When I touch my hand it touches me back:
An investigation of the illusion of self-touch

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Thesis submitted for the degree of Doctor of Philosophy
Trinity Term 2011

ACKNOWLEDGEMENTS

Heartfelt thanks to my supervisors Dr Anne Aimola Davies and Professor Martin Davies.
It is a privilege to work with a supervisor who is as inspirational, passionate, interesting, dedicated, and supportive as Anne. I am forever grateful for the rich and intellectually-stimulating learning environment that Anne creates for her students. I am also indebted to Martin, who has always provided a unique perspective on the work in this thesis, as well as endless support and encouragement. The opportunity to work with such a dynamic and brilliant team – Anne and Martin – is one of the most valuable gifts any student can be given, and I have never taken this opportunity for granted.

Thank you to Professor Kim Plunkett and the members of the Baby Lab for providing a friendly and stimulating space in which to work. Thank you also to Professor Brian Rogers who has been very supportive during my DPhil.

For financial support, I am grateful to Oxford University Press (OUP) and the Clarendon Fund, without whom I would not have had the opportunity to undertake doctoral studies in Oxford.

I am also very grateful for the support provided by Corpus Christi College. In my mind, it is one of the most beautiful, friendly, and intimate colleges in Oxford, and I consider myself very privileged to have been a member during my DPhil.

Thank you to Professor Udo Kischka who sparked my interest in the phenomenon of self-touch enhancement following stroke, and went on to facilitate the patient work at the Oxford Centre for Enablement. Thank you also to the patients (NG, CJ, SM, CA, and SK) who took part in the studies presented in Chapters 2 and 3. I am so grateful for your enthusiasm, and I thank you for being so generous with your time. Likewise I am very grateful to the participants who took part in the studies presented in Chapters 4 through 8.

Finally, a huge thank you to my Mum and Dad, who support me in everything I do – there are no words to express my appreciation for all that you have done for me; Elisabeth, James and Andrew, who make me one very lucky sister; Sue and Chris, for your encouragement and support; and Nick, who is the kindest, most encouraging, funny, and supportive person I know.

PUBLICATIONS ARISING FROM THIS THESIS

Portions of this thesis appear in the following publications:

Aimola Davies, A. M., & White, R. C (2011). Touching my face with my supernumerary hand: A cheeky illusion. *Perception, 40*, 1245-1247.

Aimola Davies, A. M., & White, R. C. A *sensation*al illusion: Vision-touch synaesthesia and the rubber hand paradigm. *Cortex.* Accepted 25 January 2012.

Aimola Davies, A.M., White, R.C., & Davies, M. (Submitted Manuscript). Spatial limits on the illusion of self-touch.

Aimola Davies, A. M., White, R. C., Thew, G., Aimola, N. M. V., & Davies, M. (2010). Visual capture of action, experience of ownership and the illusion of self touch: A new rubber hand paradigm. *Perception, 39*, 830-838.

White, R. C., & Aimola Davies, A. M. (2011). Touching my left elbow: The anatomical structure of the body affects the illusion of self-touch. *Perception, 40*, 95-98.

White, R. C., Aimola Davies, A. M., & Davies, M. (2011). Two hands are better than one: A new assessment method and a new interpretation of the non-visual illusion of self-touch. *Consciousness and Cognition, 20*, 956-964.

White, R. C., Aimola Davies, A. M., Halleen, T. J., & Davies, M. (2010). Tactile expectations and the perception of self touch: An investigation using the rubber hand paradigm. *Consciousness and Cognition, 19*, 505-519.

White, R. C., Aimola Davies, A. M., & Kischka, U. (2010). Errors of somatosensory localisation in a patient with right hemisphere stroke. *Neurocase, 16*, 238-258.

White, R. C., Aimola Davies, A. M., Kischka, U., & Davies, M. (2010). Touch and Feel? Using the rubber hand paradigm to investigate self-touch enhancement in right-hemisphere stroke patients. *Neuropsychologia*, *48*, 26-37.

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SHORT ABSTRACT

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Following stroke, a patient may fail to report touch administered by another person but claim that s/he feels touch when it is self-administered. In Part One, the self-touch rubber hand paradigm was used to investigate different explanations for this phenomenon, termed self-touch enhancement. The most important finding was that patients reported touch based on feeling rather than by using proprioceptive information. Some patients have residual sensation that could be targeted in sensory rehabilitation.

Part Two is a systematic investigation of the illusion of self-touch conducted with neurologically healthy participants. Participants used the right hand to administer touch to a prosthetic hand while the left (receptive) hand, positioned 15 cm from the prosthetic hand, received Examiner-administered touch. Proprioceptively perceived position of the administering and receptive hand was measured. Most participants experienced the single event of self-touch at the location of the receptive hand. Previous investigations have relied on measurement of only one hand and have concluded that participants experience self-touch at the location of the prosthetic hand. Our findings have implications for the role of ownership in this illusion.

There is also a series of experiments in Part Two which test four potential constraints on the illusion of self-touch – violated expectations about the object that is administering touch, increased distance between the hands, alignment mismatch, and anatomical implausibility. For example, one study uses a novel paradigm to demonstrate that, although the subjective intensity of the illusion of self-touch is diminished by anatomical implausibility, most participants report the impossible experience of touching their left elbow with their own left index finger. Taken together, these experiments highlight the malleability of body representation, and provide a comprehensive framework for understanding the illusion of self-touch.

LONG ABSTRACT

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The thesis had two main aims. The first aim was to use the self-touch rubber hand paradigm to investigate self-touch enhancement in patients following stroke. The second aim was to provide a systematic investigation of the constraints on the illusion of self-touch. The thesis achieved these two main aims, and during the course of the project, unexpected findings inspired additional experiments and new lines of enquiry. Most notably, during the investigation of the constraints on the illusion of self-touch, a new interpretation for how the participant experiences the illusion came to light. This interpretation was followed up in two experiments that were not anticipated in the original plan of research. The long abstract begins with a description of the experimental paradigm and then moves to an overview of the empirical chapters. The overview groups the different chapters by topic; first, the chapters that investigated self-touch enhancement following stroke (Chapters 2 and 3); second, the chapters that provided a new interpretation of the illusion of self-touch (Chapters 4, 5, and 6); and third, the chapters that investigated the constraints on the illusion of self-touch (Chapters 4, 7, and 8).

The experiments presented in this thesis used the self-touch rubber hand paradigm (Ehrsson, Holmes, & Passingham, 2005). In the self-touch rubber hand paradigm, the Examiner guides the participant's right hand to administer stimulation to a prosthetic hand, and at the same time, the Examiner administers stimulation to the participant's receptive left hand. (Note that the paradigm can be implemented using the converse set-up; the participant's left hand administers touch and the participant's right hand receives touch.) Participants tested with this paradigm experience the

compelling illusion that they are touching their own hand; they experience the action of the administering hand and the sensation on the receptive hand as belonging to a single event of self-touch. Prior to this thesis, the self-touch rubber hand paradigm had not been used with a patient population.

In the experiments presented in Chapters 2 and 3, the self-touch rubber hand paradigm was used to investigate sensation in patients who had experienced a right-hemisphere stroke. Following stroke, patients may fail to report touch when it is administered by another person, but they may claim that they feel touch when it is self-administered. This effect, termed *self-touch enhancement*, has been investigated in only two previous research programmes (Valentini, Kischka, & Halligan, 2008; Weiskrantz & Zhang, 1987). Chapter 2 presents experiments conducted with five patients. Four of the five patients were impaired at detecting touch from the Examiner, but showed significantly better detection when touch was self-administered; that is, these patients demonstrated self-touch enhancement. A series of experiments used the self-touch rubber hand paradigm to investigate explanations for self-touch enhancement: (1) proprioceptive information from the administering hand, (2) attentional modulation at the spatial region of the administering hand, and (3) temporal expectation. Tactile sensation was assessed with vision precluded, and with the affected hand positioned in the left and right hemispace. The Examiner administered stimulation to the patient's affected left hand while guiding the patient's right hand to administer synchronous stimulation to a prosthetic hand.

The results were striking. Even though the patients were administering touch to the prosthetic hand (with their right hand) and receiving touch (on the affected left hand) from the Examiner, patients detected the same number of stimulations as when they touched their own hand directly, and thus, they detected a significantly greater number of stimulations than in the standard Examiner-administered stimulation condition in which the patient was not involved. Patients did not report touch on sham trials, in which they were guided to administer touch to the prosthetic hand, but no touch was administered to the patient's own affected hand. Moreover, there was no decline in rates of detection when potentially informative movements of the patient's administering hand were restricted. Together, these findings rule out an explanation for self-touch enhancement in terms of the patient using proprioceptive information from the administering hand to *infer* whether he or she is being touched: Patients report self-administered touch on the basis of *feeling* rather than knowledge. When the prosthetic hand was positioned in the opposite hemispace to the patient's affected hand, so that patients administered touch and received touch in opposite sides of space, all but one patient showed self-touch enhancement. Thus, attentional modulation at the spatial region of the administering hand provided an insufficient explanation for self-touch enhancement. In a follow-up experiment, a delay between the patient's stimulation of the prosthetic hand and the Examiner's stimulation of the patient's affected hand eliminated the self-touch enhancement effect. This finding indicates an important role for temporal expectation in self-touch enhancement.

During the investigation of self-touch enhancement reported in Chapter 2, one of the patients demonstrated an unusual pattern of sensory mislocalisations. Following a right-hemisphere stroke, NG (a 21-year old patient) systematically mislocalised touch on the little finger and the ring finger of her affected left hand, and reported feeling this touch on the neighbouring rightward finger. This pattern of mislocalisation was most pronounced in the self-administered stimulation condition. In a series of experiments presented in Chapter 3, we conducted a systematic investigation of sensory localisation in Patient NG. Using the self-touch rubber hand paradigm, we manipulated the relative position of the prosthetic hand and NG's receptive hand, or considered differently, we manipulated the relative position of NG's two hands during sensory assessment of the affected hand. When NG's administering right hand was positioned to the left of her affected hand, NG demonstrated a significant improvement in sensory localisation. This finding has important theoretical and clinical implications, and these implications are outlined in the discussion of Chapter 3.

Whereas in Chapters 2 and 3 the self-touch rubber hand paradigm was used as a tool for investigating sensation following stroke, Chapters 4 to 8 were dedicated to understanding the illusion that is elicited with this paradigm. Prior to this thesis, only one study had used the self-touch rubber hand paradigm to elicit the illusion that the individual is touching her own hand (Ehrsson et al., 2005). In a theoretical paper discussing qualia, Ramachandran and Hirstein (1997) described a related paradigm that can be used to elicit the illusion that the individual is touching her nose when she is actually touching another person's nose. Thus, despite its fascinating implications for body representation and awareness, the illusion of self-touch has not been widely investigated.

In the pioneering study presented by Ehrsson et al. (2005), the illusion of self-touch was elicited with the participant's eyes closed. Participants reported that it seemed as if they were touching their own hand when they administered touch to a prosthetic hand while receiving synchronous touch from the Examiner. Subsequent to experiencing this illusion, participants demonstrated a change in the proprioceptively perceived position of the receptive hand toward the prosthetic hand: when asked to point to the index finger of the receptive hand, participants pointed to a location that was displaced toward the prosthetic hand by 3cm. Based on this proprioceptive mislocalisation, it was assumed that, when participants experienced the illusion of self-touch, they experienced touch on the receptive hand as occurring at the location of the prosthetic hand. Participants were thought to experience a "feeling of ownership of [the] touched rubber limb" (Ehrsson et al., 2005, p. 10569).

The results presented in Chapters 4, 5, and 6 provided a new interpretation of what the participant experiences when it seems that she is touching her own hand. Although some participants may experience the single event of self-touch at the location of the prosthetic hand, many participants experience the single event of self-touch at the location of the receptive hand. The first hint at this new interpretation came from the experiments presented in Chapters 4 and 5, in which a novel *visual* version of the self-touch rubber hand paradigm was introduced. In one condition, participants viewed the right hand administering touch to the prosthetic hand with the receptive left hand hidden from view, and in the second condition, participants viewed the left hand receiving touch from the Examiner with the administering right hand hidden from view. In both conditions, it seemed to participants that they were touching their own hand in the viewed location; in the first condition, the single event of self-touch was experienced as occurring at the location of the prosthetic hand (Chapter 4), and in the second condition, the single event of self-touch was experienced as occurring at the location of the participant's own receptive hand (Chapters 4 and 5). The finding that the perceived location of illusory self-touch varied depending on where the participant was looking, prompted us to question where the participant experiences the single event of self-touch when her eyes are closed. Previously it has been assumed that the participant experiences the single event of self-touch at the location of the prosthetic hand, but alternative possibilities have not been investigated.

The experiment presented in Chapter 6 investigated proprioceptively perceived hand position before and after experience of the *non-visual* illusion of self-touch. Whereas Ehrsson et al. (2005) only assessed change in the proprioceptively perceived position of the receptive hand (toward the prosthetic hand), change in the proprioceptively perceived position of both the receptive hand and the administering hand was assessed. Change in proprioceptively perceived position of the administering hand was significantly greater than change in proprioceptively perceived position of the receptive hand for some, or even most, participants. Thus, for the majority of participants, the location of the illusory self-touch event is at, or close to, the receptive hand rather than the prosthetic hand. Theoretical implications in terms of the notion of ownership in this non-visual illusion are outlined in Chapter 6.

Chapter 4 provided the first hint at a new interpretation for the non-visual illusion of self-touch, but the main objective of the experiment presented in Chapter 4 was to investigate the *tactile* constraints on the illusion of self-touch. Participants used the index finger to administer touch to the prosthetic hand, while the Examiner used a congruent stimulus (the index finger) or an incongruent stimulus (a paintbrush) to administer touch to the participant's receptive hand. The illusion was robust to the manipulation of tactile congruence. Participants experienced the illusion of self-touch despite the use of incongruent stimuli, both when vision was precluded and when visual feedback provided clear evidence of the tactile mismatch. Moreover, in the incongruent stimulation condition, many participants reported that it seemed as if the administering index finger was a brush, thus highlighting the malleability of body representation.

In Chapter 7, the *spatial* constraints on the illusion of self-touch were investigated. In previous investigations, the prosthetic hand and the participant's receptive hand have been separated by 15 cm, and positioned side-by-side with the fingers pointing away from the participant's body. In the first experiment presented in Chapter 7, the distance (15 cm, 30 cm, 45 cm, 60 cm) between the prosthetic hand and the participant's receptive hand was manipulated. In the second experiment, the alignment of the prosthetic hand relative to the participant's receptive hand was manipulated. The illusion of self-touch was diminished as the distance between the prosthetic hand and the participant's receptive hand increased, and it was also diminished when the prosthetic hand and the participant's receptive hand were misaligned.

The experiment presented in Chapter 8 investigated the *anatomical* constraints on the illusion of self-touch. The self-touch rubber hand paradigm was adapted to investigate a new illusion: the illusion that the participant was touching her left elbow when she was actually administering touch to the Examiner's arm. In everyday life, one can touch one's left elbow with the right index finger, but not with the left index finger. The experiment investigated whether the illusion was sensitive to these anatomical rules. Participants always received touch on the left elbow, but they used either the right index finger or the left index finger to administer touch to the Examiner's arm. Illusion onset was faster and illusion ratings were higher when participants administered touch using the plausible right index finger compared with the implausible left index finger. However, whilst the illusion was diminished by anatomical implausibility, it was nonetheless the case that participants did experience self-touch in the implausible condition.

In the General Discussion, the results from all of the experiments are integrated, and the theoretical and clinical implications of the work are considered. Together, the experiments in this thesis highlight the malleability of body representation. They also provide a comprehensive framework for understanding the nature of the illusion that is elicited with the self-touch rubber hand paradigm. The experiments inspire a host of future studies, and to this end, the thesis concludes with a prospectus for further research.

CHAPTER 1: GENERAL INTRODUCTION AND OVERVIEW OF THESIS

Following stroke, a majority of patients have some form of somatosensory impairment affecting the contralesional side of the body (Connell, Lincoln, & Radford, 2008); that is, the side of the body opposite to the cerebral lesion. Somatosensory information is normally processed in the medulla, thalamus, primary somatosensory cortex, secondary somatosensory cortex, posterior parietal cortex, insular cortex, and motor and premotor areas of the frontal lobe (Dijkerman & de Haan, 2007; Romo & Salinas, 1999). Consequently, somatosensory impairments can arise following lesions to a number of different brain areas (Roland, 1987). Signs of somatosensory impairment include numbness, tingling or prickling sensations, and difficulties with texture discrimination, recognition of objects placed in the hand, proprioception, and detection and localisation of touch. These impairments can have grave and significant consequences for the patient's quality of life, engagement in daily activities, independence and functional recovery (Carey & Matyas, 2010). Thus, one cannot underestimate the importance of research aimed at investigating, and ultimately enhancing, sensation following stroke.

In routine neurological examination, sensation is assessed with the patient's eyes closed (Douglass & McDermott, 2009). In an assessment of detection of touch, the patient notifies the Examiner when she feels a stimulus administered to a specified body part, for example, when she feels a tap administered to her hand or her foot. A patient with severe loss of sensation may fail to detect even intense stimulation under these testing conditions. But the same patient may demonstrate some preserved sensation when a different method of assessment is used, specifically when the patient is permitted vision of the affected limb, or is herself involved in administering the stimulation.

The first of these effects – *visual enhancement of touch* – is well-established in the literature, and has been the subject of extensive investigation over the past decade. The second of these effects – *self-touch enhancement* – has not received the same level of research attention. Consequently, Part One of the thesis is dedicated to providing a systematic investigation of this effect. I begin with a brief review of visual enhancement of touch, because it provides a valuable foundation for the empirical investigation of self-touch enhancement following stroke.

Visual Enhancement of Touch

Halligan, Hunt, Marshall, and Wade (1997) wrote to 30 neurologists to establish how they conducted a somatosensory assessment, and more specifically, whether they followed the "textbook procedure" (p. 199) of requesting that the patient close her eyes. Fifteen neurologists always assessed tactile detection with the patient's eyes closed, and a further 14 neurologists did so on some occasions. The neurologists indicated that they asked patients to close their eyes because they were concerned that patients might report touch based on visual information (i.e., what they see) rather than tactile information (i.e., what they feel). But Halligan et al. had their own concerns. They noted that "it [is] difficult to extrapolate clinical findings (without vision) to performance in the patient's normal multimodal environment" (p. 200). Thus, the traditional sensory assessment may fail to detect residual sensation that deserves attention in the rehabilitation setting. Consistent with this view, Halligan et al. (1997; see also Halligan, Hunt, Marshall, & Wade, 1996; Rorden, Heutink, Greenfield, & Robertson, 1999; Serino, Farnè, Rinaldesi, Haggard, & Làdavas, 2007) went on to show that some patients demonstrate better detection of touch when they are allowed to view the body part as it receives stimulation.

The pioneering study of Halligan et al. (1997) comprised twenty stroke patients (mean time since stroke = 80 weeks; range = 1 week to 530 weeks) and twenty neurologically healthy control participants. Detection of touch was assessed with and without visual feedback, and the Examiner administered stimulation using an aesthesiometer which was calibrated to administer subthreshold stimulation; that is, it was calibrated to the intensity at which the patient detected no more than two of six stimulations on the affected hand. Prior to testing, the Examiner was careful to establish that the patients (and control participants) fully understood the task requirements. In particular, it was important that the patient answered the question "Do you feel touch on your hand?" (Halligan et al., p. 200), and did not confuse this question with possible variants such as "Do you know/ think/ believe/suspect that you are being touched?" (p. 200). During screening, the Examiner demonstrated to the patient that there was a distinction between reporting touch based on feeling versus reporting touch based on knowledge. For example, the Examiner administered touch to a confederate's hand, and asked the patient whether she *felt* the confederate's touch. By asking questions such as this, the Examiner established that the patients understood what was required; the patients knew "that they were not to report the obvious fact that (with vision) they could indeed see themselves being touched" (p. 200).

In the experiment proper, the patient received 36 stimulations with eyes closed and 36 stimulations with eyes open. Seven patients demonstrated "somewhat better performance with the eyes open" (p. 200) and two patients demonstrated superior performance with the eyes open. In these two patients, report went from 0% with eyes closed, to 100% with eyes open. That is, the patients reported all stimulations when vision of the affected hand was permitted. Twelve of the control participants showed a small advantage in the conditions permitting vision (i.e., a maximum of six additional detections), but none demonstrated visual enhancement of touch at a comparable level to that demonstrated by the two stroke patients.

A follow-up experiment was conducted with one of the two patients (DN) who showed the most striking improvement in the report of touch when vision was permitted. Sensation in Patient DN's *unaffected* hand was assessed using a subthreshold-level stimulus. DN reported 4/36 stimulations with eyes closed and 8/36 stimulations with eyes open. One hour later, the assessment was repeated and DN reported 2/36 stimulations with eyes closed and 6/36 stimulations with eyes open. If (with vision) DN had reported a significantly greater number of stimulations on the affected hand due to suggestibility, then DN would have been expected to show a comparable effect during assessment of the unaffected hand. Contrary to this, enhancement for the unaffected hand was within the range of that demonstrated by control participants without impaired sensation.

The researchers present a number of additional points that are thought to argue against an interpretation for visual enhancement of touch in terms of suggestibility. First, the two patients who showed the most pronounced visual enhancement of touch were well oriented and of above average intelligence. Second, neither patient showed any evidence of psychiatric disorder. Third, the patients were continually reminded to report touch based on feeling rather than inference. In a different article providing a more extensive account of Patient DN, the researchers note that DN eventually retorted "I'm not stupid, you know. I do know what 'feel' means" (Halligan et al., 1996, p. 23).

To explain visual enhancement of touch, Halligan et al. (1997) suggested that visual evidence may "somehow 'boost' the signal strength of neuronal circuits associated with the experience of feeling touch" (p. 202). Bimodal visual somatosensory cells respond to visual and tactile stimuli (see Macaluso, Driver, & Frith, 2003). Following stroke, limited tactile information is available and these cells may be deprived of their tactile inputs. However, when the very limited tactile information is consistent with visual information, the visual input may "boost sub-threshold tactile stimulation into conscious awareness" (Halligan et al., p. 203), thus explaining enhanced detection under conditions permitting visual feedback.

The pioneering study by Halligan et al. (1997) inspired further investigations of visual enhancement of touch. A recent study by Serino et al. (2007) used a rigorous procedure for ensuring that patients were unable to use visual information to infer touch. The study comprised ten stroke patients (mean time since stroke = 7.6 months; range = 1 month to 50 months) and thirty-two neurologically healthy control participants. The researchers investigated visual enhancement of touch using a two-point discrimination task. The patient was tapped by one stimulus, or she was simultaneously tapped by two spatially-separated stimuli. The task was to report the number of touches administered, one or two. Stimulations were administered using solenoid tappers attached to the patient's affected arm. The solenoids were invisible to the patient as they were concealed by a small wooden box that was also attached to the patient's arm. Thus the patient was able to view her arm as it was stimulated but she was not able to view the stimulation. There were two control conditions. In one control condition, the patient viewed a neutral object – a box – while she received stimulation on the affected arm. In the other control condition, the patient viewed a prosthetic foot while she received stimulation on the affected arm. Eight patients showed significant visual enhancement of touch when viewing the arm; that is, performance on the two-point discrimination task was significantly better when the patient viewed her arm than when she viewed the neutral object (i.e., the box) or the prosthetic foot. In this experiment the visual information was *non-informative* because the solenoids were concealed from view. Thus, the advantage can be attributed to viewing the arm, rather than viewing the stimulation to the arm. Moreover, the finding that performance was better when the patient viewed her arm compared with a prosthetic foot indicates that vision of a body part is insufficient to produce visual enhancement of touch. The viewed body part needs to correspond to the body part that is receiving stimulation; for example, if the patient's right arm is being stimulated, visual enhancement of touch occurs only if the patient is viewing a right arm.

There is an important finding from the study by Serino et al. (2007). Among neurologically healthy control participants, visual enhancement of touch was inversely related to tactile acuity at baseline, and significant visual enhancement of touch was only demonstrated by individuals with *poor* tactile acuity at baseline. The researchers suggest that "visual enhancement of touch occurs specifically when tactile information alone is limited" (p. 1105). They suggest that when weak unisensory stimuli are combined, multisensory systems show an enhanced response. This explanation differs from the one presented by Halligan et al. (1997) insofar as Serino et al. do not attribute the enhancement to bimodal visual somatosensory cells. Rather, they suggest that the co-occurrence of visual and tactile information elicits a short term modulation of the primary somatosensory cortex, which is usually regarded as a unisensory region of the brain. Modulation of the primary somatosensory cortex may be the result of backward projection from multisensory brain regions (e.g., the parietal lobe), or feedforward connections between visual and somatosensory brain regions.

Serino et al.'s (2007) finding that visual enhancement of touch is inversely related to tactile acuity at baseline resonates with other studies investigating neurologically healthy individuals. For example, Longo, Cardozo, and Haggard (2008) investigated tactile acuity with the gratings orientation test. There were gratings of four different widths: .75, 1, 1.25 and 1.5 mm. For each width, one grating was oriented so that it ran along the long axis of the finger, and one grating was oriented so that it ran across the finger. There were eight gratings in total. The participant's task was to identify whether she was being stimulated with the grating that ran along or across the finger. Using this task, Longo et al. demonstrated visual enhancement of touch among participants whose performance was close to chance at baseline. A similar finding was presented by Press, Taylor-Clarke, Kennett, and Haggard (2004). The researchers investigated tactile acuity using four different tasks. Participants only demonstrated visual enhancement of touch in the single most difficult task. The task required the participant to identify which of two closely-positioned 'tappers' administered touch to the participant's arm. The sight (and sound) of the tappers did not carry any information, so vision of the arm was non-informative with respect to which tapper was administering touch. In the three less difficult tasks that were assessed as part of the experimental series, participants did not demonstrate visual enhancement of touch.

Together, the studies by Longo et al. (2008), Press et al. (2004), and Serino et al. (2007) make an important theoretical contribution with regard to ruling out an explanation for visual enhancement of touch in terms of suggestibility or response bias. First, in all three studies visual information did not carry information that would allow the individual to arrive at the correct response (see also Kennett, Taylor-Clarke, & Haggard, 2001; Rorden et al., 1999). And second, all three studies used a two-alternative forced choice format, in which visual enhancement of touch cannot be accounted for by response bias (see also Fiorio & Haggard, 2005; Kennett et al., 2001; Taylor-Clarke, Kennett, & Haggard, 2002; Taylor-Clarke, Kennett, & Haggard, 2004). Consider a two-point discrimination task, in which 50% of trials involve stimulation with one point and 50% of trials involve stimulation with two points. A participant who is biased toward reporting that she is being touched with 'one' stimulus will be correct on only 50% of trials. Thus, response bias predicts chance performance in tasks involving a two-alternative forced choice format.

