>
<tr>
<th>Strongly Disagree</th>
<th>Neither/Undecided</th>
<th>Strongly Agree</th>
</tr>
</thead>
</table>

5. It felt as if my real hand were turning ‘rubbery’.

<table>
<thead>
<tr>
<th>Strongly Disagree</th>
<th>Neither/Undecided</th>
<th>Strongly Agree</th>
</tr>
</thead>
</table>
6. I felt as if the rubber hand were my hand.

7. The rubber hand began to resemble my own (real) hand, in terms of shape, skin tone, freckles or some other visual feature.

8. It appeared (visually) as if the rubber hand were drifting towards my hand.

9. It seemed as if the **cooling** I was feeling came from somewhere between my own hand and the rubber hand.

Comments:
APPENDIX D: RHI QUESTIONNAIRE FOR PASSIVE MOVEMENT

1. It felt as if my real hand were turning ‘rubbery’.
   - [Scale]
     - Strongly Disagree
     - Neither/Undecided
     - Strongly Agree

2. I felt I was **moving** in relation to where I saw the rubber hand moving rather to where I knew my own hand to be moving.
   - [Scale]
     - Strongly Disagree
     - Neither/Undecided
     - Strongly Agree

3. I felt as if the rubber hand were my hand.
   - [Scale]
     - Strongly Disagree
     - Neither/Undecided
     - Strongly Agree

4. It felt as if my real hand was drifting towards the rubber hand.
   - [Scale]
     - Strongly Disagree
     - Neither/Undecided
     - Strongly Agree

5. The rubber hand began to resemble my own (real) hand, in terms of shape, skin tone, freckles or some other visual feature.
   - [Scale]
     - Strongly Disagree
     - Neither/Undecided
     - Strongly Agree
6. It seemed as if I might have more than one left hand or arm.

7. It seemed as if the **movement** I felt came from somewhere between my own hand and the rubber hand.

8. It felt as if the **movement** I felt was caused by the movement of the rubber hand.

9. It appeared (visually) as if the rubber hand were drifting towards my hand

Comments:
APPENDIX E: RECRUITMENT MATERIALS

Seeking Volunteers for Brain Research

We are looking for healthy volunteers to participate in a study regarding limb ownership across different types of senses.

This short (~20 min) experiment involves rating what you felt after your hand is exposed to touch, coldness, vibration and movement.

You will receive a $5 Tim Hortons gift card for taking part in the study.

Interested? Contact Linda Kim for details at: Lhkim@ucalgary.ca

This study (Ethics ID: REB14-1723) has been approved by the University of Calgary Conjoint Health Research Ethics Board.
APPENDIX F: CONSENT FORM

TITLE: The Rubber Hand Illusion across different sensory modalities

SPONSOR: Alberta Innovates - Health Solutions

INVESTIGATORS: Dr. Zelma Kiss (Supervisor) and Linda Kim (MSc student), Faculty of Medicine, Department of Neuroscience, lhkim@ucalgary.ca

This consent form is only part of the process of informed consent. It should give you the basic idea of what the research is about and what your participation will involve. If you would like more detail about something mentioned here, or information not included here, please ask. Take the time to read this carefully and to understand any accompanying information. You will receive a copy of this form.

BACKGROUND
The Rubber Hand Illusion (RHI) is a party-trick illusion that is of relevance to our understanding of our bodily sensations. Touching your real hand while a rubber hand is being touched results in a feeling of ownership towards the rubber hand in some people. This ownership can be confirmed by specific questions. There are several aspects of the RHI that are not known, such as how sensory inputs modify the intensity of the illusion.

WHAT IS THE PURPOSE OF THE STUDY?
The purpose of the study is to determine how the rubber hand illusion is affected by applying different types of sensations to the hand. The four senses that will be tested are touch, temperature (cold), vibration, and movement.

Ethics ID: REB14-1723
Study Title: The Rubber Hand Illusion across different sensory modalities
PI: Dr. Zelma Kiss
Version number/date: Version #1, December 31 2014
CHREB Template date October 2012
**WHAT WOULD I HAVE TO DO?**
Each of these four sensations will be applied to your hand by the experimenter. A paint brush will evoke touch sensation, an ice cube will evoke cold, a tuning fork will induce the sensation of vibration, and movement sense by the experimenter moving your hand. We will videotape your hand and torso (not your face) to measure the speed of movement and the consistency of applications of the stimuli to your hand between trials. You will fill in a questionnaire in which you will read a series of statements and answer how much you agree or disagree with them. The study will take approximately 20 minutes of your time.

**WHAT ARE THE RISKS?**
There is no risk to participating in this study. You may feel mild discomfort associated with cold object and a vibrating tuning fork being held to your hand.

**WILL I BENEFIT IF I TAKE PART? WILL I BE PAID FOR PARTICIPATING, OR DO I HAVE TO PAY FOR ANYTHING?**
Participation in this study will not be of personal benefit to you. You should not incur any financial costs by participating in this study. If you are coming into the lab from home or a clinic visit is extended to participate in this study, we will provide you with a parking pass. If you do not require a parking pass then as a token of appreciation for your participation in the study, a $5 gift card will be given to you after completion of the study session.

**DO I HAVE TO PARTICIPATE?**
Participation is completely voluntary. You may refuse to participate altogether, may refuse to participate in parts of the study, may decline to answer any and all questions, and may withdraw from the study at any time without penalty. If new information becomes available that might affect your willingness to participate in the study, you will be informed as soon as possible.

**WILL MY RECORDS BE KEPT PRIVATE?**
Participation is completely voluntary and all information will be kept confidential. You are free to discontinue participation at any time and all the data you have contributed to the study will be destroyed. No one except the research team will have access to the information collected. There are no names on the questionnaires. Only anonymous non-identifying information (including a videotape of your hand and torso without your face) will appear in publications. The University of Calgary Conjoint Health Research Ethics Board and the University of Calgary Research Accounting will have access to the records as a means of audit.

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Version number/date: Version #1, December 31 2014
CHREB Template date October 2012
IF I SUFFER A RESEARCH-RELATED INJURY, WILL I BE COMPENSATED?
In the event that you suffer injury as a result of participating in this research, no compensation will be provided to you by Alberta Innovates - Health Solutions, the University of Calgary, Alberta Health Services or the Researchers. You still have all your legal rights. Nothing said in this consent form alters your right to seek damages.

SIGNATURES

Your signature on this form indicates that you have understood to your satisfaction the information regarding your participation in the research project and agree to participate as a participant. In no way does this waive your legal rights nor release the investigators or involved institutions from their legal and professional responsibilities. You are free to withdraw from the study at any time without jeopardizing your health care. If you have further questions concerning matters related to this research, please contact:

Dr. Zelma Kiss
Department of Clinical Neurosciences, Faculty of Medicine

[Signature]

If you have any questions concerning your rights as a possible participant in this research, please contact the Chair, Conjoint Health Research Ethics Board, University of Calgary at [Contact Information]

<table>
<thead>
<tr>
<th>Participant’s Name</th>
<th>Signature and Date</th>
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The University of Calgary Conjoint Health Research Ethics Board has approved this research study.
A signed copy of this consent form has been given to you to keep for your records and reference.

Ethics ID: REB14-1723
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CHREB Template date October 2012