Title: Higher-order cognitive factors affect subjective but not proprioceptive aspects of self-representation in the rubber hand illusion

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Acknowledgements
Professor Virginia Slaughter for helpful advice and aid in drafting this paper

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1. Introduction

Processes of multisensory integration underlie the most fundamental aspects of self-representation (Blanke, 2012; Blanke & Metzinger, 2009; Jeannerod, 2006). Indeed, it has been proposed that human bodily self-consciousness at its most basic, pre-reflexive level results from the constant presence and integration of information from our multiple sensory systems (Gallagher, 2005; Tsakiris, 2010). Bodily self-representation, however, is not as stable as it appears to the individual. Experimental perceptual illusions that disrupt body representation by manipulating multisensory inputs provide compelling evidence that, despite its perceived constancy, our representation of self can be easily and profoundly modified (Armel & Ramachandran, 2003; Botvinick & Cohen, 1998; Ehrsson, 2007; Ehrsson, Spence, & Passingham, 2004; Lenggenhager, Tadi, Metzinger, & Blanke, 2007). These findings highlight one of the most important topics in psychology and neuroscience today, the extent of human neural plasticity in immediate response to experience.

1.1. Experimental manipulation of self-representation: The rubber hand illusion

The rubber hand illusion (RHI) is a widely employed paradigm that demonstrates how perception of the body can be manipulated through the presentation of incongruous visual and tactile inputs administered to the hands (Botvinick & Cohen, 1998). Typically, in this illusion a participant's hand is concealed from view and replaced with a rubber prosthesis. The prosthesis is placed in the approximate position and angle of the participant's concealed limb, while introducing a slight spatial deviation between the two (with the rubber hand closer in towards the body midline than the real hand). The participant's own hand and the rubber hand then receive identical tactile stimulation (RHI induction), usually in the form of stroking with a paintbrush – precisely synchronising the timing and location of strokes. This creates a match between what is seen on the rubber hand and what is felt on the participant's hidden hand.

During the RHI, there are a number of effects on self-representation. These effects can be divided into the general categories of **subjective** (Botvinick & Cohen, 1998; Costantini & Haggard, 2007; Ehrsson, Holmes, & Passingham, 2005; Tsakiris, Hesse, Boy, Haggard, & Fink, 2007), **proprioceptive** (Botvinick & Cohen, 1998; Holle, McLatchie, Maurer, & Ward, 2011; Rohde, Di Luca, & Ernst, 2011) and **physiological** outcomes (Barnsley et al., 2011; Moseley et al., 2008).

The subjective effects of the illusion refer to general alterations in the psychological, bodily experience of an individual i.e. changes in how their body and their body parts *feel*. These subjective outcomes are thought to reflect the experience of incorporating the rubber hand into the participant's own body representation as well as rejection of their actual hand (Botvinick & Cohen, 1998; Ehrsson et al., 2004; Tsakiris, 2010). These outcomes are generally assessed using a questionnaire or verbal report.

The RHI also produces changes in the perceived location of the participant's hand, shifting it from its actual location towards the location of the rubber hand. There are a number of methods for assessing this proprioceptive change. Typically, participants are asked to estimate the position of their hidden hand before and after RHI induction and the systematic error caused by the illusion is measured. This can be achieved through verbal report of the perceived location or pointing with the unstimulated hand (i.e. behavioural measures). This change is often referred to as proprioceptive *drift*.

Various physiological changes have been identified following RHI, including alterations in temperature (Moseley et al., 2008), immune function (Barnsley et al., 2011) and galvanic skin response (Armel & Ramachandran, 2003) in the stimulated hand compared to the control hand. These changes are thought to reflect the disruption of subjective ownership of that limb (Barnsley et al., 2011; Moseley et al., 2008).

1.2. New evidence suggests original models of RHI mechanisms are incorrect

In the popular model put forward by Tsakiris (2010), induction of the RHI produces changes in subjective self-representation which, in turn, produce the alterations in proprioception. In this conceptualisation, subjective outcomes cause proprioceptive outcomes and therefore are considered a *behavioural proxy*.

Contrary to this model, new behavioural evidence suggests that subjective and proprioceptive RHI outcomes are in fact dissociable. For example, a number of studies have demonstrated proprioceptive drift towards a rubber hand without associated increases in felt ownership over the rubber hand, when the participant's hand is kept still (Holle et al., 2011; Rohde et al., 2011) and when making point-to-target actions (Holmes, Snijders, & Spence, 2006).

Longo, Schüür, Kammers, Tsakiris and Haggard (2008a) conducted a large-scale qualitative analysis of first-person RHI experience. They found Location (representing proprioceptive change) and Ownership scales to be significant independent predictors of proprioceptive change levels, indicating that perceived limb shifts should be considered separately from subjective ownership of the rubber hand.

Subjective and proprioceptive aspects of self-representation are also shown to be distinct in their relationship with other aspects of perception (Longo et al., 2008a). Longo et al. (2008a) investigated the relationship of RHI outcomes to participant's ratings of similarity in appearance between their hand and the rubber hand. Individuals who reported high levels of subjective illusion intensity on a questionnaire reported significantly greater similarity in appearance than those who experienced low subjective levels of illusion. Notably, when comparing objective measures of similarity (made by a double-blind observer), there were no actual appearance differences between the high and low subjective illusion groups. Given the objective similarity in appearance, and that the similarity judgements were collected *following* illusion induction, the authors concluded the effectiveness of the ownership manipulation caused the rubber hand to be perceived as more similar to the participant's own hand – rather than the other way around. There was no such relationship with proprioceptive indicators of the illusion indicating shifting limb-location did not change visual perception of the rubber hand in the same way.

Neurophysiological evidence also indicates the existence of separate components of body representation that are subserved by distinct neural systems. Kammers et al. (2008) administered rTMS over the inferior posterior parietal lobe (IPL) during RHI induction. They found significant reductions in immediate proprioceptive judgements of limb position while subjective ownership over the rubber hand and ballistic action responses were unaffected.

1.3. Multimodal models of self-representation

It now appears self-representation is not supported by one homogenous neurocognitive system, and that distinct systems support proprioceptive position estimation and higher-order subjective body-representations (Kammers, de Vignemont, Verhagen, & Dijkerman, 2009; Kammers et al., 2008; Rohde et al., 2011). While the tight integration of all self-representation systems is critical to the production of a coherent, global 'sense of self', it appears these subsystems may be driven by very different processes of multisensory integration at disparate neural locations.

Subjective self-representation is thought to be governed by processes of intermodal matching (Botvinick & Cohen, 1998; Ehrsson et al., 2005; Ehrsson et al., 2004; Tsakiris, Costantini, & Haggard, 2008). In this process, sensory inputs that arise on the body in precise temporal and spatial synchrony are determined to be caused by the same event and are, therefore, integrated. This allows related multisensory body inputs to be perceived as a single, coherent percept – rather than a jumble of concurrent signals. Intermodal matching leads the object of stimulation to be identified as *self* which produces the psychological experience of subjective self-representation (Botvinick & Cohen, 1998; Ehrsson et al., 2005; Ehrsson et al., 2004; Tsakiris et al., 2008). Therefore, in the RHI, synchronicity between visual inputs *seen* on the rubber hand and tactile inputs *felt* on the participant's own hand cause incorporation of the rubber hand into the body image and the rejection of the own hand.

Activity in ventral premotor (PMv) and cerebellar areas has been associated with subjective self-representation in fMRI studies of the RHI. Ehrsson and colleages (2004;2005) found levels of BOLD activity correlated directly with reported levels of subjective illusion, and, activity-onset matched self-reported illusion onset (Ehrsson et al., 2005; Ehrsson et al., 2004). Such findings are aligned with previous research regarding the functions of the PMv and cerebellum. The PMv is known to receive inputs from visual and somatosensory areas in the posterior regions of the parietal cortex (Rizzolatti, Luppino, & Matelli, 1998) allowing detection of concurrent inputs from the body. The cerebellum has been linked functionally with parietal and premotor cortices (Dum & Strick, 2003) and is thought to be involved in the analysis of timing of sensory inputs (Blakemore, Frith, & Wolpert, 2001) making it a likely candidate for integration of inputs in the self-other discrimination process. This research suggests the critical role of the PMv and cerebellum in analysing the synchronicity of multisensory bodily inputs in determining self from non-self objects.

In contrast, the system proposed to underlie perception of body position (and thus, proprioceptive RHI outcomes) is far more simple than that supporting subjective self-representation. Under normal conditions, afferent kinasthetic and somatosensory information is the most important sensory source of information in the estimation of limb position (Guerraz et al., 2012; Teasdale et al., 1993). The RHI creates a mismatch between proprioceptive and visual limb position information causing the brain to assess the reliability of information from these two systems (van Beers, Sittig, & Dernier van der Gon, 1999). Visual information over-rides proprioceptive due to the inherent high acuity of the visual system and the [typically] high quality of the visual information available in the RHI context (e.g. high luminance, direct viewing orientation) (Rohde et al., 2011). Thus, the reweighting of sensory inputs causes the felt position of the hand to be altered to match the visual position of the hand, i.e. proprioceptive change.