Self-Touch Enhancement

Visual enhancement of touch is a well-known phenomenon that has received considerable attention in the research literature. This thesis explores a less well-known sensory effect, namely *self-touch enhancement*. Stroke patients who are unable to detect a tactile stimulus administered by another person may detect the same stimulus when it is self-administered. When the work on this thesis commenced, only two published studies had investigated self-touch enhancement: Valentini, Kischka, and Halligan (2008) and Weiskrantz and Zhang (1987). The current thesis contributes two further publications on self-touch enhancement (White, Aimola Davies, & Kischka , 2010; White, Aimola Davies, Kischka, & Davies, 2010). Here I begin with a description of the original research programmes.

Weiskrantz and Zhang (1987) were the first to report self-touch enhancement. The patient was a 56-year-old woman who, following right-hemisphere stroke, experienced left-side hemiplegia and severe left-side sensory deficits. On conventional sensory testing, the patient was unable to detect force of less than 35 grams (filament of 0.6 mm diameter) administered to her left hand. Healthy individuals detect intensities less than .07 grams. In a break between testing, Weiskrantz and Zhang observed that the patient was rubbing her left hand with her right hand. Curiously, when asked if she could feel anything, the patient reported that she could. The patient "quietly and insistently maintained that she had feeling in her left hand when it was touched by her own right hand" (p. 632).

Weiskrantz and Zhang (1987) set out to investigate the patient's claim. Testing was conducted with the patient's eyes closed. The Examiner guided the patient's right index finger to one of the fingers of the affected left hand and gently moved it three times over the affected finger (specifically, the distal pad of the affected finger). The patient was accurate in reporting where she was being touched, and observed that she "felt something definitely every time" (p. 633). In contrast, when the patient received the same stimulation from the Examiner, she rarely reported feeling the touch and on the few occasions that she did report a weak stimulation, the patient was unable to localise the sensation to a particular finger. The researchers verified that the patient's superior performance detecting self-administered stimulation was not due to skin-to-skin contact, because she continued to report most stimulations when she used a pen top, a von Frey filament or a thimble to administer touch.

In a follow-up assessment, the researchers introduced sham trials to rule out the possibility that the patient was simply reporting touch each time she administered stimulation. Stimulation was administered with a von Frey filament. The fingers of the Examiner's hand were interdigited with the fingers of the patient's affected hand. On valid trials, the Examiner guided the patient to administer stimulation to one of the patient's own fingers, whereas on sham trials, the Examiner guided the patient to administer stimulation to one of the Examiner's fingers. The patient's performance was not as good in this condition. On 17 of 32 self-touch trials, she did not report feeling any stimulation.

The results suggest that the introduction of sham trials affected the patient's response criterion for reporting that she had been touched. However, it is important to note that the patient nonetheless reported significantly more stimulations in this self-administered condition than in the standard Examiner-administered sensory assessment. On the basis of their systematic assessment, Weiskrantz and Zhang concluded that the patient enjoyed an "impressive degree of residual cutaneous sensitivity" (p. 634) when she was actively involved in the administration of touch.

Following Weiskrantz and Zhang's (1987) report of self-touch enhancement, there was a surprising lull in research investigating this phenomenon. Twenty years passed before a group of researchers re-opened the self-touch enhancement file and reignited interest in the phenomenon. In 2008, Valentini et al. set out to replicate Weiskrantz and Zhang's finding and to establish the incidence of self-touch enhancement in a large group of patients. They describe results obtained from 39 patients (22 with right-hemisphere damage and 17 with left-hemisphere damage), who were between 20 and 3308 days post-stroke.

Patients were blindfolded during testing. Stimulation was administered with a Semmes-Weinstein monofilament of 8.65 grams. There were two types of trials: self-administered stimulation trials and Examiner-administered stimulation trials. On the self-administered stimulation trials, the Examiner guided the patient's unaffected hand to administer stimulation, whereas on the Examiner-administered stimulation trials the patient was not involved in administering stimulation. Stimulation was administered to one of six locations on the patient's affected hand: the proximal phalanx of each digit, or the back of the hand. In addition, there were sham trials in which stimulation was administered to one of the Examiner's fingers, which were interdigited with the fingers of the patient's affected hand for the duration of the assessment.

Following each trial, the patient was asked (1) if she detected the stimulation, (2) to localise the stimulation, and (3) to provide an estimation of perceived intensity on a scale ranging from 0 (*no* *sensation*) to 5 (*very strong sensation/the same intensity as on the unaffected hand*). Seventeen of 22 right-hemisphere patients and five of 17 left-hemisphere patients demonstrated self-touch enhancement, operationally defined as (a) an improvement in stimulus detection, (b) an improvement in stimulus localisation, or (c) subjectively higher ratings of stimulus intensity in the self-administered stimulation condition compared with the Examiner-administered stimulation condition. Valentini et al.'s (2008) systematic research programme confirms that self-touch enhancement is a pervasive phenomenon, particularly among patients with right-hemisphere damage.

The researchers also investigated a control group of ten neurologically healthy individuals. None of the control participants demonstrated self-touch enhancement, and two of the control participants actually demonstrated the reverse effect – enhanced detection of Examiner-administered (rather than self-administered) stimulation. This is consistent with a large body of research investigating a phenomenon that has been termed *self-touch attenuation*. In neurologically healthy individuals, self-administered stimuli are perceived as less intense (as well as less pleasant and less tickly) than externally-administered stimuli (see Bays, Flanagan, & Wolpert, 2006; Blakemore, Frith, & Wolpert, 1999; Blakemore, Wolpert, & Frith, 1998, 2000; Claxton, 1975; Hesse, Nishitani, Fink, Jousmäki, & Hari, 2010; Weiskrantz, Elliot, & Darlington, 1971). Self-touch attenuation is explained in terms of internal forward models that make predictions about expected sensory feedback. When an individual generates a motor command, an efference copy of the motor command is created. This efference copy predicts the sensory consequences of the individual's action. When the individual executes the action, the predicted sensory consequences are compared to the actual sensory consequences. The predictable component is attenuated, thereby allowing the individual to distinguish the sensory consequences of her own action from "sensory signals due to changes in the outside world" (Blakemore et al., 1998, p. 635). A simple visual schematic of the internal forward model is presented in Figure 1.

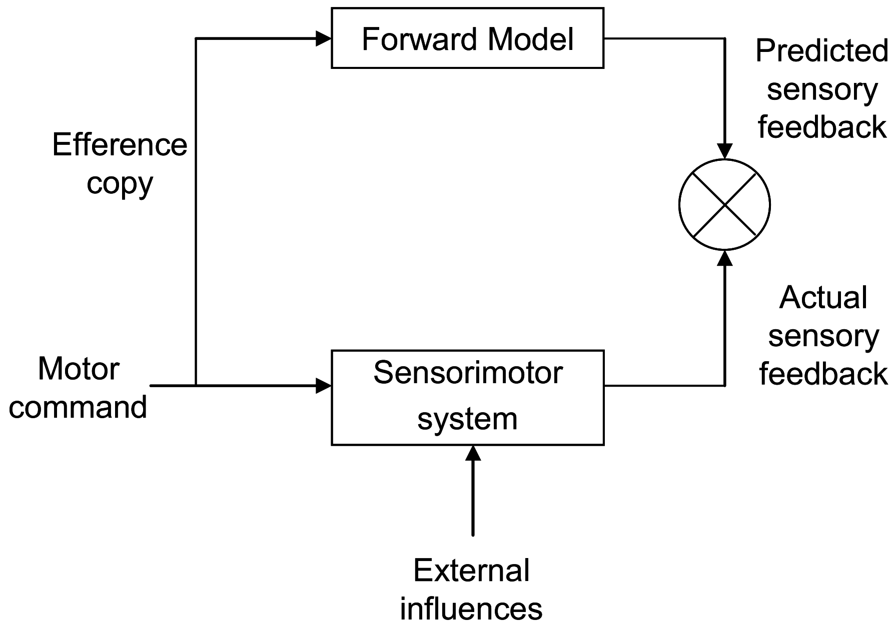

Figure 1. Internal forward model for distinguishing the sensory consequences of one's own actions and the sensory consequences of external events. On the basis of an efference copy, the forward model predicts the sensory feedback that would be expected to result from the individual's action. The predicted sensory feedback is compared to the actual sensory feedback (X = comparator). Discrepancy indicates that the sensation that an individual is experiencing is externally-produced, or modulated by external influences. This model is adapted from Bays and Wolpert (2007); Blakemore et al. (1999); Blakemore et al. (2000).

How are we to explain self-touch enhancement in patients following stroke? One explanation is that under conditions of self-touch, the patient may use *proprioceptive information* to infer whether she is being touched. That is, the patient may infer stimulation based on the relative position of her two hands. If the patient's administering hand is positioned above her affected hand, and if the patient lowers her administering hand, then she knows that she is touching her own hand. The patient may report touch based on knowledge (i.e., information derived through proprioception) rather than feeling.

The sham trials that were used in the pioneering studies provide some protection against this criticism. On sham trials, the Examiner guided the patient to administer stimulation to one of the Examiner's fingers, which were interdigited with the fingers of the patient's affected hand. If the patient reported touch only on valid trials (and not on sham trials) this provided an indication that the patient was *feeling* touch when she administered stimulation to her own hand. But, it is still possible in principle that the patient may have used proprioceptive information to distinguish valid from sham trials. That is, the patient may have used subtle differences in the location of her administering hand to distinguish valid from sham stimulations, given that she was guided to a slightly different location on these two trial types.

Valentini et al. (2008) mention another possible explanation for self-touch enhancement. These researchers suggest that the administering hand directs the patient's attention to the affected hand. They cite a study by Coslett and Lie (2004) as providing evidence for this type of attentional modulation. Coslett and Lie studied two patients with sensory deficits following right-hemisphere stroke. The first patient was a 52-year-old man who exhibited sensory extinction, failing to report touch administered to the left hand when both hands were concurrently stimulated. The second patient was a 55-year-old man with left-side hemiplegia. He exhibited severe left-side sensory deficits affecting unilateral touch, proprioception and temperature discrimination. In both patients, report of Examiner-administered stimulation on the left hand improved when the patients' right and left hands were in contact during stimulation. Coslett and Lie proposed that the unaffected hand serves as an *attentional wand or focus* "that enhances sensory processing in those regions with which it is in contact" (Coslett & Lie, p. 1873).

A Proposal for Investigating Self-Touch Enhancement

Part One of this thesis will use a novel experimental paradigm to investigate different explanations for self-touch enhancement. The *self-touch rubber hand paradigm*, also called the somatic rubber hand paradigm (Ehrsson, Holmes, & Passingham, 2005), is a simple paradigm that has been used with neurologically healthy individuals to create the illusion that the individual is touching her own hand when she is actually touching a prosthetic hand. The Examiner guides the participant to administer touch to a prosthetic hand, and at the same time, the Examiner administers touch to the participant's other hand. (Henceforth, the participant's two hands are referred to as the administering hand and the receptive hand.) When the touch that the participant administers to the prosthetic hand is synchronous with the touch that the Examiner administers to the participant's receptive hand, the participant experiences the touch on her receptive hand as if it is self-produced; that is, it seems to the participant that she is touching her own hand.

This paradigm should prove very valuable for investigating self-touch enhancement. The *action* of the patient's administering hand is matched to the condition where there is actual self-touch. The *stimulation* on the patient's receptive hand is matched to the condition where there is actual self-touch. And importantly, the *timing* of these two events (administering and receiving touch) is matched, although the paradigm also allows for the timing to be manipulated. The only detail that distinguishes the patient's experience (in the self-touch rubber hand paradigm versus actual self-touch) is the relative location of her two hands. In the self-touch rubber hand paradigm, the patient's hands are in two different locations, whereas in actual self-touch, the patient's hands are in the same location. This is precisely the detail that we wish to manipulate to rule out the possibility that the patient uses proprioceptive information to infer whether she is being touched.

Thus, the first objective of this thesis is to use the self-touch rubber hand paradigm to distinguish explanations for self-touch enhancement based on feeling from explanations based on knowledge. If patients have residual sensation that is evident under conditions of self-touch, they should continue to demonstrate self-touch enhancement when they are tested with the self-touch rubber hand paradigm. Alternatively, if patients use information about relative hand position to infer that they are being touched, they will no longer demonstrate self-touch enhancement when they are tested with the self-touch rubber hand paradigm. If we do find that patients demonstrate self-touch enhancement under conditions of the self-touch rubber hand paradigm, we can use the paradigm to investigate alternative explanations for self-touch enhancement. For example, by manipulating the position of the prosthetic hand (to which the patient administers stimulation) relative to the patient's affected hand, we can assess the attentional wand explanation.

In Chapters Two and Three of the thesis, the self-touch rubber hand paradigm will be used to investigate sensation in patients following stroke. Before turning to these experiments, I would like to review the research context in which the self-touch rubber hand paradigm was developed.

The Rubber Hand Paradigm: Visual and Non-Visual Versions

The self-touch rubber hand paradigm was developed by Ehrsson et al. (2005) as a *non-visual version* of the widely investigated visual rubber hand paradigm (Botvinick & Cohen, 1998). In 1998, Botvinick and Cohen authored a one-page *Nature* article titled "Rubber hands 'feel' touch that eyes see". In this seminal paper, the researchers introduced a simple experimental paradigm that elicits a striking body illusion. The participant looks at a prosthetic hand being touched by the Examiner while the participant's own hand – hidden from view – is also touched by the Examiner. When touches administered to the prosthetic hand and to the participant's hidden hand are synchronous, the participant has an experience in which she seems to "feel the touch not of the hidden brush but that of the viewed brush, as if the rubber hand ha[s] sensed the touch" (Botvinick & Cohen, 1998, p. 756). This experience is referred to as *visual capture of touch*. It may also seem to the participant that the prosthetic hand is her own hand. This is commonly referred to as the *illusion of ownership*, where ownership is defined as "the phenomenological experience that 'this body is mine'" (Tessari, Tsakiris, Borghi, & Serino, 2010, p. 643) and the "sense that I am the one undergoing an experience" (Gallagher, 2000, p. 15).

When the participant experiences the rubber hand illusion, she does not perceive the prosthetic hand as a third or *supernumerary* hand (Longo, Schüür, Kammers, Tsakiris, & Haggard, 2008; Newport, Pearce, & Preston, 2010). Therefore, it does not seem to the participant that she is feeling touch in the location of her hidden hand as well as in the location of the viewed prosthetic hand. Rather, the prosthetic hand *replaces* the participant's hidden hand (Ehrsson, Wiech, Weiskopf, Dolan, & Passingham, 2007; Lewis & Lloyd, 2010; Longo et al., 2008; Moseley et al., 2008, but see Folegatti, de Vignemont, Pavani, Rossetti, & Farnè, 2009). The participant experiences the *felt* and *seen* events of touch as belonging to a single event, and because visual information about limb position (usually) has less variance than proprioceptive information about limb position (Ernst & Bülthoff, 2004; van Beers, Sittig, & Denier van der Gon, 1999), the participant perceives that the felt and seen touch are both occurring at the location of the viewed prosthetic hand.

A number of methods have been developed to assess the participant's experience of the visual rubber hand illusion. The majority of studies use some type of subjective questionnaire. Experience of the illusion is reflected in the participant's agreement with statements such as "It seemed as if I were feeling the touch of the paintbrush in the location where I saw the rubber hand touched" and "I felt as if the rubber hand were my hand" (Botvinick & Cohen, 1998, p. 756). Given that questionnaire responses are subjective and prone to response bias, researchers commonly use a second method for corroborating the participant's report. For example, a popular assessment method involves measuring change in the proprioceptively perceived position of the participant's receptive hand. This change is referred to as *proprioceptive drift*. To allow the reader to visualise most easily what is meant by proprioceptive drift, it is necessary to describe the experimental set-up and the typical positioning of the hands (see Figure 2).

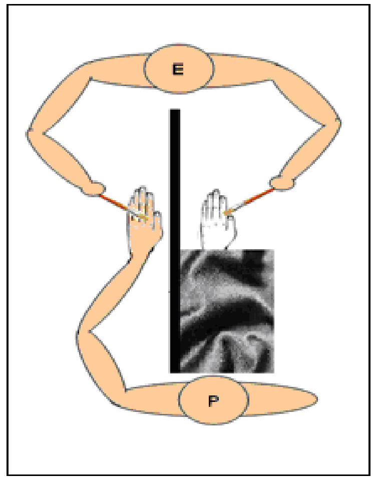

Figure 2. Example of the experimental set-up for a study investigating the visual rubber hand illusion. E = Examiner, P = Participant.

In most rubber hand studies, the prosthetic hand is positioned at the participant's body midline, with the fingers of the prosthetic hand pointing straight ahead. The participant's own hand is positioned to the left or the right of the viewed prosthetic hand, behind (or beneath) a visual divider. Therefore, the participant can see the prosthetic hand, but she cannot see her own hand. Before and after the experimental trial (and thus before and after the participant experiences the illusion), the participant indicates the position of her *hidden* receptive hand. For example, the participant might point to the index finger of the hidden receptive hand, or the participant might read the number on a ruler that corresponds to the position of the index finger of the hidden receptive hand. (The different methods that have been used to assess proprioceptively perceived hand position are reported in a Table in Appendix 1.) After experiencing the illusion, the participant proprioceptively perceives her hidden hand as being in a location that is shifted toward the location of the viewed prosthetic hand by about 15-30% of the full distance between the real hand and the prosthetic hand (Makin, Holmes, & Ehrsson, 2008). There is thus an adaptation in the proprioceptively perceived position of the receptive hand.

Additional methods that have been used to assess the participant's experience include open-ended descriptions, skin conductance responses, temperature measurements, crossmodal congruency tasks, performance on tactile tasks, electroencephalography, and imaging techniques (e.g., fMRI, MEG, and PET).[1] For examples of how experience of the rubber hand illusion is reflected in the results of each of these assessment methods, see Table 1.

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[1] References for each of the studies that have used these different assessment methods are provided in a table in Appendix 2.

Table 1

Different methods for assessing the visual rubber hand illusion, and examples of how experience of the illusion is reflected in the results of each method

Method	**Example Result**
Questionnaire	The participant responds affirmatively to statements assessing the experiences of feeling touch in the location of the viewed hand (visual capture of touch) and it seeming as if the viewed hand is the participant's own hand (illusion of ownership).
Proprioceptive drift	The participant proprioceptively perceives her hidden hand as being in a location that is shifted toward the location of the viewed prosthetic hand.
Open-ended descriptions	The participant employs terms of ownership in her open-ended descriptions, for example "I found myself looking at the dummy hand thinking it was actually my own" (Botvinick & Cohen, 1998, p. 756).
Skin conductance response	The participant demonstrates increased skin conductance response, a sign of autonomic nervous system arousal, when the viewed prosthetic hand is threatened (e.g., with a needle).
Temperature measurements	Experience of the visual rubber hand illusion is accompanied by a drop in the temperature of the participant's hidden hand.
Crossmodal congruency task	The task is to report the finger of the participant's hidden hand that has received vibrotactile stimulation. The participant views a prosthetic hand, on which distractor lights are activated. The location of the lights can be congruent (same finger) or incongruent (different finger) with the location of vibrotactile stimulation on the participant's hidden hand. The participant is faster to report the location of vibrotactile stimulation on congruent trials, and the difference in reaction times on congruent and incongruent trials is referred to as the *crossmodal congruency effect*. The standard result from studies using this method to assess the visual rubber hand illusion is that the participant demonstrates a larger crossmodal congruency effect when she perceives that the viewed hand is her own hand.
Tactile task	A number of different tactile tasks have been used to assess experience of the visual rubber hand illusion. The illusion that the viewed prosthetic hand is the participant's own hand affects the perception of tactile events at the location of the participant's hidden hand. For example, if the viewed hand is larger than the participant's hidden hand, this affects her perception of the size (Bruno & Bertamini, 2010) or weight (Haggard & Jundi, 2009) of objects placed in the hidden hand.
Electroencephalography	Example findings from EEG studies measuring oscillatory brain activity during experience of the visual rubber hand illusion include high frequency activity in the gamma band (Kanayama, Sato, & Ohira, 2007) and increased power spectrum density (Blefari, Cipriani, & Carrozza, 2011).
Imaging techniques	*fMRI*: The participant demonstrates significant activation of the premotor cortex when she experiences the visual rubber hand illusion (Ehrsson et al., 2004). *PET*: The participant demonstrates significant activity in the right posterior insula and the right frontal operculum (Tsakiris, Hesse, Boy, Haggard, & Fink, 2007).

Ehrsson, Spence, and Passingham (2004) conducted the first fMRI investigation of the visual rubber hand illusion. In this pioneering study, the researchers demonstrated significant bilateral activation of the premotor cortex and attributed this to the "the feeling of ownership of a seen limb" (p. 877). In a commentary on this fMRI investigation, Botvinick (2004) noted that the premotor cortex is activated when an object is seen to be approaching the body. He suggested that in the study by Ehrsson et al., the premotor activation may have resulted from the participant's visual experience of the paintbrush (i.e., the object) entering peripersonal space, rather than from the participant's experience of ownership of the viewed prosthetic hand. To evaluate Botvinick's hypothesis, Ehrsson et al. (2005) developed a version of the rubber hand paradigm in which the prosthetic hand is unseen.

This non-visual version of the rubber hand paradigm is the self-touch rubber hand paradigm. While the participant's eyes are closed, the Examiner guides the participant to administer touch to a prosthetic hand, and at the same time, the Examiner administers touch to the participant's receptive hand. When the touch that the participant administers to the prosthetic hand is synchronous with the touch that the Examiner administers to the participant's receptive hand, the participant experiences the touch on her receptive hand as if it is self-produced; that is, it seems to the participant that she is *touching her own hand*. Using fMRI, Ehrsson et al. (2005) demonstrated that this non-visual illusion was associated with activation in intraparietal and cerebellar regions as well as the premotor cortex. Given that the participant's eyes were closed, the premotor activation could not be attributed to the visual experience of an object entering peripersonal space. Ehrsson et al. suggested that intraparietal, cerebellar and premotor regions detect correlated multisensory signals, and the detection of correlated signals by these brain regions may be the mechanism for the experience of body ownership.

Since this pioneering work by Ehrsson et al. (2005), there have been *no* further investigations using the self-touch rubber hand paradigm, other than those presented in this thesis (Aimola Davies & White, Under Revision; Aimola Davies, White, Thew, Aimola, & Davies, 2010; White & Aimola Davies, 2011; White, Aimola Davies, & Davies, 2011; White, Aimola Davies, Halleen, & Davies, 2010). This is in contrast with the visual rubber hand paradigm, which has been the subject of extensive investigation over the past decade, and particularly over the last six years. Figure 3 presents a plot of empirical studies using the visual rubber hand paradigm that were published between 1998 (the year in which the paradigm was introduced by Botvinick and Cohen) and 2011. These studies were identified (1) from the PubMed database using the following key terms: 'rubber hands feel touch' OR 'rubber hand illusion' OR 'rubber hand paradigm' OR 'fake hand', and (2) from references included in the PubMed-retrieved articles. In total, 81 relevant articles were identified: 12 published between 1998 and 2005 and 69 published between 2006 and 2011. The 81 studies plotted in Figure 3 are also included in a Table in Appendix 2 which provides an overview of the methodological details of each study. These methodological details informed the design of the experiments in this thesis.

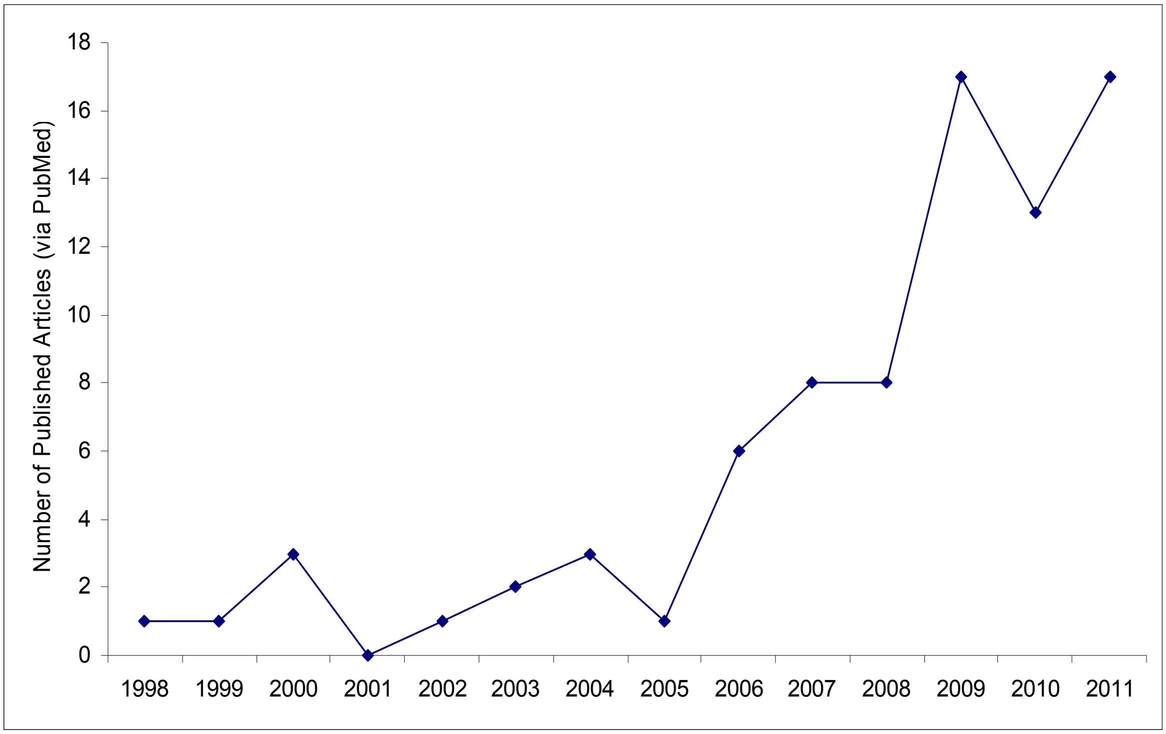

Figure 3. Number of empirical studies using the visual rubber hand paradigm as a function of year of publication.

Not surprisingly, the literature is rich with descriptions of the conditions in which the visual rubber hand illusion is elicited but lacking in descriptions of the constraints on the non-visual illusion of self-touch. Consequently, Part Two of the thesis is dedicated to investigating the self-touch rubber hand paradigm. The next section provides a brief review of studies that have investigated the constraints on the visual rubber hand illusion, and a description of the known constraints on the non-visual illusion of self-touch as determined by Ehrsson et al. (2005).

The Constraints on the Visual Rubber Hand Illusion

Many researchers investigating the visual rubber hand illusion have set out to establish the conditions in which the illusion is (or is not) elicited. To establish the constraints on the visual rubber hand illusion, researchers have manipulated (1) *timing* of stimulation, whether the stimulation of the viewed prosthetic hand and the stimulation of the participant's hidden hand are synchronous, (2) *structural description of the body*, whether the viewed hand matches the participant's hidden hand, (3) *object administering stimulation*, whether the stimulus that is used to administer touch to the viewed hand matches the stimulus that is used to administer touch to the participant's hidden hand, (4) *distance*, between the viewed hand and the participant's hidden hand, (5) *alignment*, of the viewed hand relative to the participant's hidden hand, and (6) *anatomical plausibility*, the likelihood that the viewed hand could belong to the participant's body. The thesis presents experiments which aim to build up a similar understanding with regard to the constraints on the non-visual illusion of self-touch. This introduction provides a brief outline of the results from visual studies using each of these manipulations: timing, structural description of the body, object administering stimulation, distance, alignment, and anatomical plausibility. The relevant chapters of the thesis provide a more focused review.

Timing

To elicit the visual rubber hand illusion, the Examiner's stimulation of the viewed hand must be synchronous with stimulation of the participant's hidden hand. Temporal discrepancies of more than 300 ms diminish the visual rubber hand illusion, and temporal discrepancies of more than 500 ms abolish the visual rubber hand illusion (Shimada, Fukuda, & Hiraki, 2009). The role of synchrony can be explained within a cue integration or causal inference framework: individuals are more likely to perceive two events as having a common cause when they are close to one another in time (Körding, Beierholm, Ma, Quartz, Tenenbaum, & Shams, 2007). In the visual rubber hand paradigm, the two events are the visually perceived event of the prosthetic hand being touched and the tactually perceived event of one's hidden hand being touched. The two events do not need to be perfectly synchronous (i.e., 0 ms discrepancy) because the low temporal resolution of neural processing (see van Mierlo, Brenner, & Smeets, 2007) means that multisensory integration operates within a wide temporal window (Spence & Squire, 2003). Given that the rubber hand illusion is not elicited when stimulation is asynchronous (i.e., 500 ms discrepancy), it is common for researchers to include asynchronous trials as a control or baseline condition.

Structural Description of the Body

Similarity of the viewed hand to the participant's hidden hand is also important. Tsakiris (2010) suggested that the participant compares the visual form of the viewed object against a body model which "contains a reference description of the visual, anatomical and structural properties of the body" (p. 707, see also Tsakiris, Costantini, & Haggard, 2008; Tsakiris et al., 2010). If the viewed object does not fit with this body model, the participant will not experience the visual rubber hand illusion. Importantly, the body model seems to contain information about the human body generally, rather than the participant's body specifically; the viewed hand does not need to resemble the participant's *own* hand in terms of skin tone and hand shape (i.e., slenderness versus fatness) for the rubber hand illusion to be elicited (Longo, Schüür, Kammers, Tsakiris, & Haggard, 2009). But it does need to resemble a *human* hand, with the same laterality (left or right: Tsakiris & Haggard, 2005; Tsakiris et al., 2007) and orientation (palm upward or palm downward: Austen, Soto-Faraco, Enns, & Kingstone, 2004) as the participant's hidden hand. When the rubber hand paradigm is conducted using a non-hand-object (e.g., stick: Tsakiris & Haggard, 2005; block of wood with a hand-like structure: Tsakiris, Carpenter, James, & Fotopoulou, 2010; tabletop: Haans, IJsselsteijn, & de Kort, 2008), the participant does not experience the rubber hand illusion (but see Armel & Ramachandran, 2003; Hohwy & Paton, 2010).

Object Administering Stimulation

The visual rubber hand illusion can be elicited when the stimulus that is administered to the viewed prosthetic hand is different from the stimulus that is administered to the participant's hidden receptive hand. In a study by Schütz-Bosbach, Tausche, and Weiss (2009), the participant viewed a prosthetic hand being touched with a piece of soft cotton while the participant received stimulation to her own hand from a rough sponge. This condition was also conducted in reverse, with the prosthetic hand being touched with a rough sponge while the participant's hidden hand received stimulation from soft cotton. Participants experienced a compelling visual rubber hand illusion under conditions of incongruent tactile stimulation. A series of screening measures established that participants could feel the difference between the two stimuli on the hand, and that they could discern what the stimulus administered to the viewed prosthetic hand should feel like (e.g., soft and pleasant versus rough and unpleasant) on the basis of visual information alone. Thus, it was not the case that participants were unable to *detect* a mismatch between the viewed stimulus on the prosthetic hand and the felt stimulus on the hidden hand.

Distance

There is evidence to suggest that the visual rubber hand illusion may be constrained by the positioning of the viewed prosthetic hand relative to the participant's hidden hand. Lloyd (2007) systematically manipulated the distance between the prosthetic hand and the participant's hidden hand. She set out to "quantify the spatial boundaries over which referred tactile sensations can be felt on a rubber hand" (p. 104). The prosthetic hand was positioned in one of six distances (17.5 cm, 27.5 cm, 37.5 cm, 47.5 cm, 57.5 cm, 67.5 cm) from the participant's own hand, and the order of testing of each *prosthetic* hand-placement condition was randomised between participants. The results indicated that the rubber hand illusion was strongest when the two hands were closest together (17.5 cm) and that there was a significant decline in the illusion when the hands were separated by more than 27.5 cm. Lloyd explains the effects for distance with reference to visuo-tactile bimodal cells in the premotor and parietal cortices. These cells code peripersonal space around the hand and "respond to both the visual and tactile characteristics of objects approaching and touching the hand" (p. 104). Visual receptive fields are larger than tactile receptive fields, to allow for the incorporation of tools into the body schema (see Iriki, Tanaka, & Iwamura, 1996). Lloyd's view is that the rubber hand illusion occurs when the viewed prosthetic hand falls within the region of space coded by bimodal visuo-tactile cells. That is, within the visual receptive field surrounding the tactile receptive field of the participant's stimulated hand. Thus, the fact that the visual rubber hand illusion was strongest at the 17.5 cm and 27.5 cm hand-placement conditions, and "declined significantly once the rubber hand was placed more than 27.5 cm away from the participant's own right hand" (Lloyd, p. 108), is consistent with findings that the visual receptive fields surrounding the hand extend 5 cm to 35 cm from the tactile receptive fields.

Alignment

Numerous studies have manipulated the alignment of the prosthetic hand relative to the participant's hidden hand. These studies find that the rubber hand illusion is most easily elicited when the viewed prosthetic hand is perfectly *aligned* with the participant's hidden hand. Nearly all of the studies investigating alignment have oriented the participant's hidden with the fingers pointing straight ahead, and have rotated the viewed prosthetic hand, either by 90º (Pavani, Spence, & Driver, 2000; Tsakiris & Haggard, 2005) or 180º (Ehrsson et al., 2004). These dramatic perturbations have been sufficient to abolish the rubber hand illusion.

Costantini and Haggard (2007) investigated the effect of more subtle rotations in hand position. The viewed prosthetic hand was oriented with the fingers pointing straight ahead and the participant's hidden hand was aligned with the viewed prosthetic hand or it was rotated by 10°, 20°, or 30°. Alternatively, the participant's hidden hand was oriented with the fingers pointing straight ahead and the viewed prosthetic hand was aligned with the participant's hidden hand or it was rotated by 10°, 20°, or 30°. Costantini and Haggard demonstrated that the rubber hand illusion was abolished by small changes (10º) in the orientation of the viewed prosthetic hand but not by equally small changes in the orientation of the participant's hidden hand. They concluded that small mismatches in what the participant sees (alignment of the prosthetic hand) reduce the illusion more than equivalent mismatches in what the participant feels (alignment of the participant's hidden hand).

Anatomical Plausibility

A final constraint that has been investigated is anatomical plausibility, whether the viewed prosthetic hand *could* belong to the participant's body. Anatomical plausibility is determined by the position of the viewed prosthetic hand relative to the participant's body, rather than the position of the viewed prosthetic hand relative to the participant's hidden hand. Thus an anatomically-implausible condition is one in which the viewed hand is in a position that the participant's own hand could *never* occupy. In a study by Armel and Ramachandran (2003), the viewed prosthetic hand was positioned 91 cm in front of the participant with the fingers pointing away from the participant's body. The alignment of the viewed prosthetic hand matched the alignment of the participant's hidden hand. (Note that the researchers did not specify the distance between the viewed prosthetic hand and the participant's hidden hand.) The illusion was elicited in this implausible condition, although it was diminished when compared to a more plausible hand-placement condition in which the prosthetic hand was in close proximity to the participant's body. Thus, the visual rubber hand illusion is diminished, but not necessarily abolished, by anatomical implausibility. It will be interesting for future work to use manipulations that push the boundaries of anatomical plausibility, so as to establish whether there is a point at which the illusion is abolished.

Summary

Studies investigating the constraints on the visual rubber hand illusion have paved the way for accounts of body ownership, "why and how is the rubber hand experienced as part of one's body?" (Tsakiris, 2010, p. 705), or more broadly, why and how do we experience our body as our own. The visual rubber hand paradigm provides a unique opportunity for investigating questions about body ownership. It allows researchers to turn 'on and off' the experience of ownership of a viewed hand, thus side-stepping a potential problem for this field of research, which is the simple fact that the body is "always there" (James, 1890, p. 242).

In the visual rubber hand illusion, "vision of tactile stimulation on the rubber hand captures the tactile sensation on the participant's own hand, and this visual capture results in a mislocalization of the felt location of one's own hand towards the spatial location of the visual percept" (Tsakiris, 2010, p. 705). While the paradigm is being implemented, it seems to the participant that she is being touched in the location of the viewed prosthetic hand (visual capture of touch) and it may also seem to the participant that the viewed prosthetic hand is the participant's own hand. Studies investigating the constraints on the illusion demonstrate that synchronous stimulation of the viewed prosthetic hand and the participant's hidden hand is necessary, but insufficient to produce this illusion. The illusion is most easily elicited when the viewed hand is the same laterality (left or right) as the participant's hidden hand (Tsakiris & Haggard, 2005; Tsakiris et al., 2007), close to the participant's hidden hand (Lloyd, 2007), and aligned with the participant's hidden hand (Costantini & Haggard, 2007; Ehrsson et al., 2004; Pavani et al., 2000; Tsakiris & Haggard, 2005).

Constraints on the Non-Visual Rubber Hand Illusion

The pioneering study of the self-touch rubber hand paradigm[2] (Ehrsson et al., 2005) provided information about two constraints on the illusion of self-touch, namely timing and whether the *touched* object fit with the structural description of the human body. Part Two of the thesis investigates four further constraints on the illusion of self-touch: object administering stimulation, distance, alignment, and anatomical plausibility. Before turning to the experiments, I would like to review the findings from the study by Ehrsson et al.

In the study by Ehrsson et al. (2005), experience of the illusion was assessed in four ways: subjective questionnaire, time of illusion onset, proprioceptive drift of perceived hand position, and fMRI. Here I present the findings for the *illusion condition* in which the participant administered touch to a prosthetic hand while the Examiner administered synchronous touch to the participant's receptive hand. In Experiment 1, experience of the illusion was assessed with a questionnaire. Twenty-five of 32 participants experienced the illusion of self-touch, indicated by agreement with the statement "I felt as if I was touching my right hand with my left hand" (p. 10565). In Experiment 2,

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[2] Note that Ramachandran and Hirstein (1997) have described a similar paradigm that can also be used to elicit an illusion of self-touch. The participant is guided to tap and stroke another person's nose while the Examiner administers corresponding taps and strokes to the participant's nose. After a few seconds, and depending on where the other person is sitting relative to the participant, the participant "develops the uncanny illusion that his nose has either been dislocated, or has been stretched out several feet forwards or off to the side" (p. 452). Ramachandran and Hirstein do not present empirical studies using this paradigm but they do report that the illusion is quite robust, as it was experienced by 12 of 18 naïve individuals.

the same participants were asked to report when the illusion started. The mean illusion onset was 9.7 s after synchronous stimulation of the two hands commenced. In Experiment 3, 28 of the 32 participants were assessed with a measure of proprioceptive drift of perceived hand position. Before and after the experimental trial (and thus before and after the participant experienced the illusion, and not while the participant experienced the illusion), the participant indicated the position of her receptive hand, by sliding her administering index finger along the table until it was in line with the proprioceptively perceived position of the receptive index finger. This measure was taken with the participant's eyes closed. Pointing error, or change in the proprioceptively perceived position of the receptive hand, was calculated as "the difference between the two index fingers after the stimulation period minus the distance between the index fingers before the stimulation period" (p. 10565). The results from 28 participants tested with this measure showed that, on average, participants proprioceptively perceived the receptive hand as being shifted by 3 cm toward the prosthetic hand (26% of the distance between the two hands). The fMRI experiment was conducted as a follow-up study. Fifteen participants were invited to take part, and these participants were randomly selected from the 25 participants who indicated that they experienced the illusion on the questionnaire (in Experiment 1). Experience of the illusion was associated with activation in intraparietal and cerebellar regions as well as the premotor cortex. Ehrsson et al. suggested that intraparietal, cerebellar and premotor regions detect correlated multisensory signals, and the detection of correlated signals by these brain regions may be the mechanism for the experience of body ownership.

The study included two types of control condition, each of which provided information about the constraints on the illusion of self-touch. The first control condition involved asynchronous stimulation. The participant administered touch to a prosthetic hand while the Examiner administered *asynchronous* touch to the participant's receptive hand. The illusion of self-touch was not elicited in this control condition: participants did not agree with the illusion statement on the questionnaire, they did not demonstrate proprioceptive drift of perceived hand position (*M* = .1cm, +/- 1.7cm), and they showed significantly less activation in the intraparietal and cerebellar regions and the premotor cortex than in the standard illusion condition. (Given that participants did not experience an illusion, time of illusion onset was not assessed.) Thus, the illusion of self-touch is constrained by the timing of stimulation administered to the prosthetic hand by the participant and the participant's receptive hand by the Examiner.

In the second control condition, the participant administered touch to the bristles of a dish brush (rather than a prosthetic hand) while the Examiner administered synchronous touch to the participant's receptive hand. The illusion of self-touch was not elicited in this control condition: participants did not agree with the illusion statement on the questionnaire and they showed significantly less activation in the intraparietal and cerebellar regions and the premotor cortex than in the standard illusion condition. (Time of illusion onset and proprioceptive drift in perceived hand position were not assessed.) The results indicate that the illusion of self-touch is constrained by the object of stimulation. Participants do not experience the illusion of self-touch when administering touch to a dish brush because the dish brush does not fit with the structural description of the body. Notably, in the self-touch rubber hand paradigm, the participant detects a match or mismatch with the structural description of the body using tactile rather than visual cues. That is, the participant identifies the object through touch, in contrast with the visual rubber hand paradigm, in which the participant is looking at the object as it receives stimulation from the Examiner.

As noted above, the current thesis will investigate four further constraints on the non-visual illusion of self-touch – object administering stimulation, distance, alignment, and anatomical plausibility – so as to build up a comprehensive framework for understanding this illusion. Before moving to the experimental chapters, I provide an outline of the thesis, and a brief summary of the seven experimental chapters.

Outline of Experimental Chapters

The thesis is divided into two sections. Part One investigates self-touch enhancement in patients following stroke, and Part Two investigates the illusion of self-touch in neurologically healthy individuals. There are seven empirical chapters, and twenty experiments are presented.

Part One

- *Chapter 2* presents six experiments investigating self-touch enhancement in patients who have experienced a right-hemisphere stroke (see White, Aimola Davies, Kischka, & Davies, 2010).
- *Chapter 3* presents six experiments investigating sensory localisation in a 21-year-old stroke patient who demonstrated systematic errors of sensory localisation under conditions of self-administered touch (see White, Aimola Davies, & Kischka, 2010).

Part Two

- *Chapter 4* presents three experiments investigating whether the illusion of self-touch is constrained by the object administering stimulation. The experiments manipulate the match between the stimulus used to administer touch to the prosthetic hand and the stimulus used to administer touch to the participant's hand. The first two experiments are conducted without vision, as is customary for studies investigating the illusion of self-touch. The third experiment is conducted with vision, and it is the first time in this area of research that the illusion of self-touch has been investigated with vision of the hands permitted (see White, Aimola Davies, Halleen, & Davies, 2010).

- *Chapter 5* presents one experiment investigating the visual version of the illusion of self-touch using both the questionnaire method used in Chapter 4, and a measure of proprioceptive drift of perceived hand position (see Aimola Davies, White, Thew, Aimola, & Davies, 2010).
- *Chapter 6* presents one experiment investigating the proprioceptively perceived position not only of the participant's receptive hand as is customary, but also of the participant's administering hand. This is the first time that proprioceptive drift of more than one of the participant's hands has been measured in the non-visual illusion of self-touch. Consequently this chapter presents a new interpretation of the illusion with respect to what the participant experiences when it seems that she is touching her own hand (see White, Aimola Davies, & Davies, 2011).
- *Chapter 7* presents two experiments investigating whether the illusion of self-touch is constrained by spatial factors. The first experiment manipulates distance and the second experiment manipulates alignment, of the prosthetic hand relative to the participant's receptive hand (Aimola Davies, White, & Davies, submitted manuscript).
- *Chapter 8* presents one experiment investigating whether the illusion of self-touch is constrained by anatomical plausibility. Specifically, the question asked is whether the participant can experience the illusion that she is touching a part of her body that she is unable to touch in everyday life (White & Aimola Davies, 2011).

PART ONE: SELF-TOUCH ENHANCEMENT FOLLOWING STROKE

CHAPTER 2: AN INVESTIGATION OF SELF-TOUCH ENHANCEMENT IN PATIENTS FOLLOWING RIGHT-HEMISPHERE STROKE

Following stroke, a patient may fail to report touch administered by another person but claim that she feels touch when it is self-administered. We investigated three explanations for self-touch enhancement: (1) proprioceptive information from the administering hand, (2) attentional modulation, and (3) temporal expectation. Tactile sensation was assessed with vision precluded, and with the affected hand positioned in the left and right hemispace. In four of six experiments, the self-touch rubber hand paradigm was used: the Examiner administered stimulation to the patient's affected left hand while guiding the patient's right hand to administer synchronous stimulation to a prosthetic hand. Even though the patient's two hands were not in contact, patients detected the same number of stimulations as when they touched their own hand directly (self-administered condition). Moreover, there was no decline in rates of detection when potentially informative movements of the administering hand were restricted. This demonstrates that patients feel rather than infer stimulation under conditions of self-touch. When patients received stimulation to the affected hand in the opposite hemispace to the hand administering touch to the prosthetic hand, all but one showed self-touch enhancement. Thus, neither proprioceptive information nor attentional modulation at the spatial region of the administering hand provided a sufficient explanation for self-touch enhancement. A follow-up experiment indicated an important role for temporal expectation: a delay, between the patient's stimulation of the prosthetic hand and the Examiner's stimulation of the patient's affected hand, eliminated the self-touch enhancement effect.

Weiskrantz and Zhang (1987) were the first to report self-touch enhancement in a right-hemisphere stroke patient. On conventional sensory testing, the patient was unable to detect force of less than 35 grams (filament of 0.6 mm diameter) administered to her left hand: healthy individuals detect intensities less than .07 grams. Despite clear sensory deficits, the patient "quietly and insistently maintained that she had feeling in her left hand when it was touched by her own right hand" (p. 632). Following a systematic assessment, Weiskrantz and Zhang confirmed that the patient enjoyed an "impressive degree of residual cutaneous sensitivity" (p. 634) when she was actively involved in the administration of touch.

Valentini et al. (2008) have recently assessed self-touch enhancement in 39 patients (22 with right-hemisphere damage and 17 with left-hemisphere damage), who were between 20 and 3308 days post-stroke. Seventeen right-hemisphere patients and five left-hemisphere patients demonstrated self-touch enhancement, operationally defined as (a) an improvement in stimulus detection, (b) an improvement in stimulus localisation, or (c) subjectively higher ratings of stimulus intensity under conditions of self-administered touch. The laterality bias (i.e., the higher rate of self-touch enhancement among patients with right-hemisphere damage) cannot be explained by concomitant visuospatial neglect. Self-touch enhancement was exhibited by patients with ($n = 5$) and without ($n = 17$) visuospatial neglect. Valentini et al.'s systematic research programme confirms that self-touch enhancement is a pervasive phenomenon, particularly among patients with right-hemisphere damage. However, the precise mechanisms underlying self-touch enhancement are yet to be established. Here we consider explanations in terms of (1) the patient using proprioceptive information from the administering hand to infer touch, and (2) the patient's administering hand directing attention to the affected body part.

Proprioceptive Information

Under conditions of self-touch, a patient may use proprioceptive information from the administering hand to infer stimulation. By judging the position of her administering hand relative to the affected body part, the patient may infer that she is being touched and she may report stimulation based on knowledge rather than feeling. The pioneering studies on self-touch enhancement took important steps to restrict the patient's use of proprioceptive information. To eliminate cues based on skin-to-skin contact, the patient used an instrument to administer stimulation (Valentini et al., 2008; Weiskrantz & Zhang, 1987); to make localisation more difficult, the Examiner moved the patient's administering hand between trials (Valentini et al., 2008). Sham trials provided an additional measure for ensuring the reliability of patient responses (Valentini et al., 2008; Weiskrantz & Zhang, 1987). On sham trials, the Examiner guided the patient to administer stimulation to one of the Examiner's fingers, which were inter-digited with the fingers of the patient's affected hand. If the patient reported touch only on valid trials (and not on sham trials) this provided an indication that the patient was *feeling* touch when she administered stimulation to her own hand. But, it is also possible that the patient may have used subtle differences in the location of her administering hand to distinguish valid from sham stimulations, given that she was guided to a slightly different location on these two trial types.

Each of the measures introduced by Valentini et al. (2008) and Weiskrantz and Zhang (1987) *reduces* proprioceptive information. To discount completely the explanation of proprioceptive information playing a role in self-touch enhancement, we use the self-touch rubber hand paradigm (Ehrsson et al., 2005). In the self-touch rubber hand paradigm, the Examiner administers stimulation to the patient's affected hand while guiding the patient's unaffected hand to administer synchronous stimulation to a prosthetic hand. Using this paradigm, neurologically healthy individuals have been shown to experience the powerful illusion of self-touch, even though the two hands are separated by 15 cm (Ehrsson et al). This illusion is driven by multisensory correlations between proprioceptive and tactile inputs – the participant *administers* stimulation (to the prosthetic hand) and *receives* corresponding stimulation on her receptive hand. We can use this paradigm to investigate possible explanations for self-touch enhancement, by holding constant the conditions of actual self-touch (i.e., the action of the patient's administering hand, the stimulation to the patient's affected hand, and the temporal correspondence between these two events) but removing the proprioceptive correspondence between the patient's administering and receptive hand. An explanation for self-touch enhancement based on the patient using proprioceptive information to infer touch is eliminated. The patient can no longer infer stimulation based on the relative position of her two hands because she is now administering and receiving touch in two distinct spatial locations, and this is true regardless of whether the patient has the subjective impression that she is touching her own hand.[3] Moreover, on sham trials, no stimulation is administered to the patient's affected hand (by the Examiner) but the patient is guided to administer stimulation to the prosthetic hand (as she is on valid stimulation trials). Because the location of the patient's administering hand is identical on valid and sham trials, she cannot use subtle differences in hand position to distinguish these two trial types. Consequently, our first prediction: if the explanation for self-touch enhancement is that the patient uses relative hand position to determine *whether* she has been touched, detection will decline when the patient is no longer able to use hand position to infer stimulation.

Even if the patient does not use relative hand position to decide whether she is being touched, she may use subtle movements of her administering hand to focus attention. For example, if the patient detects a stimulation to her middle finger, and the next movement of the administering hand is leftward, she may use this information to focus attention now on the ring and little finger. But these potentially informative movements of the administering hand can be held to a minimum by guiding the patient to stimulate the same location on all trials (the back of the prosthetic hand), while each of her five digits continues to receive stimulation from the Examiner. Our second prediction: if the patient uses subtle movements of the administering hand to focus attention, *detection* should decline when movements of the hand are restricted. Alternatively, if the patient uses subtle movements to localise felt sensations, *localisation* (but not detection) should decline when movements of the hand are restricted.

[3] If a patient experiences the illusion that she is touching her own hand, then this is evidence in itself that the patient feels tactile stimulation under conditions of self-touch, rather than reports stimulation based on knowledge derived from relative hand position. To experience the subjective impression that the touch on one's receptive hand is due to the action of one's administering hand (i.e., the illusion of self-touch), one must *feel* the stimulation on the receptive hand. That is, there must be a correlation between the proprioceptively-experienced action of the administering hand and the tactile inputs to the affected hand. Touching the prosthetic hand does not in itself lead to the *illusion* of self-touch. Rather, the illusion occurs if the individual touches the prosthetic hand and *feels* corresponding tactile sensations on the receptive hand. If a patient does not experience the illusion of self-touch, the paradigm is nonetheless well-suited to investigating self-touch enhancement. The stimulation on the patient's affected hand (by the Examiner) and the action of the patient's administering hand (relative to the prosthetic hand) are matched to the condition of actual self-touch. That is, the patient receives stimulation to her own hand as she administers stimulation.

Attentional Modulation

Valentini et al. (2008) have proposed that self-touch enhancement may be due to attentional modulation. Impetus for this proposal comes from research conducted by Coslett and Lie (2004) demonstrating that the unaffected hand serves as an 'attentional wand' which directs processing resources to the affected side of the body. Coslett and Lie (2004) present two patients with sensory deficits following right-hemisphere stroke. The first patient exhibited sensory extinction, failing to report touch to the left hand under conditions of bilateral stimulation. The second patient exhibited severe left-side sensory deficits affecting unilateral touch, proprioception and temperature discrimination. In both patients, report of Examiner-administered stimuli on the left hand improved when the patients' right and left hands were in contact during stimulation. This enhancement was proposed to result from attentional modulation, driven by the behavioural salience of the unaffected hand (Coslett & Lie, 2004).