It was once thought that under all situations of uncertainty, proprioceptive position would be 'captured' to match visual position (Hay, Pick, & Ikeda, 1965; Rock & Victor, 1964; Singer & Day, 1969). In fact, it now appears that the central nervous system selects the sense with the optimal reliability to make the required judgement on a case-by-case basis. This flexibility allows for the construction of the most accurate perception of body position based on available sensory information (Ernst & Bülthoff, 2004; Fitzpatrick & McCloskey, 1994; Guerraz et al., 2012; van Beers et al., 1999).

As mentioned previously, rTMS of the IPL produces a marked reduction in proprioceptive RHI outcomes suggesting this area is critical to on-line modulation of body perception. Damage to the left IPL has been linked with clinical deficits in the ability to locate and position body parts (autotopagnosia; Ogawa & Inui, 2007; Ogden, 1985) further supporting its role in analysis of the current body state and spatial relationships between limbs. Activation in the right insular cortex and frontal operculum has been found to correlate positively with proprioceptive change levels (Tsakiris et al., 2007). This activation appears to represent the alteration in proprioceptive position sense to match the visual rubber hand position (Kammers et al., 2008) again supporting the role of the insular and operculum in proprioceptive self-representation.

1.4. Effect of top-down factors in the RHI: Revision to previous theories

A number of studies report extinction of RHI effects when visual information about the rubber hand conflicts with internal information about the actual limb state or posture; for example, when the rubber hand is rotated to an anatomically impossible position with-respect-to the real hand position (180°, Ehrsson et al., 2004; 90°, Tsakiris & Haggard, 2005). Even minor postural adjustments of the rubber hand (10 or 30°, Costantini & Haggard, 2007) have been reported to attenuate RHI effects. In the light of these results, Botvinick and Cohen's original (1998) theory was expanded to include the modulation of bottom-up sensory effects by top-down cognitive functions (Tsakiris, Carpenter, James, & Fotopoulou, 2010). In this model, a 'goodness-of-fit' comparison occurs between incoming sensory information and internal body models. If there is a sufficient fit between them, intermodal matching processes will occur. A mismatch leads to rejection of the sensory information.

We believe a revision of this 'goodness-of-fit' model may be required to reflect these separable aspects of self-representation. Indeed, it appears higher-order cognitive factors may not, in fact, modulate <u>both</u> components of self-representation as was once thought. Holle et al. (2011) found that while subjective illusion was eliminated for hands rotated by 180°, proprioceptive change was still present, though reduced. They suggested previous studies (Costantini & Haggard, 2007; Tsakiris & Haggard, 2005) that failed to demonstrate drift to rotated hands simply lacked power to identify this small effect. Similarly, when taking frequent measurements of proprioceptive change (every 10 or 40 seconds) Rohde et al. (2011) produced significant drift in synchronous, asynchronous and vision-only control (no tactile stimulation) conditions. Therefore, even when sensory inputs did not match, drift still occurred. In the light of this information, we suggest that while proprioceptive self-representation is resistant to both mismatches in posture and incongruent multisensory inputs (i.e. violations of top-down body information), subjective self-representation is not. Inconsistent information about the body appears to disrupt these higher-order psychological aspects of self-recognition, although at this stage this cannot be concluded with much certainty. The current study aims to explore the differential effect of top-down cognitive factors on subjective and proprioceptive aspects of self-representation under a novel situation of illusory location manipulation where self-location is drawn *away* from the actual body position.

1.5. Is it possible to draw felt position <u>away</u> from the locus of the body, towards extracorporeal space?

Traditionally, RHI experiments have been conducted with the participant's real hand displaced laterally away from the body midline, with the rubber hand located medially, towards the body – often in line with the approximate shoulder position (Armel & Ramachandran, 2003; Asai & Tanno, 2007; Costantini & Haggard, 2007; Heed et al., 2011). From these experiments it is clear that proprioceptive alterations (drift) can be produced towards the body. Additionally, it is clear that subjective embodied position can also be drawn in, towards the body. We wish to determine whether both aspects of self-representation can be shifted away from the body location, towards extracorporeal space. Further to this, we wish to investigate the relationship between subjective and proprioceptive RHI outcomes – is the relationship between these outcomes altered when the RHI occurs away from the body.

Explicitly shifting the locus of the self away from the body is contrary to natural proprioceptive drift and top-down expectation

In the absence of visual body information, felt location of the limb has been demonstrated to shift towards the body in a radial direction when at rest (Wann & Ibrahim, 1992) and when making reach-to-grasp movements (Holmes et al., 2006) [though see (Desmurget, Vindras, Grea, Viviani, & Grafton, 2000)]. In this way, shifting the locus of self away from the body position, into extracorporeal space can be seen as a violation of top-down cognitive expectation because it contradicts the natural orientation of perceptual shifts i.e. towards the body, which is a default of the biomechanics of the limb.

Further to this, cases where self-localisation *is* shifted away from the body (as in autoscopic hallucinations, out-of-body experiences and heautoscopy) are reported to produce unnatural and bizarre subjective experiences, feelings of derealisation and generally represents a striking disturbance of conscious bodily experience (Blanke & Arzy, 2005; Blanke, Landis, Spinelli, & Seeck, 2004). These experiences are thought to be at least partly caused by a break-down of normal multisensory integration processes (Blanke & Metzinger, 2009). These experiences have also been found to be associated with pathological sensations of movement and position (Blanke et al., 2004) and body distortion processing (Braithwaite, Samson, Apperly, Broglia, & Hulleman, 2011).

In a non-clinical population, it is possible to induce a similar shift in the location of self – out from the body, outside the physical bodily borders – using full-body illusions (Lenggenhager et al., 2007). Subjects report their experience in such experiments as being highly 'strange' and 'weird' and many found the experiment to be cause subjective 'irritation' (Lenggenhager et al., 2007). These whole body illusion experiments reveal that global localisation and identification of the 'self' rely on similar multisensory mechanisms as with individual body parts, as in the RHI (Lenggenhager et al., 2007).

In contrast, when the illusory shift in self-identification and ownership occurs <u>at</u> the site of the own-body – as in the body-swap illusion, where the subject sees (via a head mounted display) a virtual avatar in place of their body and change is induced via visuo-tactile manipulations – these subjective alterations occur quickly and easily, and subjects report feeling natural about the shift of the position of their 'self' into this new body. This occurs even when subjects shake hands with their own real-body via the video illusion (Petkova & Ehrsson, 2008).

Thus it appears that as a natural default of the proprioceptive system, felt position will shift in towards central body space. To draw this location out and away from the body into extracorporeal space, therefore, would require an explicit cognitive shift – as achieved in our experiment, and in the Lenggenhager et al. (2007) experiments. Such a change, however, is by design contrary to natural bodily experience and higher-level knowledge about the body position.

Aims and hypotheses

If, as we propose, bodily perception results from a simple bottom-up process that is resistant to the effects of top-down factors it should be possible to produce proprioceptive drift in and out from the body, despite the mismatch created between the illusory, seen position of the hand and actual body position. Conversely, mismatches between external (sensory) and internal information about the body state or position may extinguish subjective ownership and embodiment. If this is indeed the case, using the RHI to draw the locus of the subjective self away from the actual body position would diminish subjective incorporation of the rubber hand into the self. To investigate the conditions that produce proprioceptive drift and whether they are indeed distinct from those required for higher-order subjective bodily experiences, our study induced illusory location shifts towards (In condition) and away from the body position (Out condition). The relationship between self-rated illusion experience and proprioceptive judgements was investigated separately within the In and Out conditions. The use of a detailed, multi-scaled questionnaire (Longo et al., 2008a) allowed a more comprehensive picture of subjective RHI experience than that provided by traditional measures (Botvinick & Cohen, 1998).

Previous findings suggest subjective embodiment (but not proprioceptive change) alters visual perception of the rubber hand (Longo, Schüür, Kammers, Tsakiris, & Haggard, 2009). In the light of such results, two measures of second-order perception were included in the current study. These were self-rated *similarity in appearance* between the real and rubber hand (as in Longo et al., 2009), and a novel measure, the *similarity in* [felt] *brushing* seen on the rubber hand and felt on the participant's own hand. It was predicted that the reduction in subjective incorporation of the rubber hand in the Out condition would lead to lower visual and tactile similarity ratings – compared to the In condition. Such a result would further support the modulation of subjective RHI outcomes between conditions as well as demonstrate, for the first time, the manipulation of tactile perception by the RHI induction.