Reed, Garza, and Roberts (2007) review the role of the body in spatial attention. The researchers observe an important role for the hands in the allocation of attention, noting that this role depends on whether the hand is static (e.g., the unaffected hand in Coslett & Lie, 2004) or in action (e.g., the unaffected hand in Valentini et al., 2008 and Weiskrantz and Zhang, 1987). When the hand is static, the "region near the hand may be prioritized so that the potential relevance of cues and targets appearing in that space is increased" (p. 47). By contrast, when the hand is moving, attention shifts to the "functional spatial range of the action" (p. 51) rather than the hand itself. Given this distinction, it is possible that the sensory enhancement exhibited by Coslett and Lie's patients is driven by a different attentional process to that exhibited by the patients with self-touch enhancement in the studies of Weiskrantz and Zhang and Valentini et al.

It may be possible to shed further light on the attentional modulation theory using the self-touch rubber hand paradigm. If the prosthetic hand were positioned in the opposite hemispace to the patient's affected hand, the patient would administer touch (to the prosthetic hand) in one hemispace and receive touch (on the affected hand) in the opposite hemispace. In this condition, the patient's affected hand would not fall "within the functional spatial range" (Reed et al., 2007, p. 57) of the administering hand action. Our third prediction: if self-touch enhancement occurs because attention is enhanced in the region of space in which a motor programme unfolds (see Rizzolatti, Riggio, Dascola, & Umilta, 1987; Umilta, 2000), detection should decline when the patient administers and receives stimulation in opposite sides of space.

Overview of Experiments

Experiments 1 and 2 provided baseline rates for Examiner- and self-administered stimulation. Following on from these experiments, the self-touch rubber hand paradigm was used to investigate an explanation for self-touch enhancement based on proprioceptive information from the administering hand. In Experiment 3, the patient administered stimulation to the digit of the prosthetic hand corresponding to the digit of her own hand receiving stimulation from the Examiner. In this experiment, the patient could not use the relative position of her two hands to infer stimulation. In Experiment 4, the patient administered stimulation to the same location on the back of the prosthetic hand on all trials. In this experiment, potentially informative movements of the patient's administering hand were held to a minimum. In Experiment 5, the self-touch rubber hand paradigm was used to investigate an explanation for self-touch enhancement based on attentional modulation. The prosthetic hand and the patient's affected hand were positioned so that the patient administered and received stimulation in distinct spatial regions, one hand in each hemispace. In this experiment, the administering hand directed the patient's attention away from the affected hand.

General Methods

Patient Recruitment

Five right-hemisphere stroke patients were examined as Valentini et al. (2008) have shown that self-touch enhancement occurs more frequently among patients with right-hemisphere damage. Three patients (Patients NG, SM, SK) were recruited from the inpatient rehabilitation ward at the Oxford Centre for Enablement, and two patients (Patients CJ, CA) from the outpatient services of the Oxford Centre for Enablement. Patients CJ and CA were chosen specifically because they were attending therapy sessions on the day of inpatient recruitment. On the day of patient recruitment, there were 17 patients on the inpatient ward, 10 were stroke patients (four with right-hemisphere lesions, five with left-hemisphere lesions and one patient with bilateral lesions). One of the four inpatients with a right-hemisphere lesion declined to participate.

The patients were assessed following a protocol approved by the NHS Oxfordshire Research Ethics Committee C, and in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki. Patients gave informed consent prior to participating in this study.

Patient Assessment

Patient demographics and details from the neuropsychological assessment are presented in Table 2. The Mini-Mental State Examination (MMSE: Folstein, Folstein, & McHugh, 1975) was used as a brief screen of cognitive function. Handedness was evaluated using the Edinburgh Handedness

Inventory (Oldfield, 1971). Patients were assessed for personal and peripersonal neglect. Zoccolotti and Judica's (1991) personal neglect battery was used (with the scoring system proposed by McIntosh, Brodie, Beschin, & Robertson, 2000), along with Bisiach's 'reach test' in which the patient reaches for his or her contralesional thumb using the ipsilesional hand (Bisiach, Vallar, Perani, Papagno, & Berti, 1986). Bisiach's reach test also provides a measure of position sense, as the patient needs to locate the affected thumb without vision. All patients reached for their thumb without hesitation, and in a single movement. Peripersonal neglect was assessed using Star Cancellation, Letter Cancellation and Line Bisection subtests from the Behavioural Inattention Test (Wilson, Cockburn, & Halligan, 1987), Schenkenberg's Line Bisection test (Schenkenberg, Bradford, & Ajax, 1980), Baking Tray test (Tham & Tegnér, 1996), Scene Copying (adapted from Ogden, 1985) and two drawing tasks (Self-Portrait and "Draw a Man"; Goodenough, 1926).

Motor and sensory functions were assessed using the Motricity Index for Motor Impairments after Stroke (Collin &Wade, 1990; Demeurisse, Demol, & Robaye, 1980), the Revised Nottingham Sensory Assessment (Lincoln, Jackson, & Adams, 1998) and a standardised confrontation method. The confrontation method was used to assess neglect (failure to report contralesional events) and extinction (failure to report contralesional events on bilateral, but not unilateral, stimulus trials) in the visual, auditory and somatosensory modality. In each modality, the patient was presented with 10 unilateral right, 10 unilateral left and 20 bilateral stimulus trials. The patient indicated awareness of the stimulus by saying 'right' if the stimulus was on the right, 'left' if the stimulus was on the left, or 'both' if there were two simultaneously presented stimuli.

Sensory Thresholds

In the experiments investigating self-touch enhancement, stimulation was administered using Semmes-Weinstein monofilaments. Prior to testing, each patient's sensory threshold for Examiner-administered stimulation was established: the Examiner stimulated the proximal phalanx of each of the fingers and the thumb with vision of the hand precluded. Each digit received three stimulations, and threshold was defined as the lowest intensity at which the patient detected one stimulation (minimum) to at least three digits. This criterion avoided a ceiling effect in Experiment 1, which was the Examiner-administered stimulation condition. Once established, this intensity was used for all experiments (.6958 grams: NG, SM; 2.052 grams: CJ; 3.632 grams: CA; .0275 grams: SK). Four patients (NG, SM, CJ, CA) exhibited a sensory impairment on threshold testing, and the experimental results for these four patients are presented. The fifth patient (SK) exhibited normal sensory function and no change in stimulus detection when Examiner- and self-administered stimulation conditions were compared (including conditions using the self-touch rubber hand paradigm). The experimental results for this patient are not presented.

Table 2

Patient Test Results

		NG	CJ	SM	AC	SK
Patient Profile	Sex	F	F	M	M	M
	Age	21	42	69	67	69
	Time Since Stroke	3.5 m	19 m	10 m	58 m	2.5 m
	Lesion Location	R(F)	R (FP)	R MCA	R MCA	R Lacunar
Screen	MMSE	24	30	29	26	30
	Handedness	100	82	100	100	82
Personal Neglect	Comb Test	-	-	+	-	-
	Razor/Powder Test	-	-	-	-	-
	Bisiach Reach Test	-	-	-	-	-
Peripersonal Neglect	Star Cancellation	-	-	-	-	-
	Letter Cancellation	-	+	-	-	-
	Line Bisection	-	-	+	-	-
	Schenkenberg's Line Bisection	-	-	+	+	-
	Baking Tray Test	-	-	+	-	-
	Scene Copying (1)	-	+	+	-	-
	Scene Copying (2)	+	+	-	-	-
	Drawing: Person	-	-	-	-	-
	Drawing: Self Portrait	-	-	-	-	-
Motricity Index	Arm (L/R)	84/100	77/100	1/81	60/100	40/100
	Leg (L/R)	54/100	60/100	43/100	49/81	51/100
	Side of Body (L/R)	69/100	68.5/100	22/90.5	54.5/90.5	45.5/100
Nottingham Sensory Assessment	Light Touch (L/R): hand	-/-	-/-	-/-	-/-	-/-
	Light Touch (L/R): elbow	-/-	-/-	+/+	-/-	-/-
	Deep Pressure (L/R): hand	-/-	-/-	-/-	-/-	-/-
	Deep Pressure (L/R): elbow	-/-	-/-	-/-	-/-	-/-
	Localisation (L/R): hand	+/nt	+/-	+/nt	+/+	-/nt
	Localisation (L/R): elbow	-/nt	+/+	+/nt	+/nt	-/nt
	Temperature (L/R): hand	-/-	-/-	+/-	+/-	-/-
	Temperature (L/R): elbow	-/-	-/-	-/+	-/-	-/-
	Proprioception (L/R): wrist	-/-	-/-	+/nt	-/nt	-/nt
	Proprioception (L/R): elbow	-/-	-/-	nt/nt	-/nt	-/nt
	Stereognosis (L)	-	+	+	-	-
	Two-point discrimination (L)	-	-	+	nt	nt
Confrontation Method	Visual	-	-	Neglect	-	-
	Auditory	-	-	Neglect	Extinction	-
	Somatosensory	-	-	Neglect	Extinction	-

Lesion Location: 'F' = frontal, 'P' = parietal, 'MCA' = middle cerebral artery, 'Lacunar' = lacunar infarct.

Handedness: Positive values of 40+ indicate right-handedness.

Task performance: '+' = presence of deficit; '-' = absence of deficit; 'nt' = not tested.

Motricity Index: Minimum score equals 0, maximum score equals 100.

Experiment 1

Experiment 1 was used to establish each patient's baseline performance for stimulation administered by the Examiner.

Method

Patients were seated comfortably and blindfolded. The patient's left (affected) hand was positioned palm downwards on a testing table. The patient's right (unaffected) hand was positioned on the patient's lap. Sensation was assessed with the patient's left hand positioned first in the left hemispace and then in the right hemispace. The patient's middle finger was positioned 20 cm from body midline. Stimulation was administered at five locations on the left hand (the dorsal proximal phalanx of the thumb and each of the fingers) and at an unpredictable pace (approximately one stimulation every 5–8 s).

In each of the left and right hemispace conditions, the patient received 10 stimulations to each digit. There were also 10 sham stimulations in which no touch was administered. Sham trials were included to screen for unreliable responders, defined as patients responding to more than two sham trials in an experimental condition. Following each trial, the patient was asked whether he or she could (a) detect the tactile stimulation and (b) localise the tactile stimulation. The patient indicated which digit had been touched either by name or by number (thumb: 1, index: 2, middle: 3, ring/fourth: 4, little: 5). Patients frequently offered this information as soon as the digit was stimulated; that is, prior to the Examiner's prompt.

Statistical Analyses

Statistical analyses were conducted using the Q' test (see Michael, 2007), which tests the hypothesis of equal proportions and is appropriate for single-case analyses. The Q' statistic has a χ^2 distribution with $K - 1$ degrees of freedom, where K equals the number of experimental conditions.

Results

None of the patients responded to more than two sham trials in any of the left or right hemispace conditions. As this is true of all experiments reported herein, no patient was excluded due to unreliable responses.

Effect of Hemispace

Detection and localisation. Experiment 1 provides baseline detection and localisation rates under conditions of Examiner-administered stimulation. Detections are reported as a raw score out of 50 (Table 3). Mislocalisations are reported as a percentage of the *detected* stimulations (Table 4). No patient exhibited a difference in stimulus detection or stimulus localisation when the affected hand was positioned in the left versus the right hemispace. Due to stiffness in Patient CA's elbow and wrist, the desired positioning of the hand was possible in the left hemispace only.

Table 3

*Stimulus Detection (/50) for Experiments 1 through 5. Detection rates in Experiments 2 through 5 were analysed against Experiment 1 (shaded column) to assess for sensory enhancement. Significant results are indicated with **

	Patient	Exp. 1	Exp. 2	P	Sig.	Exp. 3	P	Sig.	Exp. 4	P	Sig.	Exp. 5	P	Sig.
Left Hemispace	NG	31	43	.019	*	48	.000	***	50	.000	***	48	.001	**
	CJ	32	46	.003	**	48	.000	***	50	.000	***	49	.000	***
	SM	36	48	.005	**	47	.013	*	43	.150		44	.093	
	CA	27	41	.009	*	41	.009	*	37	.076		40	.010	*
Right Hemispace	NG	36	46	.028	*	49	.001	**	48	.005	**	49	.001	**
	CJ	32	49	.000	***	50	.000	***	49	.000	***	50	.000	***
	SM	31	42	.034	*	46	.002	**	45	.004	**	34	.597	
	CA	-	-			-			-			-		

Significance: * $p < 0.05$, ** $p < 0.005$, *** $p < 0.0005$.

Table 4

*Stimulus Mislocalisation (% detected stimulations) for Experiments 1 through 5. Mislocalisation rates in Experiments 2 through 5 were analysed against Experiment 1 (shaded column) to assess for changes in localisation contingent upon self-involvement. Significant results are indicated with **

	Patient	Exp. 1	Exp. 2	P	Sig.	Exp. 3	P	Sig.	Exp. 4	P	Sig.	Exp. 5	P	Sig.
Left Hemispace	NG	9.7%	16.3%	.493		22.9%	.189		26%	.111		20.8%	.259	
	CJ	62.5%	56.5%	.590		66.7%	.744		74%	.351		32.7%	.020	*
	SM	44.4%	35.4%	.476		34%	.412		58.1%	.017	*	36.4%	.533	
	CA	48.1%	14.6%	.009	*	51.2%	.830		54.1%	.687		40%	.569	
Right Hemispace	NG	19.4%	23.9%	.683		4%	.075		16.7%	.785		6.1%	.136	
	CJ	56.3%	59.2%	.823		32%	.060		63.2%	.589		44%	.351	
	SM	41.9%	16.7%	.042	*	23.9%	.155		64.4%	.092		64.7%	.110	
	CA	-	-			-			-			-		

Significance: * $p < 0.05$, ** $p < 0.005$, *** $p < 0.0005$.

Experiment 2

Experiment 2 was designed to replicate the self-touch enhancement effect (Valentini et al., 2008; Weiskrantz & Zhang, 1987). Positioning of the affected hand was not described in the previous studies of self-touch enhancement. We assess sensation with the affected hand positioned first in the left hemispace and then in the right hemispace. Studies investigating somatosensory extinction have shown that detection of stimuli administered to a patient's left hand may be enhanced when the left hand is positioned to the right of body midline, or to the right of the unaffected right hand (e.g., Moro, Zampini, & Aglioti, 2004; Smania & Aglioti, 1995). Given that somatosensory processing has been shown to occur within spatial frames of reference (see Vallar, 1997), it is hypothesised that patients with neglect or extinction may exhibit a superior sensory enhancement effect when administering touch in the non-neglected side of space.

Method

The procedure was as for Experiment 1, with the exception that in the previous experiment the stimulation was administered by the Examiner without patient involvement, whereas in this experiment the patient's right hand was guided by the Examiner so that the patient self-administered touch to his or her affected left hand. On sham trials, the patient administered touch to the Examiner's hand, which was positioned in close proximity to (but without touching) the patient's hand.

Results

Effect of Experimental Manipulation

Detection. All four patients exhibited self-touch enhancement, indicated by a higher rate of detection under conditions of patient-administered stimulation, compared to the baseline Examiner-administered stimulation of Experiment 1 (Table 3).

Localisation. Patient SM and Patient CA exhibited enhanced stimulus localisation (i.e., a lower rate of stimulus mislocalisations) under conditions of self-administered touch. For Patient SM, this effect was only apparent when the affected left hand was positioned in the right hemispace. For Patients NG and CJ there was no change in stimulus localisation compared to Experiment 1, in which stimulation was administered by the Examiner (Table 4).

Effect of Hemispace

Detection and localisation. Position of the affected hand (left versus right hemispace condition) did not make a significant difference to detection or to localisation of stimuli. Although there was no significant hemispace effect for any of the patients, Patient SM did exhibit a trend towards enhanced stimulus localisation (i.e., lower rates of stimulus mislocalisation) when his left hand was positioned in the right hemispace ($p = 0.08$), and Patient CA was only assessed in the left hemispace.

Experiment 3

In Experiment 3, the self-touch rubber hand paradigm (Ehrsson et al., 2005) was used to investigate whether the self-touch enhancement effect is maintained when the patient is unable to use knowledge about the relative position of each of the hands to infer stimulation.

Method

Stimulation was again administered using a Semmes-Weinstein monofilament, but this time the patient administered stimulation to the prosthetic hand (Regal brand) rather than to his or her own hand. The prosthetic hand was positioned on a testing unit above the patient's affected hand. The testing unit measured 30 cm (length) × 25 cm (width) × 13 cm (height).

The Examiner administered stimulation to the patient's affected left hand (as in Experiment 1), while the patient's right hand was guided by the Examiner (as in Experiment 2) to administer stimulation to a prosthetic hand. Sensation was assessed with the patient's affected hand positioned first in the left hemispace and then the right. To eliminate proprioceptive correspondence, the patient's affected hand and the prosthetic hand were misaligned (by 5 cm). The patient's affected hand was positioned with the middle finger 20 cm from body midline. The prosthetic hand was positioned with the middle finger 15 cm from body midline. On sham trials, the patient administered stimulation to the prosthetic hand (as on valid trials), but no stimulation was administered to the patient's hand. The number and location of stimulations were as for Experiment 1.

Results

Effect of Experimental Manipulation

Detection. All four patients exhibited sensory enhancement in Experiment 3, even though the patient was now administering stimulation to the prosthetic hand, rather than to his or her affected hand. Sensory enhancement was indicated by a higher rate of detection when compared to the baseline Examiner-administered stimulation of Experiment 1 (Table 3).

Detection rates were also compared to Experiment 2 to assess whether there was a difference in detection when the patient was administering stimulation to his or her own hand directly. There was no difference in detection rates between Experiments 2 and 3, demonstrating that the patient does not use relative hand position to infer touch (all p values $>.05$).

Localisation. There was no change in stimulus localisation when compared to Experiment 1 in which stimulation was administered by the Examiner (Table 4). Localisation was compared to Experiment 2 to assess whether there was a difference in localisation when the patient administered stimulation to his or her hand directly. Patients CA, NG and CJ exhibited changes in stimulus localisation when administering stimulation to the prosthetic hand compared to the affected hand directly. Patient CA demonstrated a greater number of stimulus mislocalisations in the left hemispace condition (mislocalisation rates for Experiment 3 versus Experiment 2: 51.2% versus 14.6%, $Q'(1) = 9.72$, $p = 0.0018$). Patient NG and Patient CJ exhibited enhanced stimulus localisation in the right hemispace conditions (Patient NG: 4% versus 23.9%, $Q'(1) = 5.40$, $p = 0.0201$; Patient CJ: 32% versus 59.2%, $Q'(1) = 5.48$, $p = 0.0193$). For Patient SM there was no change in stimulus localisation (Figure 4).

Effect of Hemispace

Detection and localisation. Stimulus *detection* was not improved by positioning the affected hand in the left versus right hemispace, however stimulus *localisation* was enhanced (i.e., a lower rate of stimulus mislocalisations) for two patients in the right hemispace condition. Patient NG mislocalised 22.9% of stimulations when her hand was positioned in the left hemispace and 4% of stimulations when her hand was positioned in the right hemispace ($Q'(1) = 5.11$, $p = 0.0238$). Patient CJ mislocalised 66.7% of stimulations when her hand was positioned in the left hemispace and 32% of stimulations when her hand was positioned in the right hemispace ($Q'(1) = 9.02$, $p = 0.0027$). Note that CA was only assessed in the left hemispace.

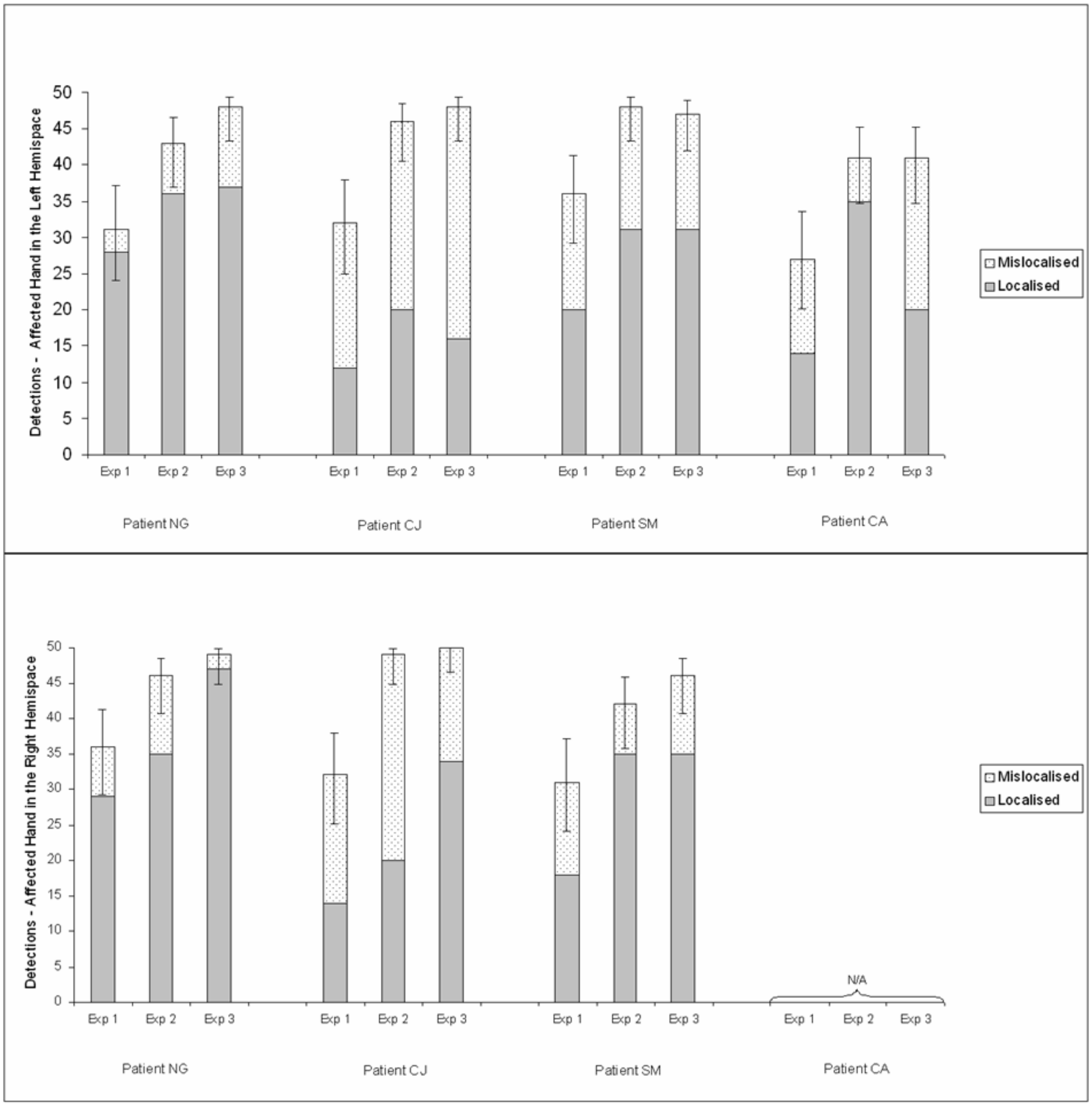

Figure 4. Detection and localisation of stimulations: Experiment 1 (Examiner administers stimulation to the patient's hand), Experiment 2 (Patient administers stimulation to the patient's hand) and Experiment 3 (Examiner administers stimulation to the patient's hand and patient administers stimulation to the prosthetic hand). Error bars indicate the 95% confidence intervals for overall detection (Wilson, 1927).

Experiment 4

Experiment 4 was designed to control for the possibility that movements of the administering hand are used as an aid to stimulus detection and localisation under conditions of self-administered touch. In Experiment 3, the patient administered touch to the digit of the prosthetic hand which *corresponded* to the digit of his or her hand receiving stimulation from the Examiner. Even though the patient could not use the relative position of each hand to judge whether the affected hand was being touched, it is still possible that subtle movements of the administering hand were used to *localise* touch. Specifically, it is possible that the patient attended to the movements made by the administering hand relative to the prosthetic hand, and used these movements to guide attention. For example, if the patient detected touch to the middle finger, and the next movement of the administering right hand to the prosthetic hand was leftward, the patient may have used this information to focus attention on the ring and little finger of his or her affected hand in preparation for the next stimulation. In Experiment 4, movements of the patient's administering hand were held to a minimum.

Method

The Examiner administered stimulation to the five digits of the patient's affected left hand (as in Experiment 1), while the patient's right hand was guided by the Examiner (as in Experiment 2) to administer stimulation to the *back* of the prosthetic hand. The Examiner guided the patient's hand to the same location on every trial, in this way the patient's touch was informative with regard to the timing of stimulation but not the relative location. Sensation was assessed with the left hand positioned first in the left hemispace and then in the right hemispace. The patient's affected hand and the prosthetic hand were misaligned by 5 cm, as in Experiment 3.

On sham trials, the patient administered stimulation to the back of the prosthetic hand (as on valid trials), but no stimulation was administered to the patient's hand. The number and location of stimulations were as for Experiment 1.

Results

Effect of Experimental Manipulation

Detection. Patients NG, CJ and SM exhibited sensory enhancement, which was indicated by a higher rate of stimulus detection in Experiment 4 compared to Experiment 1. Sensory enhancement occurred even though the patient always administered stimulation to the same point on the back of the prosthetic hand, so that subtle movements of the administering hand could not be used to localise touch. For Patient SM, this sensory enhancement effect was only apparent in the right hemispace condition. Although Patient CA did not show a statistically significant sensory enhancement effect, the Q' statistic approached significance (p = 0.07) suggesting a trend towards sensory enhancement (Table 3).

Detection rates were compared to Experiment 3 to assess whether there was a difference in detection when the patient touched the digit of the prosthetic hand corresponding to the digit of his or her own hand being touched by the Examiner. Rates of stimulus detection were the same, whether the patient was administering stimulation to the digit of the prosthetic hand corresponding to the digit of his or her hand being touched (Experiment 3) or administering stimulation to the same location on the back of the prosthetic hand across all trials (Experiment 4) (all p values >0.05).