2. Methods

2.1. Participants

The sample consisted of 50 undergraduate students from The University of Queensland who completed the experiment for course credit. To avoid potential carry-over effects of the two directions of RHI manipulation, a between-groups design was used. There were 22 in the In Condition (11 male, 11 female) and 28 in the Out condition (9 male, 19 female). Mean ages were 20 (Range: 17-27, SD = 2.4) and 21.50 (Range: 17-31; SD = 4.5) for the In and Out conditions respectively. Participants were predominantly of Caucasian skin-tone (54%), with 34% Asian and the remainder (12%) of a darker skin-tone classification [Independent groups t-tests demonstrated there were no significant differences in skin tone between the In and Out groups, $t(48) = -.305$, $p = .761$].

Out of 50 participants, 45 were right-handed (EHI = 65.99, SE =3.39) using the EHI classification of handedness (Oldfield, 1971). All had normal or corrected-to-normal vision. There were no significant differences in the distribution of gender, age, skin-tone, handedness (EHI), medical issues (vision, hearing) between the In & Out conditions.

2.2. Apparatus

The experiment was conducted on a specially constructed apparatus consisting of three equidistant shelves [see Figure[1a] below]. A LCD computer screen was fitted into the top shelf, facing downwards, for presentation of experimental stimuli onto a mirror below. Participants sat at the apparatus with their hands placed on the lowermost shelf. A black cloth placed over the participant's shoulders prevented visual information about the position of their arms. Looking into the mirror participants saw the hand images reflected at the same approximate position, depth plane and size as their own hands, creating a convincing illusion.

#Figure[1a] and [1b] approximately here #

2.3. Hand images: Appearance and positioning of participants' hands with respect to hand image

The hand image stimuli consisted of a left and right hand of Caucasian skin tone, medium size and indeterminate gender (i.e. nails were short, fingers were of intermediate width). In the In Condition, the participant's hands were positioned 7cm in from either edge of the computer screen and the hand images were 15cm in. Positions were inverted in the Out condition (participant's hands at 15cm, and hand image at 7cm from the screen edge). Distance between the real hand and the hand images (8cm) [Figure[1b]] was kept constant so proprioceptive drift could be compared for relative position alone (as previous research has shown separation distance effects drift magnitude, Lloyd, 2007).

2.4. Measurement of change in bodily perception: Proprioceptive drift magnitude

Measurements of static proprioceptive hand position were made using a digital image of a ruler displayed on-screen. Rather than presenting the same ruler repeatedly, one of a set of 15 rulers (starting point varied, e.g. ruler 1 spanning 1cm to 30cm, ruler 2 5cm to 35cm) was randomly selected to appear on screen at each trial. The use of multiple rulers prevented participants learning or remembering the position of their finger on the ruler.

The ruler was presented on-screen so their position and depth plane matched that of the tip of the participants' finger middle finger [see Figure[1b]]. Subjects were asked to estimate the location of their hidden left middle finger by reporting the number on the ruler closest to its position. This was reported verbally and recorded by the experimenter to ensure participant's hands could remain still, in position for the entire trial duration.

Position judgements were taken before and after RHI induction at each of the nine trials. Pre-RHI error was subtracted from post-RHI error to give an absolute value of movement towards the hand image following induction. This score was labelled drift magnitude and represented the alteration in proprioceptive self-representation caused by the RHI. Positive scores represented movement of perceived position from the actual hand position towards the hand image, negative scores represented movement away.

2.5. Assessment of subjective self-representation: The RHI Questionnaire or RHIQ

Longo and colleagues (2008a) used a comprehensive qualitative analysis and principle components analysis to separate subjective RHI experience into five distinct subcomponents. These were *Embodiment* [subscales: Ownership, Location, Agency], collectively representing feelings that the object (rubber hand or own hand) is part of the self, and is owned and controlled by the individual. *Loss of Own Hand* gauges feelings that the participant's own hand had 'disappeared' during the illusion. *Movement* assesses sensations that the participant's hand had shifted in space from its original location. *Affect* assesses whether participants felt the experience was positive or negative. Finally, the *Sensation* scale asks about the presence or absence of perceptual sensations resulting from the illusion such as pins and needles or numbness [see Footnote[a] for an example item for each scale or Supplementary Materials, item A for the full 25 item questionnaire].

This 25 item scale was employed (over the traditional seven-item Botvinick & Cohen (1998) scale) in order to comprehensively assess the complexity in first-person RHI experience. Question one, two and seven of the Longo et al.(2008a) scale form the Ownership scale from the original Botvinick and Cohen (1998) questionnaire allowing direct comparability of our subjective results with previous studies that employ this scale. Interestingly, these three items typically are the only questions of the seven Botvinick and Cohen (1998) items to receive significant positive endorsement (Botvinick & Cohen, 1998; Rohde et al., 2011) suggesting the full-scale may be of limited usefulness.

Footnote[a]. Sample questions for each of the five separate components of subjective self-representation as described by Longo et al. (2008a)
Embodiment: "It seemed like the hand image was part of my body" (Q3)
Loss of Own Hand: "It seemed like my hand disappeared" (Q16)
Movement: "It seemed like my hand was moving towards the hand image" (Q18)
Affect: "I found the experience enjoyable" (Q20)
Sensation: "I had the sensation of pins and needles in my hand" (Q22)

Participants respond on a seven-point Likert Scale ranging from strongly disagree to strongly agree. This was later recoded to range from -3 to +3 in line with traditional RHI scoring practices.

The questionnaire was employed on two separate trials directly following RHI induction. Position of these trials was randomised throughout the nine trials. A measurement of proprioceptive drift was taken following the questionnaires but not included in the general drift analysis.

2.6. RHI Induction procedure

Participant's hands were positioned by the experimenter at the beginning of each trial. The ruler was presented on the screen 2500ms after hand placement, at which time participants made their pre-RHI estimation of hand position. Both the real hand and the hand image were brushed in synchrony at approximately 1Hz for a period of 90 seconds using a set of soft brushes [approximately .5cm diameter] affixed to the apparatus to ensure pressure and contact of the brush remained constant over participants. At the finish of the RHI induction there was a 2500ms pause before the ruler was presented on the screen and participants made their post-RHI judgement. Between trials, participants were instructed to move their hand onto their lap. Inter-trial interval (ITI) was 90 seconds [to match RHI induction duration].

Some RHI experiments include a condition of asynchronous stimulation where tactile stimulation is applied to both the real and rubber hand surfaces, but does not match. This is done to assess the effects of intermodal matching on RHI effects. The presence of drift in synchronous and absence in asynchronous conditions has been widely demonstrated by previous research (Botvinick & Cohen, 1998; Ehrsson et al., 2005; Ehrsson et al., 2004; Tsakiris et al., 2010; Tsakiris & Haggard, 2005). Indeed, some recent studies suggest that visuo-tactile stimulation is unnecessary for the production of proprioceptive drift, but rather, illusory hand information alone is required (Rohde et al., 2011).

The purpose of the current study was not to investigate what *arrests* the experience of RHI, but how it manifests under certain conditions (In and Out from the body), meaning the comparison of synchronous and asynchronous conditions was not of direct relevance to the study's aims. For this reason an asynchronous condition was not included in this study [as in Botvinick & Cohen's original 1998 study that also employed synchronous stroking only], rather we compared the effect of our direction manipulation on synchronous conditions alone.

2.7. *Experimenter and participant ratings of similarity in appearance and brushing*

2.7.1. Participant ratings

At the completion of the experiment, participants were asked a series of questions regarding how similar they believed the rubber hand was in appearance to their own hand (similarity in appearance measure) and, secondly, how similar the brushing on their hand was to the brushing they saw on the hand on the screen (similarity in brushing measure). These ratings were made on a Likert scale from one to ten, with one representing 'very dissimilar' and ten 'very similar'.

2.7.2. Experimenter ratings

Prior to experiment onset, the experimenter recorded the skin-tone of the participant on a trichotomous scale (1: fair – e.g. Caucasian, 2: mid-tone – e.g. Chinese, Japanese, 3: dark-tone – e.g. Pakistani, African). Gender was also recorded. This was done to give a blunt, objective measure of approximate hand appearance in terms of skin colour, size, hair-coverage etc.

On completion of the RHI induction at each of the nine trials, the experimenter made a rating of the visuo-tactile brushing 'effectiveness'. This rating was from 0 to 100%, with 0% representing no match and 100% representing a complete match between the brushing on the participant's own hand and the hand image (in terms of brushing angle, pressure and timing).

3. Results

3.1. Proprioceptive drift magnitude (drift)

Overall, a high number of participants demonstrated significant levels of proprioceptive change (74% had a drift magnitude significantly greater than zero using one-sample *t*-tests with Bonferroni corrections for multiple comparisons).

Post-RHI error was subtracted from pre-RHI error to create the drift magnitude score (see Table[A] for pre and post raw scores). This score was used for our experimental comparisons as it represents the absolute value of change caused by the illusion. In both conditions, One-Sample *t*-tests showed drift magnitude was significantly greater than zero – indicating a change in felt location from actual position towards the hand image when the illusory shift was towards the body (In condition, $M = 1.31$, $SE = 0.30$; $t(21) = 4.38$, $p < .001$) and away from the body (Out condition, $M = 2.60$, $SE = 0.24$; $t(27) = 11.05$, $p < .001$)[b]. Thus proprioceptive drift was successfully created in both the In and Out conditions.

Footnote[b]: An alpha level of .05 was used as the significance criterion for all statistical tests. Bonferroni corrections for multiple comparisons were applied when required.

Table A approximately here

3.2. Subjective self-representation: RHI Questionnaire (RHIQ)

Total RHIQ Scores were quite low overall, i.e. close to 0, ‘neither agree nor disagree’ (In condition, *M* = .061, *SE* = .180; Out condition, *M* = .324, *SE* = .106) [range: -3 to +3]. Indeed, Independent *t*-tests revealed Total RHIQ was significantly greater than zero in the Out ($t(27) = 3.051$, $p = .005$) but not In conditions ($t(21) = .339$, $p = .738$).

Analysis of individual scale scores revealed this low value was caused by some scales receiving positive endorsement (i.e. ‘agreement’) and some negative endorsement (i.e. ‘disagreement’). Almost all the individual scales, however, received statistically significant endorsement. Qualitative endorsement (positive or negative) of scales was identical across conditions indicating high similarity in the *nature* of subjective RHI experience between conditions [see Figure[2]]. Participants in both conditions reported experiencing changes in embodiment [Embodiment], ownership [Ownership, Botvinick & Cohen (1998) Ownership] and perceived location [Location]. All participants reported the experience being positive [Affect] and no altered sensation in their hand [Sensation].

A mixed 2x11 ANOVA compared RHI direction (In vs. Out) and RHI questionnaire condition (11 scales). It revealed a significant main effect of questionnaire condition, $F(10, 480) = 65.12$, $p < .001$, demonstrating the varying levels of endorsement across the scales. The main effect of RHI direction was not significant, $F(1,48) = 1.82$, $p = .183$, suggesting levels of subjective illusion intensity were equivalent in the In and Out conditions. Therefore, contrary to predictions, we did not see a reduction in the overall level of RHI intensity when position was shifted away from the body-position (Out), compared to when it was shifted towards the real body location (In). The interaction of questionnaire condition and direction was also non-significant, $F(10,480) = .614$, $p = .802$.

Figure[2] approximately here

3.4. Relationship between subjective and proprioceptive RHI outcomes

The relationship between subjective and proprioceptive RHI outcomes within each condition was assessed separately using Pearson’s correlation coefficients (using Bonferroni corrections for multiple comparisons – 11 comparisons, 1 per scale).

Despite the non-significant difference between subjective RHI outcomes for In and Out conditions, the relationship between proprioceptive drift and subjective illusion *did* differ between conditions. There was a significant positive correlation between the RHIQ total score and drift magnitude in the In Condition ($r = .473$, $p = .026$), whereby as level of drift increased so did endorsement of the questionnaire. Importantly, no such relationship was seen in the Out Condition ($r = .144$, $p = .464$).

A Fisher *r*-to-*z* transformation was completed to compare the significance of the correlation between drift and RHIQ total between the In and Out conditions. A significant difference was found between the correlations in these two conditions, $z = 1.21$, $p > .05$ (using a two-tailed comparison). This demonstrates, the correlation in the In condition (which was significant), was significantly larger than the correlation in the Out condition (which was null).

This result is particularly interesting because it demonstrates that, despite the overall similarity in reported illusion intensity between conditions, there was a relationship between the amount of drift and the intensity of the illusion *only* when RHI was conducted towards the body.

Looking at the subscales, the Location scale correlated significantly with drift in the In ($r = .811$, $p = .027$) but not Out ($r = .508$, $p = .134$) condition suggesting subjective location change was associated with actual proprioceptive change. The Botvinick and Cohen (1998) scale also correlated with drift in the In (*r* = .412, *p* = .05) but not Out (*r* = .158, *p* = .432) condition which is consistent with previous studies employing the same measure (Botvinick & Cohen, 1998; Lenggenhager et al., 2007; Longo et al., 2008a). Various other subscales were approaching significance in the In condition but no subscales were related to drift in the Out condition [see Table[B]].

Previous studies have demonstrated that there is variation in the experience of the RHI across participants, with some experiencing it to a greater or lesser extent (Asai, Mao, Sugimori, & Tanno, 2011; Mussap & Salton, 2006; Peled, Ritsner, Hirschmann, Geva, & Modai, 2000). It was thought that the participants who were not affected by the illusion might be reducing variability in the total proprioceptive change score by the inclusion of their mean scores which would be consistently zero or close to zero centimetres change. This could potentially obscure the relationship between subjective and proprioceptive RHI outcomes. To address this, participants experiencing high levels of illusory position change were identified and analysed as a separate group.

Participants with mean drift magnitude falling in the top quartile (25%) of scores were selected (In [*N* = 7], *M* = 3.00, *SE* = 0.41; Out [*N* = 10], *M* = 3.96, *SE* = 0.83). Within this group, the correlation between drift magnitude and Total RHIQ subjective intensity was more strongly significant (compared with the whole sample) in the In condition (*r* = .831, *p* = .021) but remained non-significant in the Out Condition (*r* = .280, *p* = .260).

Once again, a Fisher *r*-to-*z* transformations with two-tailed comparisons demonstrated the significance of the correlation between drift and RHIQ total was significantly different in the In and Out conditions, *z* = 2.97, p < .05 (with the In correlation being larger than the Out).

Also within the high-drift group, Pearson correlation statistics (corrected for multiple comparisons) showed a number of additional RHIQ subscales (Embodiment, Ownership and Sensation) became correlated with drift in the In condition though all correlations remained non-significant in the Out condition [see Table[B]].

Overall, in the In condition a relationship was seen between proprioceptive drift and, not only the RHIQ Total scale, but also a number of subscales. In the Out condition, however, there was no relationship between the amount of subjective RHI – total or scales – and drift magnitude.

Table B approximately here#

3.5. Similarity in appearance ratings

General rating statistics

Appearance scores ranged from 1 to 8 in the In Condition and 1 to 10 in Out [full range, 1 to 10] with low overall means (i.e. close to 5, ‘neither similar nor dissimilar’) in both conditions (In, *M* = 5.54, *SE* = 0.41; Out, *M* = 5.18, *SE* = 0.45). Independent-Groups *t*-tests revealed there were no significant differences in appearance ratings between In and Out conditions, *t*(48) = -.58, *p* = .565.

Relationship between appearance ratings, subjective illusion and proprioceptive drift

Pearson’s Correlation Coefficients demonstrated there was no evidence of an association between appearance ratings and drift magnitude (In, *r* = .035, *p* = .877; Out, *r* = .052, *p* = .791) or RHIQ total (In, *r* = .306, *p* = .166; Out, *r* =.249, *p* = .202) in either the In or Out conditions. This was in line with predictions in so far as proprioceptive change had no effect on visual perception of the rubber hand. Contrary to predictions, however, the relationship between similarity in appearance ratings and subjective illusion intensity seen in Longo et al. (2008a) was not demonstrated in this experimental context.

Subjective vs. objective perceptions of appearance similarity

Appearance ratings were analysed for their relationship with experimenter ratings of skin-tone and gender. This was done to assess whether participant's ratings of appearance matched these more objective markers of appearance. One-Way ANOVA tests (one per RHI direction condition) revealed there were no significant differences in appearance ratings between individuals with light (e.g. Caucasian), medium (e.g. Asian) or darker (e.g. African) skin-tone in either condition (In, $F(2) = 1.50$, $p = .249$; Out, $F(2) = 0.03$, $p = .969$), meaning actual differences in hand appearance (in terms of colour) had no effect on similarity ratings. Females reported higher ratings of similarity in appearance than males in the Out condition (Females, $M = 6.16$, $SE = .47$; Males, $M = 4.22$, $SE = .64$; $t(26) = -2.39$, $p = .024$) but not the In condition (Females, $M = 5.64$, SE = .66; Males, $M = 4.73$, $SE = .60$; $t(20) = -1.01$, $p = .324$)[c]. Therefore, only in the Out condition did gender – an objective marker of appearance similarity (in terms of size, skin-texture and hair-coverage) correlate with appearance scores. Overall, it appeared that objective similarity in appearance was not related to ratings of appearance similarity.

Footnote[c]: The hand image used was a set of Caucasian, female hands. Nails were cut short to reduce the impact of this gender-defining appearance feature, making the hands somewhat more gender-neutral.

3.6. Similarity in felt brushing ratings

General rating statistics

Unlike appearance ratings, brushing ratings were quite high, ranging from 4 to 10 with a mean of 8.55 ($SE = 0.33$) in the In condition, and from 7 to 10, mean 9.07 ($SE = 0.16$) in the Out condition. Brushing ratings were significantly higher than appearance ratings in both In ($t(21) = -6.41$, $p < .001$) and Out ($t(27) = -8.13$, $p < .001$). There were no significant differences in overall ratings of brushing similarity between conditions, $t(48) = -1.418$, $p = .166$. The data suggest that overall participants in both conditions felt the tactile stimulation they felt on their own hand matched that seen on the rubber hand.