Localisation. In the left hemispace condition, Patient SM exhibited a higher rate of stimulus mislocalisations when he was administering touch to the same point on the back of the prosthetic hand, compared to Experiment 1 in which he was not involved in the administration of touch ($p = 0.0178$) (Table 4). For Patients NG, CJ and CA, there was no change in stimulus localisation when compared to Experiment 1 in which stimulation was administered by the Examiner.

Localisation was compared to Experiment 3 to assess whether there was a difference in localisation when the patient touched the digit of the prosthetic hand corresponding to the digit of his or her hand being touched by the Examiner. Patient CJ and Patient SM exhibited a higher rate of stimulus mislocalisations when administering stimulation to the same location on the prosthetic hand across all trials (Experiment 4). For Patient CJ, this effect was only apparent in the right hemispace condition (mislocalisation rates for Experiment 4 versus Experiment 3: 63.2% versus 32%, $Q'(1) = 7.32$, $p = 0.0068$). For Patient SM, this effect was apparent in both the left (mislocalisation rates for Experiment 4 versus Experiment 3: 58.1% versus 34%, $Q'(1) = 3.88$, $p = 0.0487$) and the right hemispace conditions (mislocalisation rates for Experiment 4 versus Experiment 3: 64.4% versus 23.9%, $Q'(1) = 12.01$, $p = 0.0005$). For Patients NG and CA there was no change in stimulus localisation (Figure 5).

Effect of Hemispace

Detection and localisation. There was no significant hemispace effect for any of the patients: position of the affected hand (left versus right hemispace condition) did not make a significant difference to detection or to localisation of stimuli. Note that CA was only assessed in the left hemispace.

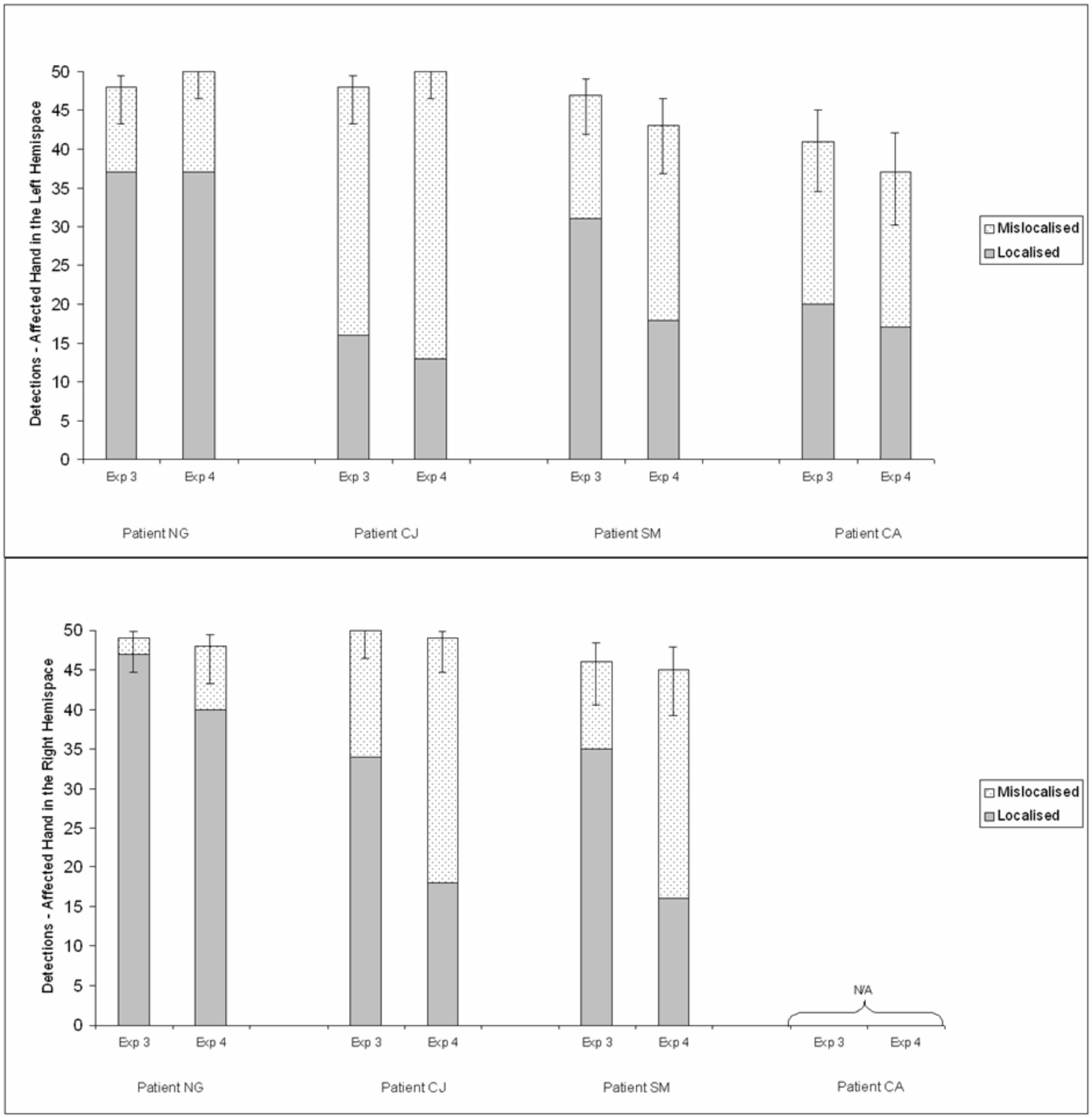

Figure 5. Detection and localisation of stimulations: Experiment 3 (localisation cues) and Experiment 4 (no localisation cues). Error bars indicate the 95% confidence intervals for overall detection (Wilson, 1927).

Experiment 5

In Experiment 5, the prosthetic hand and the patient's affected hand were positioned so that the patient administered and received stimulation in distinct spatial regions, one hand in each hemispace. It has been argued that under conditions of self-administered touch, the hand administering the stimulation (i.e., the patient's unaffected hand) may direct the patient's attention to the affected hand (Valentini et al., 2008). According to this proposal, enhanced sensory performance is a product of increased attention. If the administering hand directs attention in spatial coordinates, stimulus detection should decline when the hands are positioned in opposite sides of space.

Method

The Examiner administered stimulation to the patient's affected left hand while the patient's right hand was guided by the Examiner to administer stimulation to the prosthetic hand. The patient's affected hand and the prosthetic hand were positioned in opposite sides of space. Sensation was assessed first with the patient's affected hand positioned in the left hemispace and then with the affected hand positioned in the right hemispace. As with the previous experiments, the middle finger of the patient's hand was 20 cm from body midline and the middle finger of the prosthetic hand was 15 cm from body midline (but in the opposite hemispace). On sham trials, the patient administered stimulation to the prosthetic hand (as on valid trials), but no stimulation was administered to the patient's hand. The number and location of stimulations were as for Experiment 1.

Results

Effect of Experimental Manipulation

To assess for sensory enhancement, we compared detection and localisation rates in Experiment 1 and Experiment 5, with the position of the *affected* hand matched for each comparison. For example, detection in the left hemispace condition of Experiment 1 was compared to detection when the patient's affected hand was positioned in the left hemispace but the patient administered touch in the right hemispace.

To assess for changes contingent upon the position of the administering hand, we compared detection and localisation rates in Experiment 3 and Experiment 5, with the position of the *affected* hand matched for each comparison. For example, detection in the left hemispace condition of Experiment 3 was compared to detection when the patient's affected hand was positioned in the left hemispace but the patient administered touch in the right hemispace.

Detection. Patients NG, CJ and CA exhibited a sensory enhancement effect, which was indicated by a higher rate of stimulus detection in Experiment 5 compared to Experiment 1. Patient SM did not exhibit sensory enhancement in either hemispace, although there was a trend towards enhancement when his affected hand was positioned in the left hemispace (p = 0.09) (Table 3).

Detection was also compared to Experiment 3 to assess whether there was a difference in detection when the patient administered stimulation to the prosthetic hand positioned in the same hemispace as the affected hand. Patient SM exhibited a decline in stimulus detection in the right hemispace condition of Experiment 5 (92% Experiment 3 versus 68% Experiment 5,

$Q'(1) = 6.52$, $p = 0.0107$). For Patients NG, CJ and CA, rates of stimulus detection were the same whether the patient was administering stimulation to the prosthetic hand located in the same (Experiment 3) or the opposite (Experiment 5) hemispace to the patient's own affected hand (all p values >0.05).

Localisation. When her affected hand was positioned in the left hemispace, Patient CJ exhibited enhanced stimulus localisation (i.e., a lower rate of stimulus mislocalisations) compared to Experiment 1 in which she was not involved in the administration of touch. For Patients NG, SM and CA, there was no change in stimulus localisation when compared to Experiment 1 (Table 4).

Localisation was compared to Experiment 3 to assess whether there was a difference in localisation when the patient administered stimulation to the prosthetic hand positioned in the same hemispace as the affected hand. Localisation was affected in Patient CJ and Patient SM. Patient CJ exhibited enhanced stimulus localisation (i.e., a lower rate of stimulus mislocalisations) in the left hemispace condition of Experiment 5 (mislocalisation rates for Experiment 5 versus Experiment 3: 32.7% versus 66.7%, $Q'(1) = 8.58$, $p = 0.0034$). Patient SM exhibited a higher rate of stimulus mislocalisations in the right hemispace condition of Experiment 5 (mislocalisation rates for Experiment 5 versus Experiment 3: 64.7% versus 23.9%, $Q'(1) = 10.64$, $p = 0.0011$). For Patients NG and CA there was no change in stimulus localisation (p values >0.05).

Effect of Hemispace

Detection and localisation. Stimulus detection was not improved by positioning the affected hand in the left versus right hemispace, nor was stimulus localisation for Patients CJ and NG. However, Patient SM exhibited a higher rate of stimulus mislocalisations ($Q'(1) = 4.71$, $p = 0.03$) when his affected hand was positioned in the right hemispace (and the prosthetic hand was positioned in the left hemispace). Note that Patient CA was only assessed with his affected hand in the left hemispace.

Interim Discussion

The results from Experiments 1–5 confirm that patients with impaired sensation are better at detecting sensory stimulation when they are involved in administration. We assessed four patients with impaired sensation and found that, in these patients, enhanced sensation under conditions of self-touch was not due to patients using proprioceptive information from the administering hand to infer touch (Experiment 3). Furthermore, enhanced detection of stimulation did not depend on patients using information about subtle movements of the administering hand to focus attention on a particular digit of the affected hand, although two patients (CJ and SM) used these movements to localise stimulation (Experiment 4). For one patient (SM), an explanation of enhanced detection in terms of attentional modulation was partially supported: stimulus detection declined when the administering hand and the receptive hand were positioned in opposite sides of space (Experiment 5). For the remaining three patients enhancement was not contingent on spatial cues from the administering hand.

Having established that self-touch enhancement does not occur because the patient uses proprioceptive information from the administering hand to infer touch (explanation 1) and does not necessarily occur because the administering hand directs attention spatially (explanation 2) we must consider alternative explanations for the effect. Here we propose a new hypothesis for self-touch enhancement in terms of temporal expectation (explanation 3). The advantage for self-touch may be due to the patient using temporal cues to set attention effectively. That is, the patient knows when stimulation will be administered and can tune attention to a precise point in time. If under conditions of self-touch the action of the administering hand provides a precise temporal cue for focusing one's attention, stimulus detection should decline when the action of the administering hand and the stimulation on the affected hand are temporally disambiguated. This new hypothesis is investigated in Experiment 6 with Patient NG.

Experiment 6

Method

In Experiment 6, the Examiner administered stimulation to Patient NG's affected left hand while her right hand was guided by the Examiner to administer stimulation to the prosthetic hand. A 1-s delay was introduced: the Examiner guided the patient to administer stimulation to the prosthetic hand before the patient's affected hand was stimulated by the Examiner. The patient's affected hand and the prosthetic hand were positioned in the same side of space (as in Experiments 3 and 4). Sensation was assessed first with the patient's affected hand positioned in the left hemispace and then in the right. The number and location of stimulations were as for Experiment 1.

Results

Effect of Experimental Manipulation

Detection. NG detected 64% of stimulations when her hand was in the left hemispace and 72% of stimulations when her hand was in the right hemispace. There was no longer a self-touch enhancement effect. Detection returned to the level of the baseline Examiner-administered stimulation condition of Experiment 1: 62% (p = 0.8618) and 72% (p = 1.000) in the left and right hemispace, respectively.

Localisation. NG mislocalised 6.25% of reported stimulations when her hand was in the left hemispace and 8.33% of reported stimulations when her hand was in the right hemispace. There was no change in stimulus localisation when compared to the baseline Examiner-administered stimulation condition (9.68% of reported stimulations mislocalised ($p = 0.6965$) and 19.44% of reported stimulations mislocalised ($p = 0.2623$) in the left and right hemispace, respectively).

Effect of Hemispace

Detection and localisation. There was no significant hemispace effect: position of the affected hand (left versus right hemispace condition) did not make a significant difference to detection or to localisation of stimuli.

General Discussion

A stroke patient with impaired sensation may fail to detect stimulation when it is administered by another person but may detect identical stimulation when it is self-administered. We have used a novel method – the self-touch rubber hand paradigm (Ehrsson et al., 2005) – to investigate self-touch enhancement. The Examiner administers stimulation to the patient's affected hand, while guiding the patient's unaffected hand to administer stimulation to a prosthetic hand. Neurologically healthy individuals assessed with this paradigm experience the subjective illusion that they are touching their own hand, when they are in fact touching a prosthetic hand (Ehrsson et al.). The self-touch rubber hand paradigm allows us to tease apart the factors which may contribute to self-touch enhancement, and to consider three potential explanations: (1) the patient's administering hand is providing proprioceptive information, so that the patient infers rather than feels the sensory stimulation, (2) the patient's administering hand is acting like an attentional wand and is directing attention to the affected hand, and (3) the patient's administering hand action provides a temporal cue to focus attention at the precise time-point when stimulation is administered.

Experiments 1 and 2: Baseline Effects for Self-Touch Enhancement

In Experiments 1 and 2, we replicated the standard self-touch enhancement effect (Valentini et al., 2008; Weiskrantz & Zhang, 1987). All four patients detected significantly more self-administered stimulations, when compared to stimulations administered by the Examiner. Sham trials, in which no stimulation was administered to the patient's hand, were included to assess the reliability of the patient's responses. On sham trials, the Examiner guided the patient to administer stimulation to one of the Examiner's fingers, which was positioned in close proximity to the patient's affected hand. No patient reported feeling touch on more than two sham trials; the criterion used for patient exclusion. That patients did not report touch on sham trials does not provide unequivocal evidence that the patients *felt* the stimulation on valid trials. On sham trials, patients were guided to a different location (i.e., the Examiner's finger), and they may have used subtle differences in hand position to distinguish valid and sham stimulations.

In an extension of the two previous studies on self-touch enhancement, we assessed sensation with the patient's affected hand positioned in the left and in the right hemispace. Studies investigating somatosensory extinction have shown that detection of stimuli administered to a patient's left hand may be enhanced when the left hand is positioned to the right of body midline, or to the right of the unaffected right hand (e.g., Moro et al., 2004; Smania & Aglioti, 1995). Given that somatosensory processing has been shown to occur within spatial frames of reference (see Aglioti, Smania, & Peru, 1999; Moscovitch & Behrmann, 1994; Tinazzi, Ferrari, Zampini, & Aglioti, 2000; Vallar, 1997), we hypothesised that patients with neglect or extinction may exhibit a superior sensory enhancement effect when administering touch in the non-neglected side of space. However, we found that the spatial positioning of the hands did not differentially affect detection or localisation in the current patient sample.

Experiments 3 and 4: Ruling out the Proprioceptive Information Explanation for Self-Touch Enhancement

Experiments 3 and 4 tested the proprioceptive explanation for self-touch enhancement. In Experiment 3, the Examiner administered stimulation to the patient's affected hand while guiding the patient's unaffected hand to administer synchronous stimulation to a prosthetic hand. The stimulation on the patient's affected hand (by the Examiner) and the action of the patient's administering hand (relative to the prosthetic hand) were matched to the condition of actual self-touch. That is, the patient received stimulation on her own hand as she administered stimulation (to the prosthetic hand). But, because the patient was administering stimulation away from her own hand, she was unable to use the position of her administering hand to decide whether her affected hand had been touched. This novel manipulation resulted in the finding of enhanced sensation compared to Experiment 1, the Examiner-administered stimulation condition. The implication is that the sensory enhancement experienced under conditions of self-administered stimulation represents a true change in sensory perception. Previous studies investigating self-touch enhancement could not discount the possibility that the patient attended to the position of her hands relative to one another, and thus reported touch based on inference rather than on sensation. Experiment 3 provides evidence against this possibility. The patients demonstrated the same level of detection as in Experiment 2 (patient-administered stimulation), even though they could no longer use the relative position of the hands to infer stimulation.

In Experiment 4, movements of the patient's administering hand were held to a minimum. The patient always stimulated the same location on the back of the prosthetic hand (instead of corresponding digits of the prosthetic hand), while the Examiner stimulated each of the patient's five digits (as in Experiment 3). There was no change in stimulus detection when the results of Experiment 4 were compared to Experiment 3; that is, the patients continued to show sensory enhancement. (*Note*: Patient SM exhibited sensory enhancement in the right hemispace condition and Patient CA exhibited only a trend towards sensory enhancement.) For two patients (CJ, SM), it was evident that although detection was not affected, the administering hand movements were used as a cue for localisation of felt sensations. Both patients exhibited a decline in stimulus localisation, so that although they continued to detect stimulation, this stimulation was frequently attributed to the wrong digit.

Sham trials have an important role in these experiments. On sham trials in Experiments 3 and 4, the patient administered stimulation to the prosthetic hand but no stimulation was administered to the patient's own hand. None of the patients reported touch on more than two sham trials. Because the action, trajectory and location of the patient's administering hand was identical across sham and valid trials, the fact that patients reported touch on valid but not sham trials can be attributed to the sensations experienced in the patient's affected hand. This is to be contrasted with Experiment 2, in which the Examiner guided the patient to a 'new' location (i.e., one of the Examiner's fingers) on sham trials. Taken together, the results of Experiments 3 and 4 argue against a proprioceptive explanation for enhanced stimulus *detection* under conditions of self-administered touch. The patient does not need to touch her own hand to know that she is being touched. However, proprioceptive information may still be used by some patients to *localise* felt sensations.

Experiment 5: Support for the Attentional Modulation Explanation for Self-Touch Enhancement

Experiment 5 tested the attentional modulation explanation for self-touch enhancement. Valentini et al. (2008) suggest that self-touch enhancement may be driven by the patient's administering hand guiding attention towards the affected hand; hence the metaphor of the administering hand as an attentional wand (see also Coslett & Lie, 2004). Using the self-touch rubber hand paradigm we tested this hypothesis by creating a self-touch condition in which the patient's hands were not in contact, and were actually positioned in opposite sides of space (left versus right hemispace). If the attentional wand operates in spatial coordinates, there should be no advantage for self-administered touch when the patient's administering hand directs attention to the opposite side of space to that of the patient's affected hand.

Our results suggest that the attentional wand may be an important explanatory factor in some, but not all, patients. Patient SM exhibited a decline in stimulus detection when he administered stimulation (to the prosthetic hand) in the left hemispace while his own hand received stimulation (from the Examiner) in the right hemispace, when compared to Experiment 3 in which SM administered stimulation (to the prosthetic hand) and received stimulation (from the Examiner) in the same hemispace. The implication here is that Patient SM's hand may direct his attention so that he detects touch on the affected hand when it is positioned within the "functional spatial range" (Reed et al., 2007, p. 51) of the administering hand action. But this cannot be the whole story since SM did not show a decline in stimulus detection when the prosthetic hand was in the right hemispace and his own hand in the left. Patient SM's performance on the neuropsychological screening measures may be relevant since he exhibited sensory anti-extinction (Goodrich & Ward, 1997). When assessed using the confrontation method, Patient SM consistently failed to detect unilateral left-side events (visual, auditory and somatosensory), but bilateral trials were detected with near-perfect accuracy (as were unilateral right-side events). Patient SM may use right-side events as an attentional cue to 'check left', thus explaining detection of left-side events under conditions of bilateral stimulation. During self-administered touch, the administering *right* hand action would provide a cue to 'check left'. In Experiment 5, the prosthetic hand (the site of the administering hand action) and the patient's affected hand are positioned in opposite sides of space. When the administering hand action occurs in the right hemispace, a leftward shift of attention would result in detection of sensory stimulation on the affected hand positioned in the left hemispace. By contrast, when the administering hand action occurs in the left hemispace, a leftward shift of attention would drive the patient's attention further from his affected hand, which is now positioned in the right hemispace. This explanation is consistent with Patient SM's results profile for Experiment 5.

For the remaining three patients (NG, CJ, CA) there was no decline in stimulus detection when the patient administered stimulation to the prosthetic hand located in the opposite hemispace from the affected hand. This finding suggests that the administering hand need not be directing the patient's attention in spatial coordinates. A potential counter-argument is that the self-touch rubber hand paradigm may create proprioceptive mislocalisation of the affected hand, so that the patient has the perception that the affected hand is located in the position of the prosthetic hand and thus within the functional spatial range of the administering hand action. This argument is based on research showing that in neurologically healthy individuals the illusion of self-touch[4] is associated with a drift in the proprioceptively perceived position of the 'touched' hand towards the location of the prosthetic hand (Ehrsson et al., 2005).[5] However, proprioceptive mislocalisation can only occur if the patient is experiencing the illusion of self-touch, and to experience this illusion the patient needs to *feel* the stimulation on the affected hand. Stated differently, the patient needs to feel the stimulation on her affected hand before she can possibly mislocalise the hand, so as to perceive it within the functional spatial range of the administering hand action. Notably, all four patients detected the first stimulation in the left and right hemispace conditions of Experiment 5, before proprioceptive mislocalisation could possibly have occurred.

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[4] Although we did not collect quantitative information as to whether the patients experienced the illusion of self-touch, one patient (CJ) spontaneously exclaimed: "The logical bit of your brain tells you your hand is underneath [the testing unit] but something else tells you, no, you're wrong, it's up here and you're touching it".

[5] Data presented in Chapter Six indicates that some participants may experience the converse pattern of drift; that is, drift of the administering hand towards the location of the touched hand (White, Aimola Davies, & Davies, 2011).

Taken together, the results of Experiment 5 suggest that, for some patients, the administering hand may direct attention spatially. However, this explanation is not sufficient to account for self-touch enhancement in all patients.

Experiment 6: Support for the Temporal Expectation Explanation for Self-Touch Enhancement

Experiment 6 investigated the temporal expectation explanation for self-touch enhancement in Patient NG. We hypothesised that the action of the administering hand may provide a precise temporal cue for focusing attention on the affected hand. In Experiment 6, the action of the patient's administering hand and the stimulation on the affected hand were disambiguated. Detection returned to the level of the baseline Examiner-administered stimulation condition (Experiment 1), such that there was no longer an advantage for self-involvement. The result suggests that temporal expectation may be an important factor in self-touch enhancement. The patient need not sustain attention across a 'hazy' time window whilst waiting for inevitable stimulation from the Examiner. Instead, the patient can anticipate the precise moment at which maximal attention is required. Consistent with this, Patient SM (who was not involved in Experiment 6) spontaneously remarked that the self-administered stimulation conditions were easier because of the temporal component. He said "I know when to concentrate for the tickle because my hand is going down".

Conclusion

The results of the current experimental series confirm that patients with impaired sensation may experience enhanced sensory perception under conditions of self-administered touch. By using the self-touch rubber hand paradigm, we were able to demonstrate that the patient *feels* the stimulation under conditions of self-administered touch. The patient does not use the relative position of her two hands to infer stimulation, nor does she use subtle movements of the administering hand to focus attention on a particular region of the affected hand. An explanation for self-touch enhancement in terms of the administering hand acting like an attentional wand and guiding the patient's attention to the affected hand does not provide a sufficient account for all patients. When the prosthetic hand and the patient's hand were positioned so that the patient administered and received stimulation in distinct spatial regions (one hand in each hemispace), only one patient showed a decline in stimulus detection.

Temporal expectation was shown to be an important factor in a follow-up study with Patient NG. Here we propose that this explanation may be relevant to findings that self-touch enhancement is more common following damage to the right hemisphere (Valentini et al., 2008). The right hemisphere is activated during somatosensory tasks of sustained attention and vigilance, such as monitoring a skin region and reporting sensory stimulations (see Pardo, Fox, & Raichle, 1991). The left hemisphere is involved in temporal orienting of attention (see Coull, Frith, Büchel, & Nobre, 2000; Coull & Nobre, 1998; Nobre, 2001); that is, "direct[ing] attention to a point in time when a relevant event is expected, to optimize behavior" (Coull & Nobre, 1998, p. 7426). Reporting sensory stimulations administered by the Examiner requires sustained attention and ongoing vigilance. In contrast, when reporting self-administered stimulations, the patient may direct attention to points in time when relevant events are expected, using the timing of the administering hand as a cue to orient attention. It is possible that the tasks of detecting Examiner-administered stimulations and detecting self-administered stimulations engage the right and the left hemispheres differently. Self-touch enhancement would be anticipated to occur more frequently in patients with right-hemisphere damage, who, due to their intact left hemisphere, may benefit from the temporal cues provided by self-involvement.

CHAPTER 3: ERRORS OF SOMATOSENSORY LOCALISATION IN A PATIENT FOLLOWING RIGHT-HEMISPHERE STROKE

Following a right-hemisphere stroke, Patient NG could detect somatosensory stimulation that she was unable to localise. With vision precluded, NG systematically mislocalised touch on the little and ring finger of her affected left hand, and reported feeling this touch on the neighbouring rightward finger. This pattern of mislocalisation occurred not only when the Examiner administered touch but also when touch was self-administered. We manipulated the relative position of NG's two hands during sensory assessment of the affected hand. When NG's right hand was positioned to the left of her affected hand, NG exhibited improved localisation. Theoretical and clinical implications are discussed.