Relationship between brushing ratings, subjective illusion and proprioceptive drift

We then investigated whether RHI outcomes were related to the participant's perceived effectiveness of the visuo-tactile manipulation. As with appearance ratings, Pearson Correlation Coefficients demonstrated a non-significant relationship between drift magnitude and brushing in the In ($r = .142$, $p = .529$) and Out conditions ($r = .236$, $p = .228$). Felt shifts in location (proprioceptive alterations) did not alter tactile perception. In the In condition, brushing correlated significantly with RHIQ total ($r = .428$, $p = .047$): as subjective illusion intensity increased, so did the perceived similarity between brushing *seen* on the rubber hand and that *felt* on the participant's own hand. There was no such relationship between RHIQ total and brushing ($r = .170$, $p = .386$) in the Out condition supporting an alteration in the nature of subjective RHI experience when top-down body information was violated.

Subjective vs. objective perceptions of brushing similarity

Experimenter ratings of RHI brushing precision were analysed. Trial scores were averaged to produce an overall score for each participant. Brushing precision was deemed to be high (In, *M* = 96.82%, *SE* = 2.41; Out, *M* = 94.64%, *SE* = 1.96) and did not differ significantly across In-Out condition, $t(48) = .709$, $p = .482$. Though this measure relies on human judgement and therefore potentially susceptible to situational fluctuations, the experimenter was blind to levels of subjective and proprioceptive RHI levels which reduced the likelihood of experimenter bias confounds.

4. Discussion

4.1. Subjective and proprioceptive aspects of body representation are differentially affected by top-down factors

4.1.1. Evidence from our experiment

In the current study, we used the rubber hand illusion to create a mismatch between higher-order information about body position and body information generated by the senses. This was done by drawing felt position *away* from the veridical body position towards extracorporeal space (RHI Out condition). Subjective and proprioceptive components of self-representation were compared between this condition and a condition of traditional RHI where limb position was drawn towards the actual body position (RHI In condition).

We found two important patterns in the data. First, subjective and proprioceptive components of self-representation are distinct. Second, they are also differentially affected by top-down factors. While we were able to produce proprioceptive drift in both conditions consistently, incongruent information about body position in the Out condition modulated subjective RHI outcomes. This was most clearly demonstrated when the significant correlation between subjective and proprioceptive outcomes, found in the RHI In condition, was abolished in the Out condition.

When looking at the high proprioceptive illusion group alone, this relationship became even more evident with a much stronger correlation between subjective and proprioceptive RHI outcomes in the In condition. Analysis of the questionnaire subscales provided more detailed information about the exact nature of subjective RHI experience. We saw items assessing subjective perceptions of hand location change (Location scale) were highly related to *actual* location change (drift). The Botvinick and Cohen (1998) Ownership scale also correlated highly with proprioceptive outcomes in the In condition suggesting felt ownership of the hand was associated with drift magnitude. This finding is consistent with various previous studies that incorporated this scale in their measure of subjective RHI (Botvinick & Cohen, 1998; Lenggenhager et al., 2007; Longo et al., 2008a) supporting the validity of our RHI Total scale. Overall it appears that for movements towards the body, proprioceptive recalibration is associated with the level of change in subjective bodily experience. More specifically, as embodiment and ownership increase for the rubber hand so does the level of drift. In opposition to this, when perceived location is shifted away from the body, there is no associated change in subjective self-representation – rather the levels vary independently.

Consistent with this, in the In condition, a significant positive correlation was found between subjective RHI and self-rated similarity in tactile perceptions – in that participants reporting high levels of subjective embodiment of the hand image perceived a greater match between tactile sensations administered to the hand image and those felt on their own hand. This relationship, however, also became non-significant in the Out condition. We propose this too demonstrates the alteration of subjective embodiment of the hand image by top-down factors.

This finding adds to the new but growing body of evidence (Holle et al., 2011; Kammers et al., 2008; Rohde et al., 2011) that human self-representation consists of a number of distinct processes subserved by separate neural systems. Neurophysiological studies demonstrate the role of the inferior parietal lobule (IPL) in localising the body and body parts (Ogawa & Inui, 2007a; Ogden, 1985) and in the recalibration of limb position in the RHI (Kammers et. al., 2008; Tsakiris et al., 2007) suggesting this may be the location of body-perception systems.

Subjective body-representation on the other hand is thought to be subserved by a system encompassing ventral premotor (PMv) and cerebellar areas (Ehrsson et al., 2005; Ehrsson et al., 2004). These areas detect concurrent multisensory inputs arising from the body and integrate them to produce self-identification over the object of stimulation, subsequently producing the special perceptual experience of that object belonging to the *self* (Botvinick & Cohen, 1998; Ehrsson et al., 2005; Ehrsson et al., 2004; Tsakiris et al., 2008) – as quantified by subjective RHI measures.

While they are indeed independent constructs, many studies (including ours) have found subjective and proprioceptive RHI measures to covary. We believe this correlation most likely reflects the function of a remote common mechanism that determines susceptibility to both forms of RHI outcome, rather than a direct causative relationship as was once thought. Rohde et al. (2011) propose a strong reliance on vision in body judgements might lead to both increased visuo-proprioceptive recalibration (drift) and intermodal matching of visual and tactile inputs causing felt ownership. Thus, levels of subjective and proprioceptive outcomes would covary without directly causally affecting each other. In the light of this dissociation, relationships between other components of self-representation that are assumed to be causative (e.g. physiological RHI outcomes that are hypothesised to be caused by changes in subjective ownership) may require further exploration.

Representation of self – the role of the posterior parietal cortex

The representation of self is a complicated and multifaceted process. The RHI is a neat paradigm that can easily and quickly manipulate two particular aspects of self-representation – subjective ownership and embodiment as well as proprioceptive position. As mentioned previously, these alterations have been demonstrated to critically be subserved by the PMv and IPL respectively. In the same way as these two RHI outcomes cannot be said to represent the entire spectrum of the human experience of 'selfhood' we do not suggest here that these two brain areas support the entirety of self-representation.

One area that must be mentioned in a discussion of self-representation is the posterior parietal cortex which is critically involved in multisensory coding of body part position [in non-human primates] (Graziano, Cooke, & Taylor, 2000), recursive recalculation and updating of the current body state from sensory and motor signals (Wolpert, Goodbody, & Husain, 1998), the storage of multiple internal reference frames for the encoding and use of sensory information (Bernier & Grafton, 2010), monitoring internal versus externally generated actions (Ogawa & Inui, 2007b) and – in non-human primates – the alteration of the body schema to incorporate external objects, such as tools (Iriki, Tanaka, & Iwamura, 1996).

4.1.2. Implications for existing theories of the effects of top-down factors on self-representation

Tsakiris and colleagues (2010) developed a two-step model of self-representation to explain the interaction of top-down and bottom-up processes in the identification of an object as *self*. First, visual inputs are matched with stored information about the body. If there is a sufficient fit with this internal body image then inputs are assessed for intermodal matching, with a match leading to integration of this object into the self-image.

Our data suggest that this model is valid but may apply only to subjective self-representation. We propose that subjective bodily experience is dependent on processes of intermodal matching and requires consistency between internal and sensory information about the body (as described above). In contrast, our results suggest proprioceptive self-representation is not affected by higher-order cognitive factors. Consistent with this idea, Holle et al. (2011) were able to produce drift to a hand placed in an anatomically impossible position (thereby violating top-down body information) without felt ownership over this hand. They provided evidence that two previous studies reporting an 'attenuation' of drift to rotated limbs (Costantini & Haggard, 2007; Tsakiris & Haggard, 2005) were simply lacking in power to detect this small effect size due to insufficient sample sizes. Indeed, also contrary to traditional theories, it is becoming increasingly clear that intermodal matching is not necessary for the production of proprioceptive drift. This is supported by various studies that demonstrate drift under conditions of asynchronous stimulation (Rohde et al, 2011) or even in the *absence* of tactile stimulation all-together (Durgin, Evans, Dunphy, Klostermann, & Simmons, 2007; Rohde et al., 2011).

The robust nature of proprioceptive RHI outcomes is likely due to the simple, bottom-up mechanism that governs bodily perception. Rohde et al. (2011) suggest alterations in perceptual body position (proprioceptive drift) in the RHI occurs as a result of visuo-proprioceptive recalibration where felt position is drawn to match the false visual information about position provided by the rubber hand.

'RHI susceptibility' should be considered separately for subjective and proprioceptive outcomes

'RHI susceptibility' refers to the ability to experience the illusory effect of the RHI. Analysing the prevalence of RHI effects in different groups and under different experimental conditions can reveal important information about the necessary and sufficient conditions required to manipulate human bodily experience. We suggest that consideration of RHI outcomes as a unitary phenomenon in the past may have lead to misrepresentation of this susceptibility in the literature. Often, due to the assumed causative relationship, estimates are based on one measure (subjective *or* proprioceptive) alone and these terms are used interchangeably or combined into a blanket representation of both outcomes (Costantini & Haggard, 2007; Kammers et al., 2008; Tsakiris & Haggard, 2005).