> Ordinarily when a patient experiences a sensation we take it for granted that he can locate the site of the stimulation. We seldom request the patient to indicate the point of the stimulation because it is generally assumed that the ability to perceive is associated with the ability to localise. (Bender, 1952, pp. 54-55)

Patients with somatosensory impairments have shown surprising dissociations between tactile detection and tactile localisation. Patients may fail to detect a stimulus that they can localise, or they may fail to localise a stimulus that they can detect. Localisation without detection has been likened to blindsight in the visual modality (see Weiskrantz, 1986). Paillard, Michel, and Stelmach (1983) provide an early example in a patient with deafferentation of the right arm. The patient's sensory deficit was so severe that she could burn herself without noticing. But while the patient was unable to detect static pressure on her skin, she was able to point to the approximate locus of stimulation. Lahav (1993) describes a similar patient who, on 36 of 40 trials, was correct in guessing the locus of an 'unfelt' tactile stimulus administered to the left arm (in a two alternative forced-choice paradigm). Rossetti, Rode, and Boisson (1995) provide a further example in a patient with complete right-side hemianaesthesia. The patient could neither detect nor describe sensory stimulation administered to his right arm, yet he was able to point to the locus of stimulation with his unaffected left hand.

The reverse dissociation, intact detection accompanied by impaired localisation, is a more common consequence of neurological damage. In a pioneering study of sensation, Head and

Holmes (1911) reported localisation deficits in 12 out of 24 patients with lesions affecting the optic thalamus. Detection without localisation is revealed in statements such as "I feel you touch me, but I can't tell where it is; the touch oozes all through my hand" (p. 139). Head and Holmes note that the inability to localise stimulation can have grave consequences. Unpleasant sensations tend to spread widely when the capacity for stimulus localisation is impaired. In contrast, recognising the site of the stimulation seems to exert an inhibitory influence on the distribution of sensation, so that pain, for example, is confined to the stimulated skin region.

Halligan, Hunt, Marshall, and Wade (1995) provide another example of this dissociation in a patient following stroke. In a systematic sensory assessment, the patient was unable to localise 33% of all felt stimulations to his right arm. The researchers note that the patient expressed a clear feeling of being touched, yet "remained resolute in his report that he 'simply had no idea' where he had been touched on these trials" (p. 263). Whereas the patient presented by Halligan et al. indicated complete uncertainty regarding the locus of stimulation, localisation deficits are typically less dramatic.

Rapp, Hendel, and Medina (2002) investigated the distribution of stimulus mislocalisations in two patients following stroke. Touch was administered to 22 locations on the dorsal and ventral surfaces of each patient's affected right hand. Following stimulation, the patient was permitted vision of the hand and was asked to point to the perceived location of the prior touch. Both patients demonstrated excellent stimulus detection but had systematic impairments in stimulus localisation. Localisation judgments showed a "striking downward shift" (p. 210) away from the fingertips and in the direction of the wrist. Touch on the fingertip, for example, was perceived as displaced towards the palm. Rapp et al. concluded that "cerebral damage in humans may result in shifted and compressed perceptual representations that preserve the relative locations of the stimuli" (p. 210). According to this view, cerebral damage leads to a reorganisation of somatosensory representations whereby "pre-lesion topography" (p. 210) is preserved, but within a reduced cortical space. If a patient's body is touched at a site corresponding to the compressed part of her perceptual representation, the stimulation will be mislocalised. Although numerous other studies support the neuroplasticity of the somatosensory cortex (e.g., Calford, 1991; Elbert et al., 1994; Merzenich, Nelson, Stryker, Cynader, Schoppmann, & Zook, 1984; Mogilner et al., 1993; Ramachandran, 1993; Ramachandran, Stewart, & Rogers-Ramachandran, 1992) - the region of the brain that contains a somatotopic map of the contralateral side of the body (see Haggard, Taylor-Clarke, & Kennett, 2003) - the study by Rapp et al. is the first to consider post-stroke sensory mislocalisation in terms of reorganised cortical somatosensory maps.

In these previous cases of impaired sensory localisation, the patients have mislocalised stimulation administered by another person. The current chapter presents a patient (NG) who, following a right-hemisphere stroke, has systematic errors of stimulus localisation under conditions of self-administered touch. The patient was assessed as part of a larger study (Chapter 2), which was designed to investigate self-touch enhancement. Self-touch enhancement is demonstrated when an individual fails to detect somatosensory stimulation administered by the Examiner, but detects the same intensity stimulation when it is self-administered (see Valentini et al, 2008; Weiskrantz & Zhang, 1987).

One objective of our larger study was to rule out a proprioceptive explanation for self-touch enhancement. We were concerned that, under conditions of self-administered stimulation, the patient may attend to the relative position of her two hands and report touch based on knowledge of stimulation rather than perceived stimulation. To control for this possible confound, the self-touch rubber hand paradigm (Ehrsson et al., 2005) was used, as it has been shown to create the subjective illusion that "one is touching one's own hand" (p. 10566) when one is instead touching a prosthetic hand. The Examiner guides the patient to administer stimulation to a prosthetic hand while the Examiner administers synchronous stimulation to the patient's affected hand. This paradigm holds constant the three conditions of actual self-touch (the action of the patient's administering hand, the stimulation to the patient's affected hand and the temporal correspondence between these two events) but removes the proprioceptive correspondence between the patient's administering and receptive hands. The patient can no longer use proprioceptive information to infer touch because she is administering and receiving touch in two distinct spatial locations. Patients continued to show sensory enhancement, thereby confirming that proprioceptive information alone is not enough to explain self-touch enhancement.

Patient NG failed to detect the majority of stimulations on the little and ring finger of her affected hand when these were administered by the Examiner. We refer to these fingers as the 'impaired region' of NG's hand. When stimulation was self-administered, NG detected touch on these two fingers but perceived it to be further to the right than the actual site of sensory stimulation. For example, touch on the little finger was perceived at the location of the ring finger, and touch on the ring finger was perceived at the location of the middle finger. NG thus presents with systematic sensory mislocalisations similar to the two patients described by Rapp et al. (2002); these patients misperceived touch away from the fingertips, and in the direction of the wrist. Rapp et al. proposed that systematic mislocalisations may result from compressed perceptual representations. For the two patients in their study, the distal part of the affected hand representation (i.e., the fingertips) was thought to be compressed. For our patient, NG, the behavioural evidence suggests that it is the left side of the hand representation that is compressed.

Body representation is known to be highly malleable, insofar as "the brain's representation of the body can be rapidly and functionally changed" (Haggard et al., 2003, p. R171, see also Gandevia & Phegan, 1999) as a result of sensory deprivation or deafferentation,[6] as well as illusions that modify the way in which the body is experienced (Schaefer, Flor, Heinze, & Rotte, 2007). Here, we present four experiments demonstrating that NG's capacity to localise sensory stimulation on her affected left hand varies according to the position of her right hand at the time of the stimulation. When NG reaches to the left side of her affected hand while the Examiner administers stimulation to her impaired digits, NG demonstrates an immediate improvement in stimulus localisation. This leads us to suggest that NG's impaired hand representation may be affected by simply manipulating the relative position of her two hands.

Case History

NG is a 21-year-old right-handed (Oldfield, 1971) female, who experienced a cerebral vascular accident resulting in left-side hemiplegia. A computed-tomography (CT) scan on admission revealed a large haemorrhage affecting the right frontal lobe, with bleeding in the frontal and posterior corona radiata, the thalamus, and the lateral and third and fourth ventricles. There was associated oedema and a small degree of midline shift (Figure 6a). NG underwent surgical embolisation of the right frontal lobe ten days following her stroke. Further CT scans

[6] Examples in which sensory deprivation leads to a change in the brain's representation of the body include cerebrovascular accident (Rapp et al., 2002; Schaechter, Moore, Connell, Rosen, & Dijkhuizen, 2006) and brain tumours (Roux, Boulanouar, Ibarrola, Tremoulet, Chollet, & Berry, 2000). Examples in which deafferentation leads to a change in the brain's representation of the body include amputation (Elbert et al., 1994; Merzenich et al., 1984; Ramachandran et al., 1992), nerve injury (Braune & Schady, 1993; Wall, Huerta, & Kaas, 1992) and local anaesthesia (Björkman, Weibull, Rosén, Svensson, & Lundborg, 2009; Kew et al., 1994; Waberski, Gobbelé, Kawohl, Cordes, & Buchner, 2003). Note that cortical changes associated with local anaesthesia may be immediate.

were obtained in the three weeks following admission. These scans indicated marked improvement in the degree of midline shift, and no new features (Figure 6b).

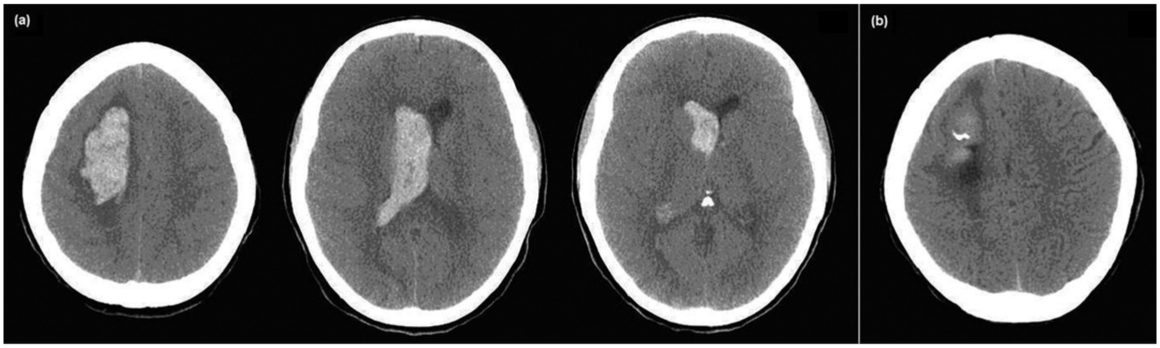


Figure 6. CT scan for NG, showing a right frontal lobe lesion. The three images in panel (a) were obtained on the day of the patient's stroke, and the image in panel (b) was obtained three weeks post-stroke and following surgical embolisation. Note that the left of the image corresponds to the right hemisphere.

We assessed NG at three-and-a-half months post-stroke in nine 40-min sessions spanning a two-and-a-half week period. She had recovered considerable motor function and was able to walk with the aid of a Zimmer frame. NG's speech was fluent, expressive and informative. She was motivated in her approach to therapy sessions in the rehabilitation hospital (e.g., physiotherapy, hydrotherapy, occupational therapy, neuropsychology), and was likewise enthusiastic to participate in our research. NG scored 24 on the Mini-Mental State Examination (MMSE: Folstein et al., 1975): two points were deducted on the orientation items (date and county), three points were deducted on the memory items (delayed recall of three items: apple, table and penny), and one point was deducted on the item requiring NG to repeat a sentence presented by the Examiner ('no ifs, ands or buts').

Personal neglect was assessed using Bisiach's 'reach test' (Bisiach et al., 1986) and Zoccolotti and Judica's (1991) personal neglect battery (with the scoring system proposed by McIntosh et al., 2000). In the 'reach test', the patient uses her ipsilesional hand to reach for her contralesional thumb. NG promptly reached for her left thumb, with and without vision. In Zoccolotti and Judica's personal neglect battery, a female patient is asked to comb her hair and to apply facial powder for 30 s each. Lateralisation bias is evidenced by a higher number of applications on one side of the body. NG did not exhibit personal neglect on this battery. She was always well-groomed and attended to both sides of her body during testing sessions.

There was no evidence of peripersonal neglect, assessed using the Star Cancellation, Letter Cancellation and Line Bisection subtests from the Behavioural Inattention Test (Wilson et al., 1987), Schenkenberg's Line Bisection test (Schenkenberg et al., 1980), the Baking Tray test (Tham & Tegnér, 1996) and drawing tests (Self-Portrait and 'Draw a Man') (Goodenough, 1926). However, NG did omit one left-side detail on a scene copying task: the chimney on the left side of a centrally-positioned house (adapted from Ogden, 1985). There was no evidence of neglect or extinction on confrontation assessment in the auditory, somatosensory and visual modalities. NG detected all unilateral and bilateral events.

Motor function was assessed using the Motricity Index for Motor Impairments after Stroke (Collin & Wade, 1990; Demeurisse et al., 1980). NG received a score of 84 for her left arm and 54 for her left leg, and 100 for both her right arm and her right leg. Sensory function of the hands and arms was assessed using the Revised Nottingham Sensory Assessment (Lincoln et al., 1998). The Revised Nottingham Sensory Assessment includes measures for light touch, deep pressure, tactile localisation, temperature discrimination, proprioception, stereognosis and two-point discrimination. NG exhibited impairments in localising stimuli administered to her left hand. All other sensory functions were normal.

General Methods

Four experiments were conducted with vision precluded. In each experiment, sensation was assessed with NG's affected left hand positioned first in the left hemispace and then in the right hemispace (Figure 7). NG's hand was positioned with the middle finger 20 cm from body midline. Stimulation was administered at five locations - the proximal phalanx of the thumb and each of the fingers of the hand - using a Semmes-Weinstein monofilament of .70 grams intensity (indicating diminished protective sensation). This monofilament corresponded to NG's sensory threshold and was used to avoid a ceiling effect.

Each hand-placement condition (i.e., left and right hemispace) comprised 60 trials: 10 stimulations to each digit and an additional 10 sham trials in which no stimulation was administered. Sham trials were included to ensure reliability in responses. NG did not report touch on more than two sham trials in any experiment, which was the criterion used to indicate unreliable responding. After each trial, NG was asked whether she detected the touch and whether she was able to localise the touch. NG provided verbal responses, indicating the stimulated digit by name.

Statistical Analyses

Statistical analyses were conducted with the *Q'* test (see Michael, 2007), used in single-case analyses to test the hypothesis of equal proportions. The *Q'* statistic has a χ^2 distribution with K-1 degrees of freedom, where K equals the number of experimental conditions.

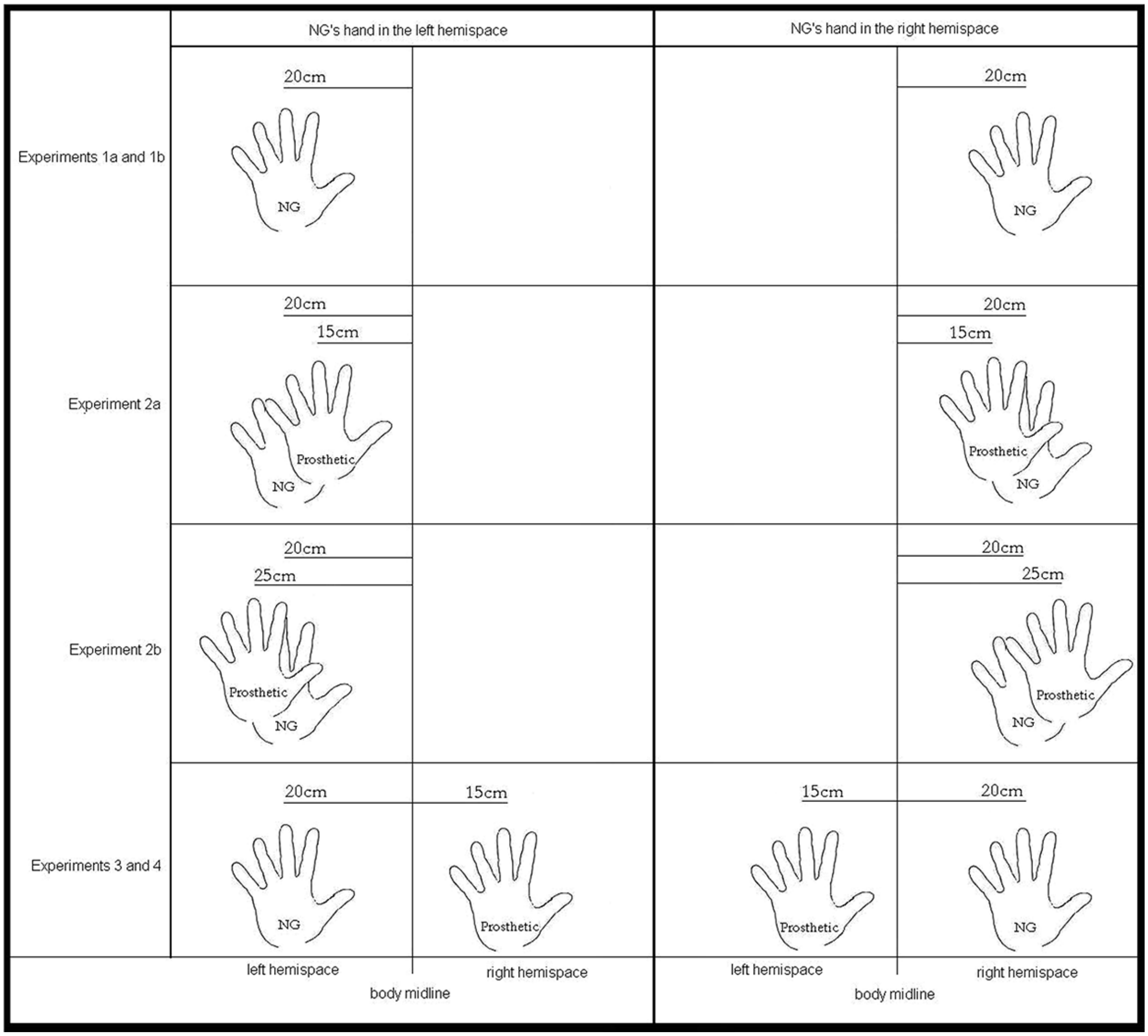


Figure 7. Hand-placement conditions in Experiments 1 through 4. Patient NG's hand was always positioned with the middle finger 20 cm from her body midline. The prosthetic hand was positioned with the middle finger 15 cm from NG's body midline in Experiments 2a, 3 and 4, and 25 cm from NG's body midline in Experiment 2b.

Experiments 1a and 1b

Experiment 1 was used to establish NG's baseline detection and localisation rates for Examiner- and patient-administered stimulation. The experiment comprised two parts: Experiments 1a and 1b. In each experiment, sensation was assessed with the middle finger of NG's left hand positioned 20 cm from her body midline, first in the left hemispace and then in the right hemispace (Figure 7).

In Experiment 1a, the Examiner administered stimulation to NG's affected left hand. On sham trials, no stimulation was administered but NG was still asked whether she detected the stimulation and whether she could localise the stimulation. In Experiment 1b, the Examiner guided NG's right hand (which was holding the Semmes-Weinstein monofilament) to self-administer stimulation to her own left hand. On sham trials, stimulation was administered to one of the Examiner's fingers, which were positioned close to (but not touching) NG's hand.

Results

Experiment 1a: Examiner-Administered Stimulation

Detection. There was no difference in overall detection of Examiner-administered stimulation in the two hemispace conditions: NG failed to detect 19 of 50 stimulations when her affected left hand was positioned in the left hemispace and 14 of 50 stimulations when positioned in the right hemispace ($Q'(1) = .80$, $p = .37$). Note that 31 of 33 missed stimulations were to either the little or the ring finger.

Localisation. There was no difference in the overall rate of stimulus mislocalisations in the two hemispace conditions: NG mislocalised 3 of 31 reported stimulations when her affected left hand was positioned in the left hemispace and 7 of 36 reported stimulations when positioned in the right hemispace ($Q'(1) = .97$, $p = .35$). In the right-hemispace condition, NG predominantly mislocalised rightward ($Q'(1) = 8.65$, $p = .003$). For example, she reported that she felt touch on her ring finger when she received stimulation on the little finger (Table 5).

Experiment 1b: Patient-Administered Stimulation

Detection. There was no difference in overall detection of self-administered stimulation in the two hemispace conditions: NG failed to detect 7 of 50 stimulations when her affected left hand was positioned in the left hemispace and 4 of 50 stimulations when positioned in the right hemispace ($Q'(1) = .60$, $p = .44$). All missed stimulations were to either the little or the ring finger.

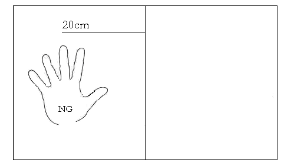
NG missed significantly fewer stimulations in the self-administered stimulation condition than in the Examiner-administered stimulation condition, both in the left hemispace ($Q'(1) = 5.46$, $p = .0195$) and in the right hemispace ($Q'(1) = 6.80$, $p = .0284$).

Table 5

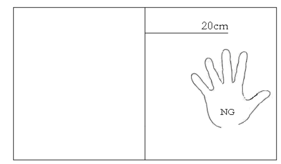
Missed or mislocalised stimuli in Experiments 1a and 1b

Experiment 1a: Examiner administers stimulation to NG's affected hand.

Patient's Hand in Left Hemispace	Little	Ring	Middle	Index	Thumb	Total
Misses	10	8		1		19
Mislocalised: Right		2				2
Mislocalised: Left				1		1
Not localised						0

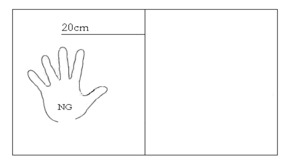


Patient's Hand in Right Hemispace	Little	Ring	Middle	Index	Thumb	Total
Misses	7	6	1			14
Mislocalised: Right	1	3	1	1		6
Mislocalised: Left				1		1
Not localised						0

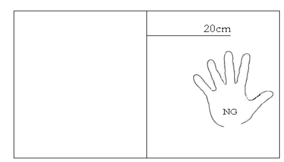


Experiment 1b: NG administers stimulation to her own affected hand.

Patient's Hand in Left Hemispace	Little	Ring	Middle	Index	Thumb	Total
Misses	4	3				7
Mislocalised: Right	1	4	1			6
Mislocalised: Left		1				1
Not localised						0



Patient's Hand in Right Hemispace	Little	Ring	Middle	Index	Thumb	Total
Misses	3	1				4
Mislocalised: Right	3	5				8
Mislocalised: Left		1				1
Not localised	1	1				2



Localisation. There was no difference in the overall rate of stimulus mislocalisations in the two hemispace conditions: NG mislocalised 7 of 43 reported stimulations when her affected left hand was positioned in the left hemispace and 11 of 46 reported stimulations when positioned in the right hemispace ($Q'(1) = .56, p = .45$). NG predominantly mislocalised rightward (Table 5), both in the left hemispace ($Q'(1) = 8.65, p = .003$) and in the right hemispace ($Q'(1) = 4.32, p = .03$).

There was no significant difference in the number of stimulations mislocalised when stimulation was self-administered (Experiment 1b) compared to when the Examiner administered stimulation (Experiment 1a), in either the left hemispace ($Q'(1) = .47, p = .4937$) or the right hemispace ($Q'(1) = .17, p = .6832$).

Interim Discussion

Experiments 1a and 1b provide baseline detection and localisation rates for NG. In Experiment 1a, the Examiner administered stimulation to NG's affected left hand. NG failed to detect the majority of stimulations administered to her little and ring finger (31 of 40). Of the nine detected stimulations to these fingers, six were mislocalised to a neighbouring digit to the right of the digit stimulated. In Experiment 1b, the Examiner guided NG to self-administer stimulation. When NG was involved in the administration of touch, her capacity to detect stimulations was significantly enhanced. Although NG detected the majority of stimulations under conditions of self-administered touch, she demonstrated the same pattern of mislocalisations as for Examiner-administered stimulation. She frequently reported that touch had occurred on a neighbouring digit, to the right of the digit stimulated. For example, when she administered touch on the little finger, she reported feeling touch on her ring finger.[7]

With this evidence that a patient is better at detecting self-administered touch, one may question whether the patient is actually feeling the self-administered touch, or whether she is reporting touch because she knows it has occurred. By judging the relative position of her administering and affected hand, the patient may infer that she has been touched. The self-touch rubber hand paradigm (Ehrsson et al., 2005) precludes the patient from using proprioceptive information to infer touch, and can be used to investigate perception of self-administered stimulation. The Examiner guides the patient to administer touch to a prosthetic hand while the Examiner administers synchronous stimulation to the patient's affected hand. This paradigm holds constant the three conditions of actual self-touch (the action of the patient's administering hand, the stimulation to the patient's affected hand and the temporal correspondence between these two events) but removes the proprioceptive correspondence between the patient's administering and receiving hands. The patient can no longer use proprioceptive information to infer touch because she is administering and receiving touch in two distinct spatial locations.

[7] To rule out an explanation in terms of practise effects, we repeated Experiments 1a and 1b at the end of the experimental series. There were no significant changes in the results.

Experiments 2a and 2b

In Experiment 2, the Examiner guided NG's right hand to administer stimulation to a prosthetic hand while the Examiner administered stimulation to the corresponding digit of NG's affected left hand. The experiment comprised two parts: Experiments 2a and 2b. In each experiment, sensation was assessed with the middle finger of NG's left hand positioned 20 cm from her body midline, first in the left hemispace and then in the right hemispace. The prosthetic hand was positioned on a testing unit 13 cm above NG's hand and in the same hemispace. The experimental manipulation distinguishing Experiment 2a from 2b was the position of the prosthetic hand relative to body midline and relative to NG's affected left hand (Figure 7).

In Experiment 2a, the middle finger of the prosthetic hand was positioned 15 cm from body midline; that is, closer to body midline than NG's own hand (20 cm). Therefore in the left-hemispace condition there was spatial overlap of the prosthetic hand and the thumb (or right) side of NG's hand, and in the right-hemispace condition there was spatial overlap of the prosthetic hand and the little finger (or left) side of NG's hand. In Experiment 2b, the middle finger of the prosthetic hand was positioned 25 cm from body midline; that is, further from body midline than NG's own hand (20 cm). This manipulation reversed the positioning of the prosthetic hand relative to NG's own hand; in the left-hemispace condition there was spatial overlap of the prosthetic hand and the little finger (or left) side of NG's hand and in the right-hemispace condition there was spatial overlap of the prosthetic hand and the thumb (or right) side of NG's hand.

The prosthetic hand was positioned on a testing unit 13 cm above NG's hand, so that any overlap between the two hands was purely spatial; that is, there was no skin-to-skin contact. On sham trials, NG administered stimulation to the prosthetic hand but no stimulation was administered to her hand.

Results

Experiment 2a: Prosthetic Hand Closer to Midline than the Patient's Hand

Detection. There was no difference in overall detection in the two hemispace conditions: NG failed to detect 2 of 50 stimulations when her affected left hand and the prosthetic hand were positioned in the left hemispace and 2 of 50 stimulations when positioned in the right hemispace ($Q'(1) = .00$, $p = 1.00$). All missed stimulations were to either the little or the ring finger.

There was no significant difference in stimulus detection when NG administered stimulation to the prosthetic hand (Experiment 2a) compared to her own hand directly (Experiment 1b), in either the left hemispace ($Q'(1) = 1.96$, $p = .16$) or the right hemispace ($Q'(1) = .42$, $p = .52$).