If proprioceptive alterations in the RHI *are* simply a product of an intersensory bias that is common to all perceptual systems than drift towards the rubber hand should occur whenever false visual information about the hand position is presented. Consistent with this idea, our study found the majority (75%) of individuals showed levels of drift significantly greater than zero. If drift is as ubiquitous as we believe, 'non-significant drift' (in our study and others) may simply be caused by experimental power that is too low to detect a small (but extant) effect.

A number of pathological groups have been identified as having altered susceptibility to the RHI in terms of intensity and time to onset of illusion. In some groups predisposition to the illusion is **increased**, as in individuals with schizophrenia (Peled et al., 2000), schizotypal personalities (Asai et al., 2011), eating disorders, particularly bulimia (Fiehler, Burke, Engel, Bien, & Rösler, 2008; Mussap & Salton, 2006), and dissociation disorder (Kanayama, Sato, & Ohira, 2007); and in some groups, **reduced**, such as those on the Autistic spectrum (Cascio, Foss-Feig, Burnette, Heacock, & Cosby, 2012). Various theories have been put forward for altered RHI experience within these groups including increased malleability of body-representation (in eating disordered individuals, Mussap & Salton, 2006), altered functional connectivity (in schizophrenics, Peled et al., 2000) and either an over-reliance on proprioceptive inputs or under-reliance on visual information (in those with autism spectrum disorder, Cascio et al., 2012).

Investigating susceptibility to subjective and proprioceptive RHI outcomes separately could provide much more specific information about the nature of body representation deficits in clinical groups than considering them together. For example, selective alterations in proprioceptive drift with the sparing of subjective embodiment and ownership may indicate an aberration in the weighting of sensory information in bodily judgements in the IPL. Specific modulation of subjective representation however could indicate a fault in intermodal matching systems in the PMv, or an alteration in the effect of higher-order cognitive factors on multisensory systems. A bimodal RHI susceptibility measure would have great utility within the field of psychopathy.

4.2. Production of drift away from the body location demonstrates proprioceptive change in the RHI is more than an attentional bias to central space

To our knowledge, this study is the first of its kind to successfully produce alterations in perceived limb position (i.e. proprioceptive drift) *away* from the body into extracorporeal space using the RHI. Given that drift had previously been created exclusively towards the body, it was impossible to know whether some, if not all, of the change previously attributed to the RHI manipulation was actually a product of a bias towards central space or natural position recalibration (not caused by the illusion).

Humans are known to have a strong attentional bias to the visual space where most manual behaviours occur, central peripersonal space (Downing & Peelen, 2011; Lloyd, Azañón, & Poliakoff, 2010; Losier & Klein, 2004). It has been suggested that in the absence of visual information felt limb position shifts in towards the body midline when the hand is kept still (Beers, Sittig, & Denier van der Gon, 1998; Ghilardi, Gordon, & Ghez, 1995; van Beers et al., 1999) and during action execution (Holmes et al., 2006) [though, see Desmurget, Vindras, Grea, Viviani (2000) who found no proprioceptive drift over time].

From these results, it could be inferred that proprioceptive change towards the body documented in RHI experiments could simply have resulted from a reduction in the ability to localise limb position (due either to lack of visual position information and/or the degradation in kinaesthetic cues due to the limb being held still over the RHI induction). The production of drift in *and* out from the body in our study demonstrates it is possible to draw felt position away from the body and supports the productive role of RHI induction in such perceptual alterations.

Interestingly, a number of disorders affecting body representation involve a shift of self-location *away* from the actual body position. These include Out of Body Experiences (and other Autoscopic Hallucinations) where the individual feels their *self* is located outside their body (Blanke & Arzy, 2005; Blanke et al., 2004) and somatoparaphrenia, where a body-part or whole side of the body is attributed *away* from the participant onto another individual (Feinberg, Venneri, Simone, Fan, & Northoff, 2010; Losada-Del Pozo et al., 2011; Vallar & Ronchi, 2009). Similarities between these disorders and the strange perceptual alterations in RHI suggest a common mechanism of multisensory integration may underlie these various disruptions of self-representation.

4.3. Subjective-embodiment can alter perceptions of touch in line with expectations

Self-representation is especially important to the experience of touch because the body forms part of the tactile experience (de Vignemont, Ehrsson, & Haggard, 2005). In the current study we found evidence that incorporation of a false hand into the self-representation can alter perception of tactile inputs on the participant's own hand, whereby felt touch on the own hand is assimilated to match seen touch on the false hand. We found that participants with high levels of subjective illusion had significantly higher ratings of matching between tactile inputs seen on the 'rubber' hand image and those felt on their own hand, compared to those experiencing low subjective illusion – even though no such differences actually existed (as determined by analysis of variations in actual tactile inputs using experimenter ratings of brushing effectiveness [see Methods, section 2.7]). This indicates that perception of tactile inputs was independent of actual variation in brushing administration. We propose that if actual tactile similarity did not affect the perceived similarity, then this is most likely caused by the incorporation of the seen hand into the body representation.

The modulation of tactile perception by visual information is supported by other experiments that demonstrate perceptions in one modality can be skewed to match information from another modality. For example, double-flash experiments where an illusory flash in a visual stimulus is caused by bursts of auditory noise (Shams, Kamitani, & Shimojo, 2002). In the opposite direction, the modulatory effect of vision on auditory perception has been well established in ventriloquist effect studies (Haans, Kaiser, Bouwhuis, & Ijsselsteijn, 2012; Shams et al., 2002) and McGurk experiments (McGurk & Macdonald, 1976).

Unlike subjective outcomes, the association of proprioceptive outcomes and brushing ratings was non-significant. This is further support for the dissociation of these two components of self-representation. It also demonstrates shifting felt position to match illusory visual position does not affect bodily perceptions in the same way as altering subjective ownership over that limb.

Previous research has demonstrated vision of the body can alter the perception of tactile inputs. For example, vision of a participants hand enhances tactile discrimination on that hand (Visual Enhancement of Touch, or VET) (Kennett, Taylor-Clarke, & Haggard, 2001; Taylor-Clarke, Kennett, & Haggard, 2002) even when this vision is non-informative. More recently Longo, Betti, Aglioti and Haggard (2009) demonstrated that it is perception of the *own* body not just *any* body that modulates tactile acuity.

While these studies demonstrate improvement of tactile perception by vision of the own body (Kennett et al., 2001; Taylor-Clarke et al., 2002), our results indicate reduced detection of tactile inputs on the body. This may be because in our study participants were provided with a visual input that aims to override tactile experience where VET studies simply provide a still image of the body – thus no alternate stimulus to skew perception. Regardless of whether vision of the body increases or decreases acuity of tactile perception, the results of these various studies demonstrate the critical role of visual information in tactile perception.

Akin to our results similar reductions in the influence of tactile inputs on perception by vision of the body have been seen in pain research. Looking at your own body while being exposed to a painful stimulus reduces both self-reported intensity <u>and</u> neural indicators of pain (Longo, Betti, et al., 2009). Interestingly, this analgesic effect is intensified when participants view an enlarged image of their hand and is reduced by a hand image smaller than veridical size (Mancini, Longo, Kammers, & Haggard, 2011).

Contrary to predictions, our study did not produce a significant relationship between subjective RHI and perceived similarity in appearance as was found by the Longo group (2009). We believe this may be because our experimental methodology altered the nature of subjective RHI experience in a way that affected this relationship. Specifically, endorsement of the Embodiment subscale was somewhat reduced in our study compared with levels in the Longo et al. (2009) study. They found this particular scale to be critically important in producing the relationship between similarity in appearance ratings and subjective illusion.

Along a different vein, this non-significant result may have been related to the phrasing of the similarity in appearance question itself. As mentioned previously, the goodness-of-fit model that compares sensory information about the body to the body image (Tsakiris, 2010) appears not to be fully specified, with some aspects of appearance affecting RHI outcomes (such as size of the hand; Pavani & Zampini, 2007) but not others (like skin colour; Farmer, Tajadura-Jimenez, & Tsakiris, 2012). Splitting the similarity in appearance question into a number of questions that independently assess these categories of appearance may reveal differences not found with our more generalised question.

4.4. Limitations of the current study

While this study provides interesting insights into the nature of top-down effects on different aspects of body-representation, one limitation that should be addressed is that other measures of proprioceptive change than the kind used here may produce different results. We employed an estimation of body position that required participants to report aloud which number on a ruler best corresponded with the position of their hidden middle finger while their hands were kept still. Other studies have utilised active estimations of body location such as intermanual reaches (Botvinick & Cohen, 1998) or reach-to-target actions (Heed et al., 2011). Evidence has recently been brought forward that suggests these different proprioceptive RHI measures are supported by different neural systems and therefore may be affected differently by RHI induction. For example, Kammers and colleagues (2009) found that immediate proprioceptive judgements of hand location are modified by rTMS over the IPL but subjective ownership over the rubber hand and ballistic motor movements are not (Kammers et al., 2009). Future experiments may include a variety of position estimations, such as action based pointing measures, to allow a more complete picture of the effect of higher-order cognitive factors on multisensory perceptual illusions.

4.5. Summary and conclusions

Human self-representation is a complex process critically dependent on systems of multisensory integration. It is becoming clear that self-representation consists of several distinct components, with neural circuits in the PMv supporting subjective, first-person bodily experience and the IPL underpinning proprioceptive body judgements and location of the self in space.

Our study suggests that these separate components are affected differentially by higher-order cognitive factors. Subjective bodily experience is sensitive to mismatch between internally stored information about the body state and information generated by the senses while body perception, as a simple sensory phenomenon, is relatively robust to such violations. We used the RHI to draw limb location away from the veridical body location into space, thereby supporting the role of the illusion in creating position change over the effects of attentional biases or natural proprioceptive recalibration towards central space. Finally, we found that incorporation of a hand image into self-representation can alter perception of tactile inputs, assimilating felt touch in line with visual touch information.

In conclusion, while original theories regarding the neural mechanisms underpinning the RHI require revision, this paradigm useful tool for navigating the complexities of human bodily experience.

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Footnotes

Footnote A

Footnote[a]. Sample questions for each of the five separate components of subjective self-representation as described by Longo et al. (2008a)
Embodiment: "It seemed like the hand image was part of my body" (Q3)
Loss of Own Hand: "It seemed like my hand disappeared" (Q16)
Movement: "It seemed like my hand was moving towards the hand image" (Q18)
Affect: "I found the experience enjoyable" (Q20)
Sensation: "I had the sensation of pins and needles in my hand" (Q22)

Footnote B

Footnote[b]: An alpha level of .05 was used as the significance criterion for all statistical tests. Bonferroni corrections for multiple comparisons were applied where necessary.

Footnote C

Footnote[c]: The hand image used was a set of Caucasian, female hands. Nails were cut short to reduce the impact of this gender-defining appearance feature, making the hands somewhat more gender-neutral.

Tables

Table A. Proprioceptive judgements for the In and Out conditions. Pre-RHI error refers to the estimation of hand position before the RHI induction, Post-RHI the estimate taken directly after RHI induction. Pre was subtracted from Post-RHI error to create a difference score, called Drift Magnitude, representing proprioceptive change resulting from the illusion.

	In Condition	Out Condition
Pre-RHI error	*M* = 2.62	*M* = 3.83
	SE = 0.37	*SE* = 0.47
Post-RHI error	*M* = 3.94	*M* = 6.43
	SE = 0.38	*SE* = 0.38
Drift Magnitude	*M* = 1.31	*M* = 2.60
	SE = 0.30	*SE* = 0.24

Table B. Pearson's Correlation Coefficients for the relationship between subjective (RHI Questionnaire Total and scales) and proprioceptive (Drift Magnitude) RHI outcomes. These are listed for the sample as a whole (left columns) and for the 'high drift group' [top quartile of Drift Magnitude scores] (right columns) alone.

		Whole sample Correlation with Drift Magnitude		**High drift group** Correlation with Drift Magnitude				**Whole sample** Correlation with Drift Magnitude		**High drift group** Correlation with Drift Magnitude	
Condition		In	Out	In	Out	**Condition**		In	Out	In	Out
RHI Total	***r***	**0.473**	**0.144**	**0.831**	**0.391**						
	p	**0.026**	**0.464**	**0.021**	**0.264**						
Embodiment	*r*	0.387	0.205	0.771	0.373	Movement	*r*	0.225	0.203	0.378	0.18
	p	0.075	0.296	0.042	0.289		*p*	0.314	0.3	0.403	0.619
Ownership	*r*	0.4	0.198	0.859	0.372	Affect	*r*	0.325	-0.014	0.558	0.053
(Embodiment Subscale)	*p*	0.065	0.312	0.013	0.29		*p*	0.141	0.943	0.193	0.885
Location	*r*	0.457	0.19	0.811	0.508	Sensation	*r*	0.109	-0.066	0.766	0.392
(Embodiment Subscale)	*p*	0.032	0.333	0.027	0.134		*p*	0.63	0.738	0.045	0.263
Agency	*r*	0.054	-0.03	0.47	-0.203	Supernumerary Limb	*r*	0.237	-0.359	-0.056	-0.179
(Embodiment Subscale)	*p*	0.81	0.881	0.287	0.574		*p*	0.289	0.061	0.904	0.621
Loss of Hand	*r*	0.41	0.177	0.062	0.113	Botvinick & Cohen	*r*	0.412	0.158	0.693	0.427
	p	0.058	0.367	0.895	0.757	Ownership	*p*	0.050	0.423	0.084	0.218

Figure

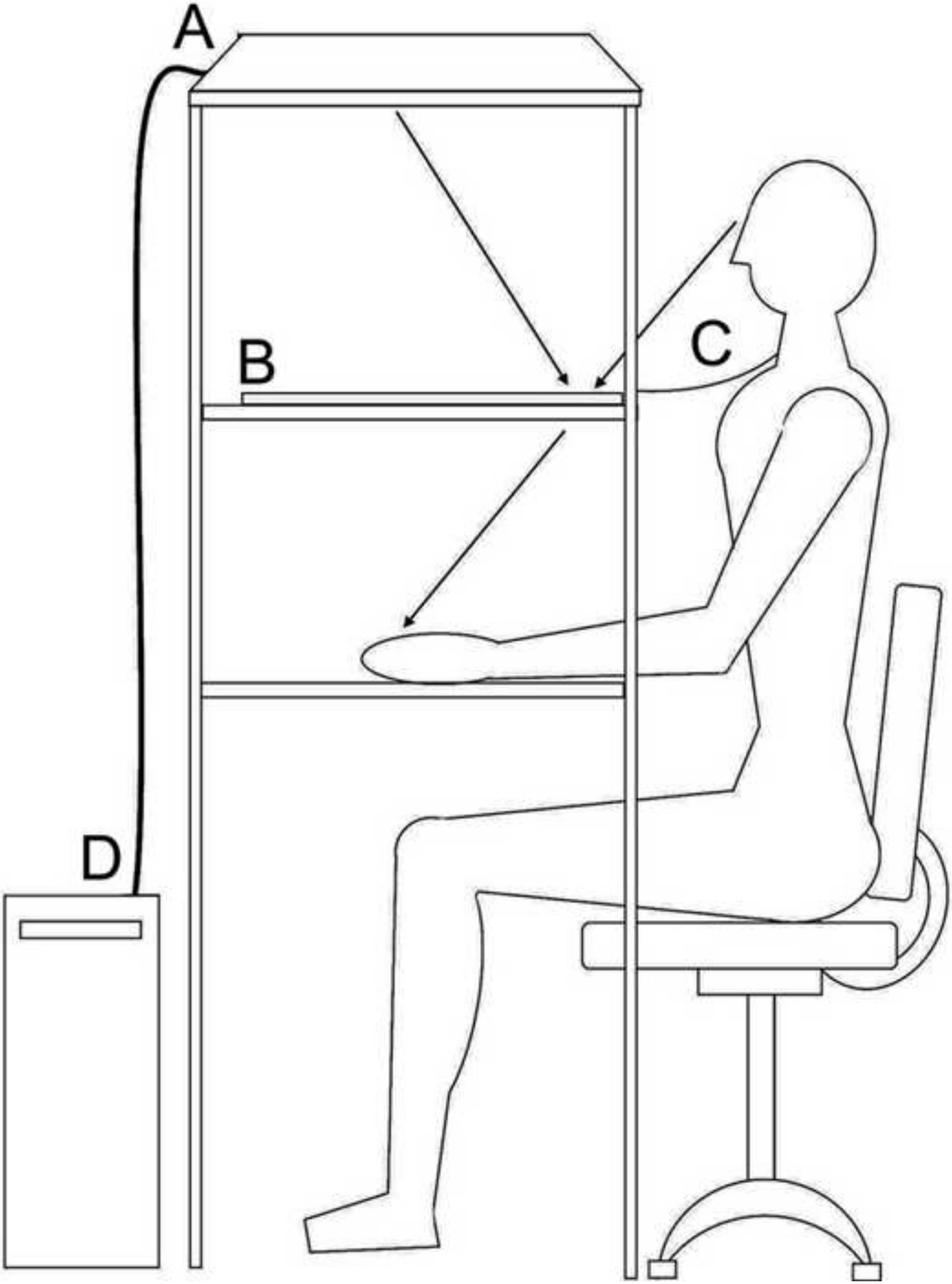
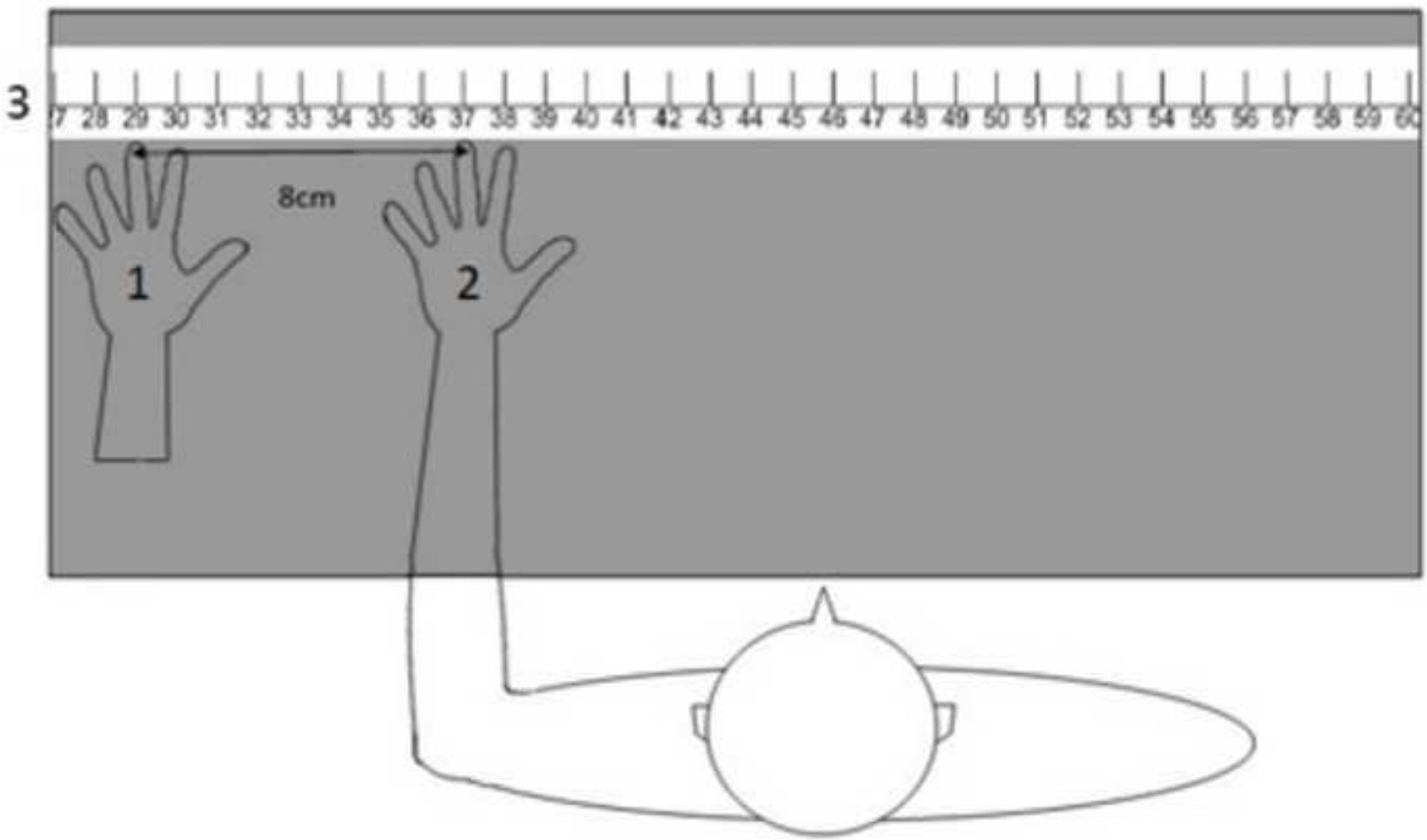