Localisation. There was a significant difference in the overall rate of stimulus mislocalisations in the two hemispace conditions: NG mislocalised 11 of 48 reported stimulations when her affected left hand and the prosthetic hand were positioned in the left hemispace and 2 of 48 reported stimulations when positioned in the right hemispace ($Q'(1) = 5.00$, $p = .03$). NG mislocalised all stimuli rightward (Table 6), both in the left hemispace ($Q'(1) = 35.63$, $p = .0001$) and in the right hemispace ($Q'(1) = 8.33$, $p = .004$). In the right-hemispace condition, NG mislocalised significantly fewer reported stimulations when she administered stimulation to the prosthetic hand (Experiment 2a) compared with when she administered stimulation to her own hand directly (Experiment 1b) ($Q'(1) = 5.29$, $p = .02$). The difference was not significant in the left-hemispace condition ($Q'(1) = .44$, $p = .51$).

Experiment 2b: Prosthetic Hand Further from Midline than the Patient's Hand

Detection. There was no difference in overall detection in the two hemispace conditions: NG detected all stimulations when her affected left hand and the prosthetic hand were positioned in the left hemispace and failed to detect 2 of 50 stimulations when positioned in the right hemispace ($Q'(1) = .86$, $p = .35$).

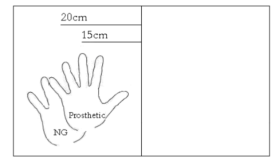
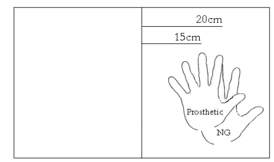
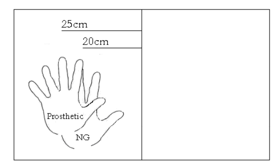
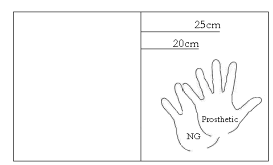
In the left-hemispace condition, NG detected significantly more stimulations when administering touch to the prosthetic hand (Experiment 2b) than when administering touch to her own hand directly (Experiment 1b) ($Q'(1) = 4.75$, $p = .03$). The difference was not significant in the right-hemispace condition ($Q'(1) = .42$, $p = .52$).

Localisation. There was a significant difference in the overall rate of stimulus mislocalisations in the two hemispace conditions: NG mislocalised 3 of 50 reported stimulations when her affected left hand and the prosthetic hand were positioned in the left hemispace and 12 of 48 reported stimulations when positioned in the right hemispace ($Q'(1) = 4.72$, $p = .03$). NG mislocalised all stimuli rightward (Table 6), both in the left hemispace ($Q'(1) = 10.89$, $p = .001$) and in the right hemispace ($Q'(1) = 39.04$, $p < .0001$).

There was no significant difference in the number of stimulations mislocalised when NG administered stimulation to the prosthetic hand (Experiment 2b) compared to her own hand directly (Experiment 1b), in either the left hemispace ($Q'(1) = 1.15$, $p = .28$) or the right hemispace ($Q'(1) = .01$, $p = .92$).

Table 6

Missed or mislocalised stimuli in Experiments 2a and 2b

Experiment 2a: Examiner administers stimulation to NG's affected hand positioned 20 cm from body midline; NG administers synchronous stimulation to the corresponding digit of a prosthetic hand positioned 15 cm from body midline.							
Patient's Hand in Left Hemispace	Little	Ring	Middle	Index	Thumb	Total	
Misses	1	1				2	
Mislocalised: Right	3	7	1			11	
Mislocalised: Left						0	
Not localised						0	
Patient's Hand in Right Hemispace	Little	Ring	Middle	Index	Thumb	Total	
Misses	1	1				2	
Mislocalised: Right	1	1				2	
Mislocalised: Left						0	
Not localised						0	
Experiment 2b: Examiner administers stimulation to NG's affected hand positioned 20 cm from body midline; NG administers synchronous stimulation to the corresponding digit of a prosthetic hand positioned 25 cm from body midline.							
Patient's Hand in Left Hemispace	Little	Ring	Middle	Index	Thumb	Total	
Misses						0	
Mislocalised: Right	2	1				3	
Mislocalised: Left						0	
Not localised						0	
Patient's Hand in Right Hemispace	Little	Ring	Middle	Index	Thumb	Total	
Misses	1		1			2	
Mislocalised: Right	3	8	1			12	
Mislocalised: Left						0	
Not localised						0	

Interim Discussion

In Experiment 2, NG administered stimulation to a prosthetic hand while the Examiner administered synchronous stimulation to the corresponding digit of NG's affected left hand. While this paradigm holds constant the conditions of actual self-touch (i.e., the temporal correspondence between the action of the patient's administering hand and the stimulation on her touched hand), it also eliminates the problem of the patient using the relative position of her own two hands to infer stimulation. The findings demonstrate that NG did not use the relative position of her two hands to infer touch, as there was no decline in detection performance when NG administered stimulation to the prosthetic hand (Experiment 2) compared to when she administered stimulation to her own hand (Experiment 1b). In Experiment 2a, the middle finger of the prosthetic hand was positioned 15 cm from body midline (on a testing unit above NG's own hand) whereas the middle finger of NG's own hand was 20 cm from body midline. NG exhibited superior localisation performance when her affected left hand and the prosthetic hand were positioned in the right hemispace: she mislocalised only 2 of 48 reported stimulations. In this right-hemispace condition, there was spatial overlap of the prosthetic hand and the little finger (impaired left) side of NG's own hand. Only in this condition was NG reaching leftward, over and beyond her own 'touched' finger when she administered touch to the corresponding digit of the prosthetic hand (Figure 7). NG's superior performance in this condition may have been due to the positioning of her affected hand in the right hemispace or, alternatively, to reaching over and beyond the impaired region (the little and ring finger) of her affected hand to administer touch to the prosthetic hand. A further experiment was conducted in which we disambiguated these factors, so that NG reached over and beyond the impaired region of her affected hand when it was positioned in the left (rather than the right) hemispace.

In Experiment 2b, the prosthetic hand was positioned further from NG's midline than her own left hand. The prosthetic hand was positioned with its middle finger 25 cm from midline while NG's affected left hand was again positioned 20 cm from the midline position. NG exhibited superior localisation performance when her affected left hand and the prosthetic hand were located in the left hemispace, so that she reached over and beyond her 'touched' finger when administering touch to the corresponding digit of the prosthetic hand. Superior performance in this condition supports the hypothesis that stimulus localisation is enhanced when NG reaches (leftward) over and beyond her affected hand to administer touch.

In the two conditions in which NG exhibited superior localisation performance; that is, the right-hemispace condition of Experiment 2a and the left-hemispace condition of Experiment 2b, the prosthetic hand was positioned on a testing unit above the patient's own hand so that there was spatial overlap of the prosthetic hand and the ring and little finger of the affected hand. Next we ask whether the improvement in localisation can be explained simply because there is spatial overlap of the prosthetic hand and the most impaired region of the patient's own hand, or whether reaching over and beyond the left part of the hand is sufficient to improve localisation.

Experiment 3

In Experiment 3, the prosthetic hand was positioned in the opposite hemispace to NG's affected left hand. NG administered touch in one hemispace and received touch in the opposite hemispace. NG's left hand was positioned with the middle finger 20 cm to the left or right of her body midline. The prosthetic hand was positioned on a testing unit, with the middle finger 15 cm from NG's body midline, and in the opposite hemispace to her affected hand. On sham trials, NG administered stimulation to the prosthetic hand but no stimulation was administered to her hand.

Results

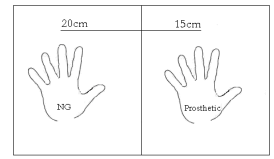
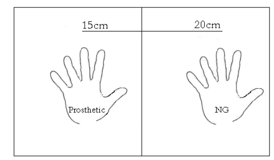
Detection. There was no difference in overall detection in the two hemispace conditions: NG failed to detect 2 of 50 stimulations when her affected left hand was positioned in the left hemispace and the prosthetic hand was positioned in the right hemispace, and 1 of 50 stimulations when her affected left hand was positioned in the right hemispace and the prosthetic hand was positioned in the left hemispace ($Q'(1) = .17$, $p = .68$).

Localisation. There was no difference in the overall rate of stimulus mislocalisations in the two hemispace conditions, although a trend towards significance was observed: NG mislocalised 10 of 48 reported stimulations when her affected left hand was positioned in the left hemispace and the prosthetic hand was positioned in the right hemispace, and 3 of 49 reported stimulations when her affected left hand was positioned in the right hemispace and the prosthetic hand was positioned in the left hemispace ($Q'(1) = 3.07$, $p = .08$). NG mislocalised all stimuli rightward (Table 7), both when her affected hand was positioned in the left hemispace

($Q'(1) = 32.26$, $p < .0001$) and when it was positioned in the right hemispace ($Q'(1) = 10.89$, $p = .001$).

Table 7

Missed or mislocalised stimuli in Experiment 3

Experiment 3: Examiner administers stimulation to NG's affected hand; NG administers synchronous stimulation to the corresponding digit of a prosthetic hand positioned in the opposite hemispace.							
Patient's Hand in Left Hemispace	Little	Ring	Middle	Index	Thumb	Total	
Misses	1	1				2	
Mislocalised: Right	4	5	1			10	
Mislocalised: Left						0	
Not localised						0	
Patient's Hand in Right Hemispace	Little	Ring	Middle	Index	Thumb	Total	
Misses				1		1	
Mislocalised: Right	2	1				3	
Mislocalised: Left						0	
Not localised						0	

Interim Discussion

Experiment 3 was designed to establish whether overlap between the prosthetic hand and the most impaired region of NG's affected hand (the ring and little finger) was necessary for enhanced localisation, or whether guiding NG to reach over and beyond the left part of her affected hand was sufficient. In this experiment, there was no overlap between the two hands because the prosthetic hand was positioned in the opposite hemispace to NG's affected left hand. NG exhibited a trend (p = .08) towards superior localisation when her affected hand was positioned in the right hemispace and the prosthetic hand was positioned in the left hemispace. In this condition, NG reached over and beyond her own 'touched' hand when administering touch to the prosthetic hand (because the prosthetic hand was positioned in the left hemispace and NG was administering touch using her right hand). The result suggests that reaching leftward, over and beyond the affected hand, may be sufficient to improve stimulus localisation.

In Experiments 2a, 2b and 3, NG touched the prosthetic hand on the digit corresponding to the touch received on her own affected hand. For example, the Examiner guided NG to administer stimulation to the middle finger of the prosthetic hand while her own middle finger was touched by the Examiner. It is possible that subtle movements of the administering hand provide a cue to stimulus localisation. For example, when NG detected touch on the index finger of her affected hand in one trial and was then guided to make a rightward movement with her administering hand in the next trial, she may have used this movement information and "knowledge about the normal configuration of the hand and fingers" (Anema et al., 2009, p. 1619, see also Anema et al., 2008; Gallagher, 2005) to focus on the thumb of her own affected hand. To exclude this possibility, a final experiment was conducted in which movements of the administering hand were restricted.

Experiment 4

The experimental set-up was identical to Experiment 3 (Figure 7). The prosthetic hand was positioned in the opposite hemispace to NG's affected left hand, and NG administered touch in one hemispace but received touch in the opposite hemispace. The difference is that in Experiment 4, NG administered touch to the same location – the back of the prosthetic hand – across all trials, while the digits of her own hand were stimulated individually (as in Experiments 1-3). On sham trials, NG administered stimulation to the prosthetic hand but no stimulation was administered to her hand.

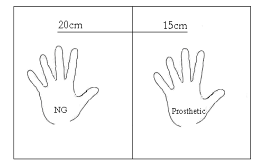
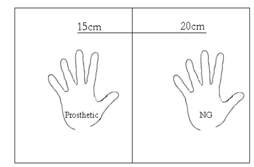
Results

Detection. NG detected all stimulations.

Localisation. There was a significant difference in the overall rate of stimulus mislocalisations in the two hemispace conditions: NG mislocalised 14 of 50 reported stimulations when her affected left hand was positioned in the left hemispace and the prosthetic hand was positioned in the right hemispace, and 3 of 50 reported stimulations when her affected left hand was positioned in the right hemispace and the prosthetic hand was positioned in the left hemispace ($Q'(1) = 6.12$, $p = .01$). NG mislocalised all stimuli rightward (Table 8), both when her affected hand was positioned in the left hemispace ($Q'(1) = 46.00$, $p < .0001$) and when it was positioned in the right hemispace ($Q'(1) = 10.89$, $p = .001$). (See Figure 8 for a comparison of all experimental conditions.)

Table 8

Missed or mislocalised stimuli in Experiment 4

Experiment 4: Examiner administers stimulation to NG's affected hand. NG administers synchronous stimulation to the back of a prosthetic hand positioned in the opposite hemispace.							
Patient's Hand in Left Hemispace	Little	Ring	Middle	Index	Thumb	Total	
Misses						0	
Mislocalised: Right	4	9	1			14	
Mislocalised: Left						0	
Not localised						0	
Patient's Hand in Right Hemispace	Little	Ring	Middle	Index	Thumb	Total	
Misses						0	
Mislocalised: Right	1	1	1			3	
Mislocalised: Left						0	
Not localised						0	

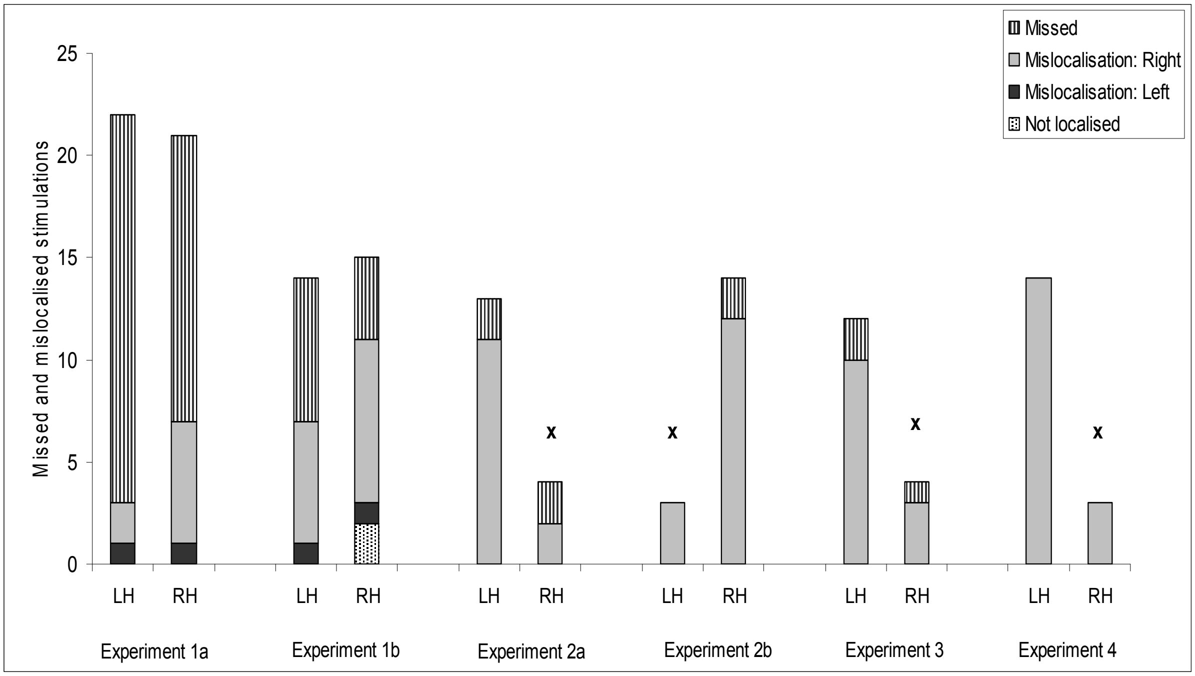


Figure 8. Missed and mislocalised stimuli for the left- (LH) and right- (RH) hemispace conditions of Experiments 1-4.

Missed, NG failed to detect the stimulation;

Mislocalisation: *Right*, NG reported that touch had occurred further to the right of where stimulation was administered. For example, touch on the ring finger was reported as touch on the middle finger;

Mislocalisation: *Left*, NG reported that touch had occurred further to the left of where stimulation was administered. For example, touch on the ring finger was reported as touch on the little finger;

Not localised, NG reported that she had felt touch but was not able to localise the felt sensation;

X, conditions in which NG reached leftward over and beyond the impaired region of her hand to administer stimulation.

Interim Discussion

In Experiment 4, subtle movements of the hand were restricted. NG always stimulated the same location on the back of the prosthetic hand while her own affected hand was stimulated at five different locations (as in Experiments 1-3). The prosthetic hand was positioned in the opposite side of space to NG's affected left hand as in Experiment 3. However, in Experiment 4, stimulation to the prosthetic hand was non-informative, insofar as NG always touched the same location on the back of the prosthetic hand. Therefore, NG could not use subtle movements of her administering hand (relative to the prosthetic hand) to focus attention on a particular region of her own hand. Nonetheless, NG exhibited superior localisation performance with her affected left hand in the right hemispace and the prosthetic hand in the left hemispace; suggesting that reaching leftward, over and beyond the impaired region of the affected hand, is sufficient to produce enhanced localisation of touch.

General Discussion

Patient NG is impaired at localising touch administered to her left hand, following a right-hemisphere stroke. Under conditions of Examiner-administered stimulation, NG exhibited poor detection of threshold-level stimuli to her little and ring finger (Experiment 1a), reporting less than a quarter of all stimulations to these digits. Of the stimulations that were detected, two-thirds were mislocalised rightward. NG exhibited a significant improvement in detecting touch on these two fingers (i.e., self-touch enhancement, see Valentini et al., 2008; Weiskrantz & Zhang, 1987) when she herself was involved in administration. However, as with detections under conditions of Examiner-administered stimulation, NG systematically mislocalised touch on the little and ring finger, and reported that touch had occurred further to the right of the digit that was actually stimulated (Experiment 1b). For example, touch on the little finger was perceived at the location of the ring finger, and touch on the ring finger was perceived at the location of the middle finger.

This pattern of mislocalisations to the neighbouring finger is consistent with that exhibited by neurologically healthy individuals when assessed using threshold-level stimuli. In a study designed to assess stimulus mislocalisations across the human hand, Schweizer, Maier, Braun, and Birbaumer (2000) found that the distribution of inter-finger mislocalisations was different to that expected by chance. Mislocalisations were mostly to the neighbouring finger (see also Braun, Ladda, Burkhardt, Wiech, Preissl, & Roberts, 2005), suggesting that participants have information about stimulus location, albeit at a lower spatial resolution, and that somatosensory receptive fields can cross digits. However, whereas neurologically healthy individuals mislocalise stimulations to the neighbouring finger to the left or to the right of the finger stimulated, NG systematically mislocalised stimulations to the right. Of the 84 stimulations that were mislocalised (across all four experiments), 83 were mislocalised to the neighbouring finger (99%) and, of these 83 mislocalised stimulations, 79 were mislocalised towards the right (95%).[8] The behavioural data thus suggest that NG has an impaired representation of her affected hand. Systematic sensory mislocalisations are proposed to result from a compressed perceptual representation of the affected body part (see Rapp et al., 2002), and NG's results are consistent with an impaired and compressed representation of the left side of her affected hand.

It is particularly relevant that NG's mislocalisations occurred not only for Examiner-administered stimulation but also for self-administered stimulation. Under conditions of self-administered touch, a person may use information from the administering hand and/or the receptive hand to aid stimulus localisation (see Schütz-Bosbach, Musil, & Haggard, 2009). That is, the patient may localise the tactile stimulus by using the position of the administering hand to calculate the location of stimulation in external spatial coordinates, or alternatively, she may "identify the stimulated region of skin by using a mapped representation" of the stimulated hand – a somatotopic body map (Haggard, Kitadono, Press, & Taylor-Clarke, 2005, p. 94). By using the self-touch rubber hand paradigm (Ehrsson et al., 2005), NG was prevented from relying on information from the administering hand, either (a) to infer whether she was being touched or (b) to localise felt stimulations. The Examiner guided NG to administer stimulation to a prosthetic hand while the Examiner administered synchronous stimulation to NG's affected hand. This experimental set-up is known to create the illusion of self-touch (Ehrsson et al., 2005). NG exhibited a significant improvement in stimulus localisation when she was required to reach

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[8] In the larger study to which NG belongs (Chapter Two) a further three patients with impaired sensation were assessed. For these three patients, the majority of mislocalised stimulations were also to the neighbouring finger (CJ = 74.7% of mislocalisations to the neighbouring finger; SM = 81.4% of mislocalisations to the neighbouring finger; CA = 80% of mislocalisations to the neighbouring finger). But, in contrast to Patient NG, the mislocalisations were to either the right or the left of the digit that received stimulation. Neurologically healthy control subjects were not included, as previous research demonstrates that individuals without a sensory impairment do not exhibit self-touch enhancement (Valentini et al., 2008); instead, they exhibit the reverse effect: self-touch attenuation (Bays et al., 2006; Bays, Wolpert, & Flanagan, 2005; Blakemore et al., 1998, 1999; Claxton, 1975; Weiskrantz et al., 1971).

(leftward) over and beyond the impaired region (i.e., the ring and little finger) of her affected left hand to administer touch to the prosthetic hand (Figure 8; conditions marked with an X). This effect occurred independently of subtle movements of her administering hand; that is, even in Experiment 4 when her administering hand was stimulating the same location on the back of the prosthetic hand across all trials.

It is important to note that simply guiding NG to reach into the left hemispace was insufficient to enhance stimulus localisation. This means that the improvement in certain conditions cannot be explained by an attentional bias which was ameliorated when NG's right hand cued her attention to the left of body midline (see Schwartz, Barrett, Kim, & Heilman, 1999). Rather, localisation was enhanced in the left and the right hemispace, provided NG was administering stimulation leftward of her affected hand.

A theoretical framework needs to account not only for the malleability of NG's compressed representation of her affected hand but also for the selective improvement across experimental conditions. That is, the enhancement of localisation only in conditions in which NG reached to the left of her own affected hand to administer touch to the prosthetic hand. Two theoretical frameworks are considered: the first discusses the role of self-touch in body representation and the possibility that the self-touch rubber hand paradigm leads to the impression of a laterally elongated left hand, and the second aligns the self-touch rubber hand paradigm with prism adaptation.

Self-Touch and Body Representation

The experience of self-touch contributes to body representation (see Schütz-Bosbach, Musil, & Haggard, 2009), insofar as information about the size, shape and position of one's body parts can be derived through the process of self-touch. The Pinocchio Illusion (see Lackner, 1988) provides a striking example. If an individual holds the tip of her nose (between her index finger and thumb) while her biceps tendon is passively vibrated (to give the impression of an outstretched arm), she experiences the startling illusion of an elongated nose (see also de Vignemont, Ehrsson, & Haggard, 2005). As humans, we find "good solutions" (Lackner, p. 292) to explain patterns of sensory stimulation and what these imply about body configuration: I am touching my nose and it feels as if my arm is outstretched, therefore, my nose is long.

In the current set of experiments, we created the illusion of self-touch with the affected left hand and the administering right hand laterally displaced by either 5 cm (Experiments 2a and 2b) or 35 cm (Experiments 3 and 4). It is possible that NG experienced the subjective impression of a laterally elongated left hand (akin to the Pinocchio Illusion) when she experienced the illusion of self-touch. This impression would provide a 'good solution' for NG's experience of self-touch when her right hand was reaching beyond the spatial position occupied by her left hand. More specifically, when her right hand was guided to the left of her affected hand, NG may have had the impression that her left hand was extending to the left, and when her right hand was guided to the right of her affected hand, NG may have had the impression that her left hand was extending to the right. In the former case, the subjective leftward elongation of the affected hand may have prompted an expansion of the compressed left side of NG's perceptual representation of her hand. This would explain the improvement in stimulus localisation.

Support for this first proposal, that the illusory elongation of a body part can affect perceptual body representations (at the cortical level), comes from a recent study by Schaefer et al. (2007). The researchers created the visual illusion that participants had an elongated left arm (i.e., a 20-cm extension) by attaching a long prosthetic arm to the participant's body and precluding vision of the participant's own left arm. Neuromagnetic source imaging indicated that this illusion, which evokes a change in the "perception of the size or shape of one's own body" (p. 703), was associated with dynamic modulations to the topography of the primary somatosensory cortex.

The Self-Touch Rubber Hand Paradigm as a Tactile Analogue of Prism Adaptation

A second explanation for our findings is that the self-touch rubber hand paradigm may have induced short-term sensorimotor adaptation, opening the left side of NG's compressed perceptual representation of her hand in a manner analogous to the effects of prism adaptation (Luauté et al., 2009) in patients with neglect (Rode, Rossetti, & Boisson, 2001).

Prismatic lenses displace the viewed field to the left or to the right. As the patient adapts to the lenses, she is required to point to objects. When the patient is wearing rightward-displacing prismatic lenses, the object will appear to be further to the right than is actually the case. Therefore, the patient will initially make rightward pointing errors (Phase 1: Pre-adaptation). However, the patient rapidly adjusts to this displacement, learning that she must point to the left of where she perceives an object in order to touch it. Thus, there is a realignment of the patient's visual and proprioceptive spatial coordinate systems (Phase 2: Adaptation). When the prismatic lenses are removed, the patient's pointing errors are in the opposite direction; that is, to the left of the object (Phase 3: Post-adaptation). (For a review of prism adaptation theory and method, see Redding & Wallace, 2006.)

Prism adaptation has been shown to reduce visual (e.g., Frassinetti, Angeli, Meneghello, Avanzi, & Làdavas, 2002; Rossetti et al., 1998), motor (e.g., Jacquin-Courtois, Rode, Pisella, Boisson, & Rossetti, 2008) and somatosensory (e.g., Dijkerman, Webeling, ter Wal, Groet, & van Zandvoort, 2004; Maravita, McNeil, Malhotra, Greenwood, Husain, & Driver, 2003) symptoms of neglect, and to improve performance on purely representational tasks (Rode et al., 2001). For example, Rode et al. found that neglect of left-side information in mental images was reduced following prism adaptation. Two patients were asked to imagine a map of France and to name as many towns as possible in two minutes. Prior to wearing the prismatic lenses, the patients' reports were largely restricted to towns on the right side of France; following prism adaptation, report of information on the left side of the mental image was significantly improved.

Prism adaptation can also affect a patient's representation of her own body, and this is true of patients with and without neglect. Patients with right-hemisphere lesions frequently experience postural imbalance, whereby the centre of pressure is displaced to the right. Tilikete et al. (Tilikete, Rode, Rossetti, Pichon, Li, & Boisson, 2001) reported improved postural control following adaptation to rightward-displacing prisms, and suggested that prism adaptation may affect a patient's internal postural map. Michel, Rossetti, Rode, and Tilikete (2003) extended this work, demonstrating that adaptation to leftward-displacing prisms can affect body representation in neurologically healthy individuals by shifting a person's subjective body-midline to the right, and thereby inducing a type of "postural neglect-like imbalance" (p. 224).