Figure
Click here to download high resolution image



Figure
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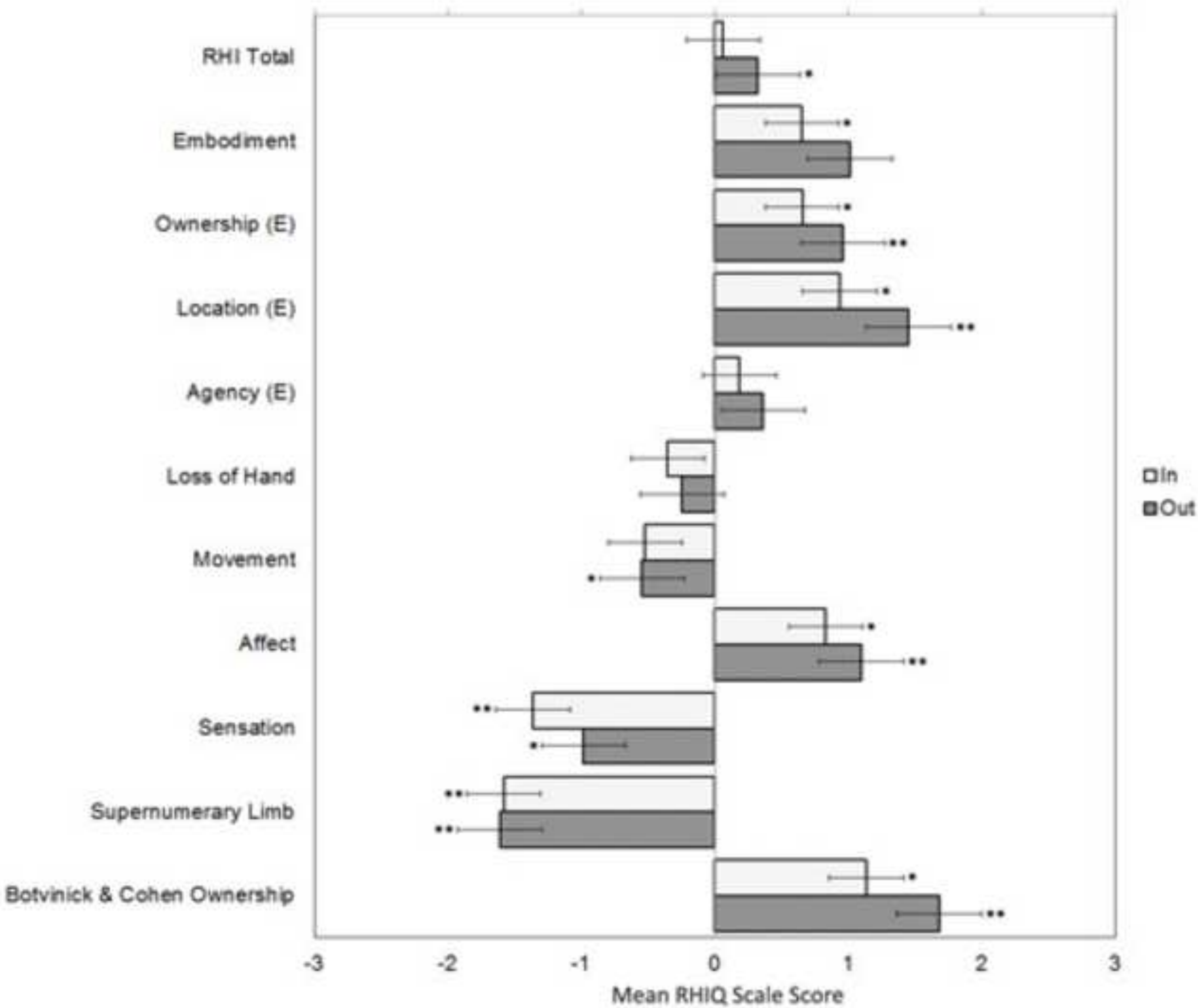

Figure

Figure Captions

Figure[1a]. Schematic of experimental apparatus for RHI induction. A. Computer monitor, B. Mirror for reflection of hand image stimuli (presented on screen (A) above, C. Cloth draped over subject's shoulders to prevent visual information about arm/ body position, D. Computer tower

Figure[1b]. Representation of the locations of the real hand and hand image ['1' & '2']. In the RHI In condition the subject's hand was positioned at location '1' and the hand image appeared on the computer screen at '2'(8cm apart) so the direction of illusory location change was in, towards the body. Positions were swapped in the Out condition so the subject's hand was at '2' and the hand image appeared at '1 [as seen in Figure 1[b] above]'. '3' represents the location at which the ruler for proprioceptive estimation appeared on the computer screen – one of a set of 15 rulers was randomly selected to appear in this position.

*Figure[2]. Mean endorsement of RHI Questionnaire Total and Scale Scores for the In [light grey bars] and Out [dark grey bars] conditions. Bars projecting to the right represent positive endorsement of that scale. Projections to the left represent negative endorsement. Asterisks represent comparison of mean scale score with zero (using t-tests with Bonferroni corrections for multiple-comparisons), * indicates significance at or below .05 alpha and ** indicates significance at or below .001.*

Supplementary Material

Click here to download Supplementary Material: Supplementary Materials, item A. Assessment of subjective self-representation