Here we propose that the self-touch rubber hand paradigm may have affected NG's compressed perceptual representation of her hand in a manner analogous to prismatic adaptation with rightward-displacing lenses. To recap, when a patient adapts to rightward-displacing prismatic lenses, she learns that she must reach to the left of an object's visually-perceived position to touch it (i.e., Phase 2: Adaptation), because the visually-perceived position is rightward of the object's veridical location. Prism adaptation leads to a "realignment of visual and proprioceptive spatial coordinates" (Luauté et al., 2009, p. 169, see also Redding & Wallace, 2006). Although the patient initially feels as if she is reaching to the left of where she sees the object, she has feedback to indicate that she has succeeded in touching the object. Thus the visual perception on the right and the leftward reaching are bound together.

The self-touch rubber hand paradigm leads to a realignment of sensory coordinates – tactile and proprioceptive – because the patient feels touch (tactile feedback) in a different spatial location to that at which she administers touch (proprioceptive feedback), and yet she experiences the illusion of self-touch. That is, the patient experiences the illusion that the tactile sensations on the affected hand are due to the action of the administering hand. A type of adaptation, akin to prism adaptation, may explain NG's superior localisation performance in the conditions in which she reached leftward, over and beyond her affected hand to touch the prosthetic hand. In these conditions, the (tactile-motor) adaptation would have been in the same direction as the (visual-motor) adaptation created with rightward-displacing prismatic lenses. NG's tactile percept was to the right of her leftward reaching hand (whereas in prism adaptation, it is the visual percept that is to the right of the leftward reaching hand). The tactile perception on the right and the leftward reaching were bound together because the paradigm creates the illusion of self-touch; that is, the illusion of spatial coincidence between the two hands.

The analogy between prism adaptation and the self-touch rubber hand paradigm has important theoretical implications, raising the possibility that in the same way that visuomotor adaptation may "modulate higher-level processes involved in spatial cognition" (Luauté et al., 2009, p. 169), so too may sensorimotor adaptation but in the complete absence of vision. The current experimental findings also have clinical implications. The self-touch rubber hand paradigm may provide an alternative to prism adaptation for use in the rehabilitation of body representation impairments. The paradigm does not require the specialist equipment of prism adaptation, and is perhaps more likely to be implemented.

This proposal is timely given recent research by Kitadono and Humphreys (2007) demonstrating potential clinical benefits associated with the visual version of the rubber hand paradigm (Botvinick & Cohen, 1998). In the visual rubber hand paradigm, the participant views stimulation on a prosthetic hand while her own (hidden) hand receives corresponding stimulation. The participant may experience the illusion that she is feeling touch at the location where she sees the prosthetic hand being touched; thus the paradigm evokes a recalibration in perceived proprioceptive location. Depending on the position of the prosthetic hand relative to the participant's own hand, this remapping involves either a leftward or a rightward shift. If the prosthetic hand is positioned to the left of the participant's own hand, the shift in perceived proprioceptive location is leftward, but if the prosthetic hand is positioned to the right of the participant's own hand, the shift in perceived proprioceptive location is rightward. Kitadono and Humphreys described a patient who demonstrated reduced visuospatial neglect on a midline-pointing task and a letter-cancellation task with the visual rubber hand paradigm. The prosthetic hand was positioned to the left of the patient's right hand, so that he had the impression of being touched to the left of the veridical location (i.e., the location in which he was actually touched). The researchers suggested that the improvement in neglect may have resulted from use of a paradigm that altered the patient's body schema, shifting his "egocentric representation of space to the left" (p. 269). Kitadono and Humphreys' pioneering work, together with the current results, suggests that the visual and non-visual rubber hand paradigms may be important clinical tools for rehabilitation following stroke.

Conclusion

Patient NG mislocalised Examiner- and self-administered touch to her affected left hand following a right-hemisphere stroke. We used the self-touch rubber hand paradigm to create the illusion of self-touch when NG's administering right hand and affected left hand were spatially separated. In a series of four experiments, we demonstrated that NG's capacity to localise touch was dependent on the position of her right hand when her affected left hand received stimulation. When NG's right hand was positioned to the left of her affected hand, she exhibited a marked improvement in her localisation of touch. The theoretical and clinical implications of the current results are striking, and we hope that these findings will inspire further studies investigating the use of the self-touch rubber hand paradigm in sensory rehabilitation following stroke.

PART TWO: THE ILLUSION OF SELF-TOUCH

CHAPTER 4: TACTILE EXPECTATION AND THE ILLUSION OF SELF-TOUCH

The self-touch rubber hand paradigm is used to create the illusion of self-touch, by having the participant administer stimulation to a prosthetic hand while the Examiner administers stimulation to the participant's receptive hand. With synchronous stimulation, participants experience the compelling illusion that they are touching their own hand. In the current study, the robustness of this illusion was assessed using incongruent stimuli. The participant used the index finger of the right hand to administer stimulation to a prosthetic hand while the Examiner used a paintbrush to administer stimulation to the participant's left hand. The results indicate that this violation of tactile expectations does not diminish the illusion of self-touch. Participants experienced the illusion despite the use of incongruent stimuli, both when vision was precluded and when visual feedback provided clear evidence of the tactile mismatch.

How do you know that the hand that you see before you is your own? The systematic study of body ownership poses a challenge to cognitive psychologists for the simple reason that the body is always there (James, 1890), existing as "a backdrop to whatever one is thinking, experiencing, or doing, though its various parts are not being monitored" (Kinsbourne, 1995, p. 217). Over the past decade, the visual rubber hand paradigm (Botvinick & Cohen, 1998) has provided an invaluable tool for experimental investigations into body ownership. With this paradigm, individuals experience a sense of ownership over a viewed prosthetic limb. Researchers have used this illusion of ownership to understand body awareness better. They manipulate factors thought to underlie self-attribution of body parts, and they assess the impact of these manipulations on the sense of ownership of the prosthetic limb. Candidate factors which may play a role in self-attribution of body parts include: visual signals, somatosensory signals, proprioceptive signals and higher-order representations of the body.

In the visual rubber hand paradigm, the participant looks at a prosthetic hand being touched with a paintbrush by the Examiner while the participant's own hand – hidden from view – is also touched with a paintbrush by the Examiner. When the touch administered to the prosthetic hand and to the participant's hidden hand is synchronous, the participant has an experience in which she seems to "feel the touch not of the hidden brush but that of the viewed brush, as if the rubber hand ha[s] sensed the touch" (Botvinick & Cohen, 1998, p. 756). This is referred to as visual capture of touch. It may also seem to the participant that the viewed prosthetic hand is her own hand.

The following conditions are best for demonstrating the visual rubber hand illusion: (1) stimulation on the viewed prosthetic hand is synchronous with stimulation on the participant's hidden hand (Shimada et al., 2009); and (2) alignment of the viewed prosthetic hand is matched to that of the participant's hidden hand (Costantini & Haggard, 2007; Ehrsson et al., 2004; Pavani et al., 2000; Tsakiris & Haggard, 2005), with the viewed prosthetic hand positioned (2a) close to the participant's hidden hand (Lloyd, 2007, but see Zopf, Savage, & Williams, 2010) and (2b) in an anatomically-plausible location relative to the participant's body (Armel & Ramachandran, 2003). It may also be important for the viewed prosthetic hand to correspond to the *structural description of the body*, an aspect of higher-order body representation. However, the research literature is divided on this point.

Armel and Ramachandran (2003) found that the visual rubber hand illusion was elicited despite visual inconsistencies between the prosthetic hand and the participant's hand, including skin tone, hand size and distinguishing visual features such as nail polish (see also Longo et al., 2009). Moreover, they reported that the illusion could even be elicited in the absence of a prosthetic hand, insofar as participants "often reported sensations arising from the table surface" (p. 1499) when it was stroked and tapped in precise synchrony with the stimulation administered to the participant's hidden hand. This finding was not supported by Haans et al. (2008), who found that the subjective experience of the visual rubber hand illusion (as measured by questionnaire items) was significantly diminished when the participant viewed the table (rather than a prosthetic hand) being stimulated. Likewise, Tsakiris and Haggard (2005) found that synchronous stimulation of a wooden stick and the participant's hidden hand did not produce the illusion. Tsakiris et al. (2007) have also shown that the illusion is not elicited if the participant is viewing stimulation on a prosthetic left hand while her own (hidden) right hand is stimulated.

How do we account for these findings that the visual rubber hand illusion may be diminished when the participant views stimulation on a non-hand or wrong-hand object? One possible explanation is that it may be more difficult for the participant to experience ownership of an object that does not correspond to her *higher-order body representation*, simply because the object conflicts with the participant's stored representation of what belongs to the human body (Longo et al., 2009). An alternative explanation is that the participant may *expect* the stimulation on her own hand to feel a certain way and this expectation may depend on the viewed object. If the viewed object has a non-skin texture, stimulation on the participant's own skin may feel different from what she would expect given the texture of the viewed object (Armel & Ramachandran, 2003; Haans et al., 2008) and this violation of tactile expectation may be sufficient to abolish the visual rubber hand illusion.

These alternative views are best conceptualised using cases from the literature. Armel and Ramachandran (2003) described four participants (out of 120) with particularly hairy hands who spontaneously indicated that "the illusion was ruined when their hand was touched in areas of high hair density" (p. 1504). The researchers suggested that it was "a mismatch in the expected (from visual information) versus felt type of touch, rather than just the visual inconsistencies of hair versus no hair, that diminished the illusion" (p. 1504). Not dissimilarly, Haans et al. (2008) found that, when the visual rubber hand illusion was elicited using a prosthetic hand wearing a latex glove rather than a prosthetic hand of natural skin texture, "several participants remarked that their tactile sensations did not match those generally perceived while wearing gloves" (p. 393). But, as noted by Haans et al., visual similarity and tactile expectation are confounded in these examples – the sensations on the participant's hand match expectations when viewing the visually similar object but not when viewing the visually dissimilar object. Hence, it is not clear whether the visual rubber hand illusion is affected by use of a visually dissimilar hand that the participant is not able to incorporate into a higher-order body representation, or by the violation of tactile expectation.

Schütz-Bosbach, Tausche, and Weiss (2009) have very recently isolated the role of tactile expectation, thus addressing the concern that higher-order body representation and tactile expectation are confounded in previous research. Rather than manipulating the match between tactile properties of the viewed prosthetic hand and of the participant's hidden hand, the researchers manipulated the match between tactile properties of the stimulus that was administered to the viewed prosthetic hand and of the stimulus administered to the participant's hidden hand. For example, the participant viewed a prosthetic hand being touched with a soft fabric while receiving stimulation from a rough fabric on her own (hidden) hand. In this case there was no confound. The participant's tactile expectation was violated but the participant was viewing stimulation on a realistic prosthetic hand that could be incorporated into her higher-order body representation. Participants experienced the visual rubber hand illusion even when tactile expectation was violated. When considered together with previous studies demonstrating that the visual rubber hand illusion is diminished if the participant views stimulation on a non-hand or wrong-hand object (or a hand that is markedly dissimilar to the participant's own hairy hand; Armel & Ramachandran, 2003), Schütz-Bosbach et al.'s finding suggests that the disruption to the visual rubber hand illusion occurs because the viewed object cannot be incorporated into the participant's higher-order body representation, rather than because the participant's tactile expectations are violated.

The current study considers the interplay of higher-order body representation and tactile expectation as it applies to the *non-visual* self-touch rubber hand paradigm (Ehrsson et al., 2005). With vision precluded, the Examiner guides the participant's hand in administering stimulation to a prosthetic hand while the Examiner administers synchronous stimulation to the participant's other hand. The participant may experience the illusion that she is touching her own hand, even when the two hands are separated by 15 cm. In the pioneering study by Ehrsson et al., the "participants, the experimenter, and the rubber hand all wore identical plastic surgical gloves to make the tactile surfaces of the two hands [participant and prosthetic] as similar as possible to each other" (p. 10565). When the participant's stimulation of the prosthetic hand and the Examiner's stimulation of the participant's receptive hand were synchronous, the participant experienced the compelling illusion that she was touching her own hand. In a control condition, the Examiner guided the participant instead to tap the bristles of a small dish brush with one hand while the Examiner synchronously stimulated the participant's other hand. In this condition, "no illusion of self-touch was typically elicited" (p. 10566), but it is not clear whether this was due to the violation of higher-order body representation or the violation of tactile expectation since these factors were confounded. Higher-order body representation was violated because a dish brush does not fit with the structural description of the human body, and tactile expectation was violated because under conditions of self-touch the participant would expect her administering index finger to feel a skin-like surface rather than the bristles of a brush.

The current study investigates the role of tactile expectation in the illusion of self-touch, without confounding higher-order body representation and tactile expectation. We manipulate tactile properties of the administering stimulus (as in Schütz-Bosbach, Tausche, & Weiss, 2009) rather than tactile properties of the object to which the participant administers stimulation. If the illusion of self-touch requires a match between expected and felt sensations, the participant will not experience the illusion when she is touching the prosthetic hand with one stimulus and receiving stimulation from a different stimulus. Alternatively, if expectations about tactile sensation do not affect the illusion, the impression of self-touch should persist provided there is synchronous stimulation of the two hands.

Overview of Experiments

Three experiments are presented. Experiments 1a and 1b assessed whether the illusion of self-touch could be elicited when the participant administered stimulation to the prosthetic hand using her index finger while her other hand was touched with – an incongruent stimulus – a paintbrush. This tactile mismatch has an effect on both of the participant's hands: the participant's administering hand is receiving tactile sensations consistent with touching a prosthetic hand while the receptive hand is receiving tactile sensations consistent with being touched with a paintbrush. These experiments were conducted with vision precluded.

Experiment 2 combined the methodologies of the traditional visual rubber hand paradigm (Botvinick & Cohen, 1998) and the non-visual self-touch rubber hand paradigm (Ehrsson et al., 2005). The participants were involved in the administration of touch as they are in the non-visual paradigm, but the paradigm was conducted with vision permitted. Stimulation was either congruent or incongruent. In the congruent condition, the participant administered stimulation to the prosthetic hand using her index finger while her other hand was touched with – a congruent stimulus – the Examiner's index finger. In the incongruent condition, the participant administered stimulation to the prosthetic hand using her index finger while her other hand was touched with – an incongruent stimulus – a paintbrush. On a given trial, the participant had vision either of her right hand administering stimulation to the prosthetic hand or of her left hand receiving stimulation from the Examiner.

Experiment 1a

Method

Participants

Ten right-handed participants (aged 19–33 years; 5 female, 5 male) were assessed following a protocol approved by the University of Oxford Research Ethics Committee, and in accordance with ethical standards laid down in the 2008 Helsinki Declaration. All participants were naïve to the experimental objectives.

Materials and Procedure

The participant was seated at a testing table with a prosthetic left hand positioned at body midline. The participant's own left hand was positioned to the left of the prosthetic hand with the two index fingers 15 cm apart.

The Examiner sat on the opposite side of the table to the participant. The Examiner guided the participant's right hand in administering stimulation to the index finger of the prosthetic hand, using the participant's index finger. The participant was instructed to keep her eyes closed throughout the experimental trial, and to relax and allow her right hand to be guided by the Examiner. At the same time, the Examiner administered stimulation to the index finger of the participant's left hand with an index finger (congruent stimulation – Trial 1) or with a paintbrush (incongruent stimulation – Trial 2, see Figure 9). The Examiner's stimulation of the participant's left hand was timed to be synchronous with the stimulation that the participant administered to the prosthetic hand.

Stimulation comprised strokes and taps administered to the proximal phalanx of the index finger (including the metacarpal phalangeal joint and the proximal interphalangeal joint). Strokes were always unidirectional toward the finger tip. Each trial lasted for 60 s.

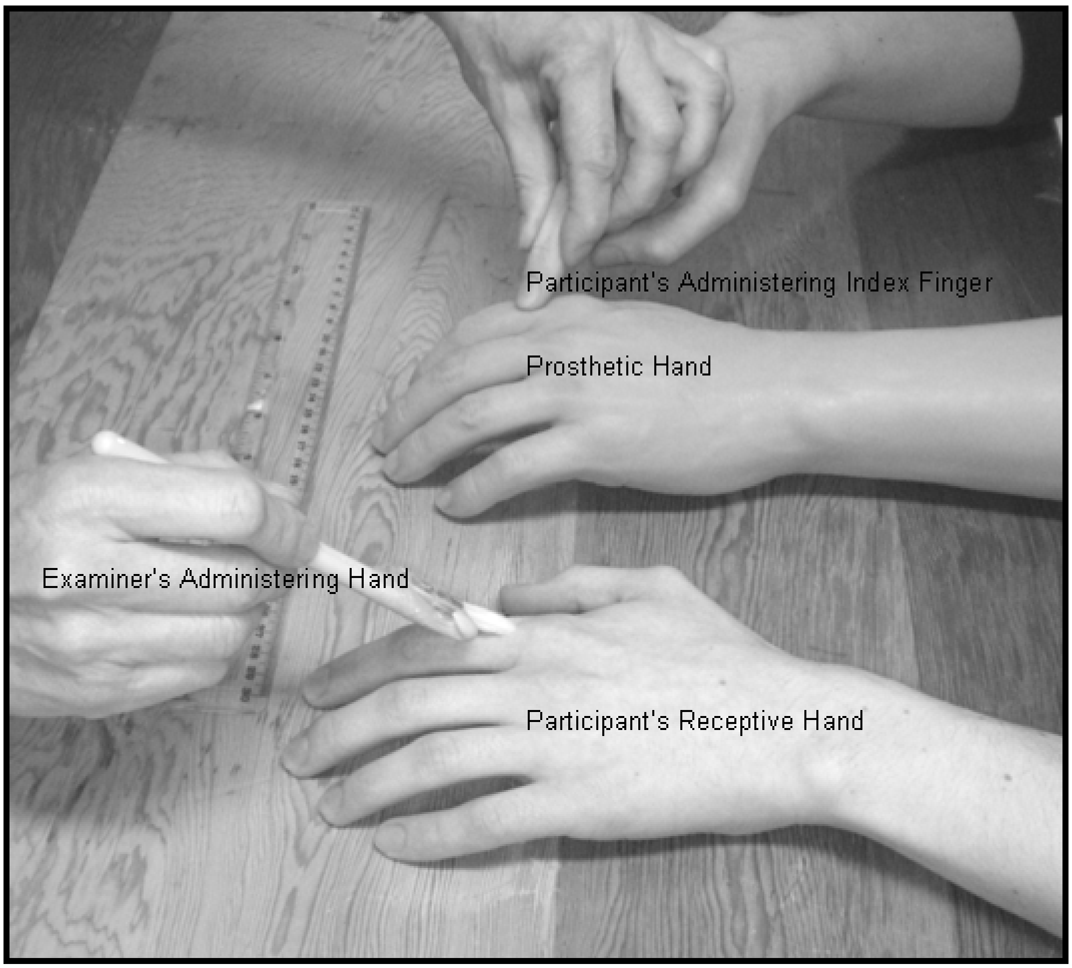

Figure 9. The basic procedure for eliciting the illusion of self-touch: the Examiner guides the participant to administer touch to a prosthetic hand while the Examiner administers touch to the participant's receptive hand. The Figure depicts the incongruent (finger-paintbrush) stimulation trial.

Self-Touch Illusion Questionnaire

Following each trial, the participant indicated her level of agreement with two statements:

(1) It felt as if I were touching my own hand.

(2) It felt as if my left hand were shrinking.

The first statement was adapted from Ehrsson et al. (2005) and was used to measure the participant's subjective experience of the illusion of self-touch. The second statement served as a control for suggestibility; that is, a statement about an experience that the paradigm was not designed to elicit. A seven-point scale (0 = *not at all*; 1 = *slightly agree*; 3 = *moderately agree*; 5 = *strongly agree*; 6 = *very strongly agree*) was used to rate agreement with the statements.

Note that the strength of the rubber hand illusion is frequently measured using a seven-point scale with negative through positive values. Participants provide an agreement rating with statements probing experience of the illusion (e.g., −3 = *strongly disagree*; +3 = *strongly agree*). However, it has been argued recently (Miles, 2008, April) that participants who do not experience the illusion may find it difficult to rate non-agreement (i.e., −1 vs. −2 vs. −3). Therefore we use a scale in which failure to experience the illusion receives a zero rating (*not at all*) and experience of the illusion is rated 1 through 6 (*very strongly agree*). This scale provides greater range for rating relative strength for the vast majority of participants who do experience the illusion.

Proprioceptive Drift

To examine the extent of proprioceptive drift associated with the illusion of self-touch, we adapted the calibration method used by Ehrsson et al. (2005). Three measurements were obtained: two pre-stimulation measurements and one post-stimulation measurement. The pre-stimulation measurements were averaged to give a baseline measure of proprioceptively perceived position. Proprioceptive drift was calculated as the change in the proprioceptively perceived position of the index finger from baseline. The prosthetic hand was removed from the table when these measurements were taken, immediately before and after each 60-s trial.

The participant was instructed to maintain the position of her receptive left hand and to extend her right arm, which the Examiner positioned at 45° to the right of the midsagittal plane of the participant's body. The participant was then asked to point quickly by sliding her right index finger along the table, in a single movement, until it was in line with the felt position of her left index finger. The Examiner recorded the distance between the participant's indicated and actual finger position. Note that the participant closed her eyes prior to the two pre-stimulation measurements, and was asked to maintain eyes closed for the duration of the experimental trial; that is, during the stimulation period and until the post-stimulation measure of proprioceptively perceived position was obtained.

Open-Ended Description

At the end of the experiment, the participant was invited to provide a written open-ended description about her experience.

Results

Self-Touch Illusion Questionnaire

Questionnaire ratings were analysed using a Wilcoxon Signed-Rank Test (the non-parametric alternative of a paired *t*-test). The results indicated that ratings for the illusion statement did not differ when stimulation was congruent (*Md* = 3.5) compared with incongruent (*Md* = 2.5)(z = -.412, p = .680)(Figure 10). Visual inspection of Figure 10 reveals that the median ratings for the control statement were zero for both conditions.

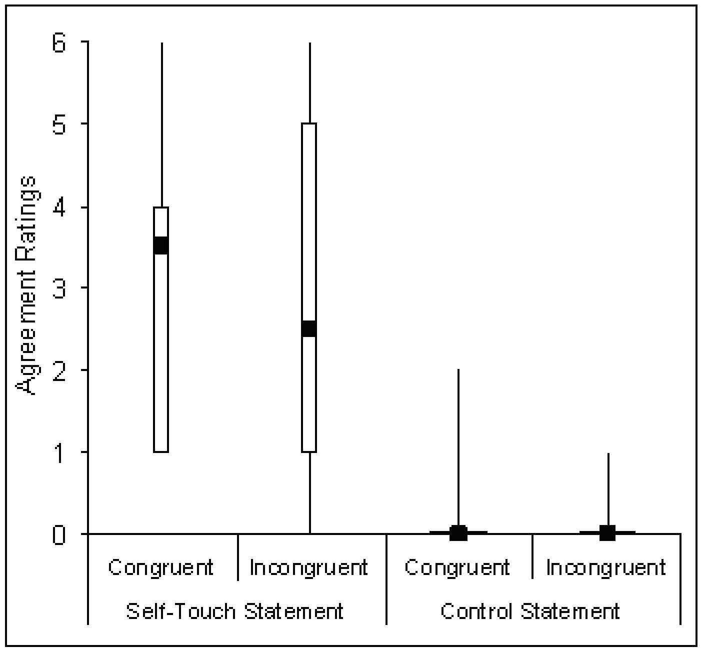

Figure 10. Median agreement ratings for the self-touch illusion questionnaire. The black filled-in square indicates the median value, the box indicates the interquartile range, and the whiskers indicate the full range of responses.

Proprioceptive Drift

Proprioceptive drift was analysed using a paired *t*-test. The results indicated that proprioceptive drift did not differ when stimulation was congruent (*M* = 1.00 cm) compared with incongruent (*M* = 1.9 cm)($t(9)$ = -1.230, p = .250)(Figure 11).

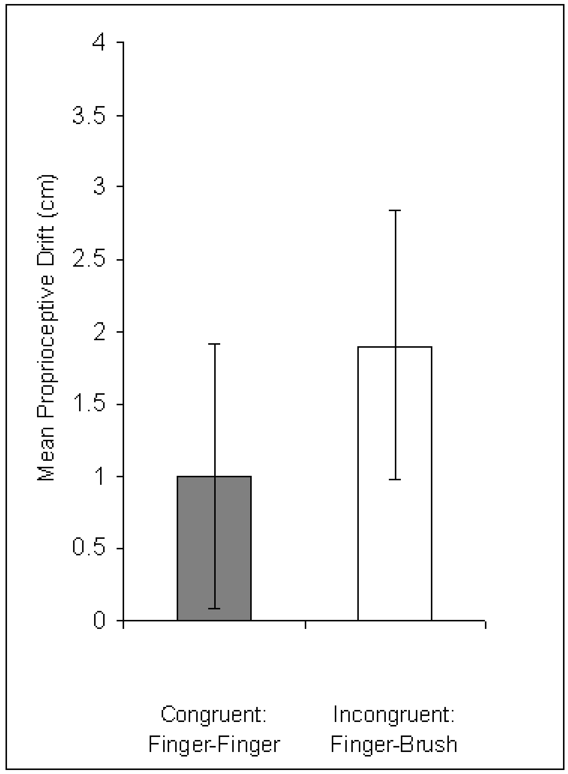

Figure 11. Mean proprioceptive drift (cm) under conditions of congruent and incongruent stimulation. Error bars indicate one standard error of the mean.

Open-Ended Descriptions

Participants mainly described the experience of self-touch. However, three participants explicitly commented on the incongruent stimulation:

P3. "When touched with a brush while using my finger, it felt like there was a glove or rough surface covering my hand which explained why the hand felt rough to touch."

P4. "In the brush condition, I felt ownership over both brush and hand. This is hard to describe but I felt like my finger was a brush or like I really needed to moisturise."

P5. "Whilst I knew that my finger was not administering the sensations to my left hand, with the movements synchronised I found it quite easy to suspend my disbelief and

> experienced at times a strange fusion of sensations, e.g., a brush-like finger. In part I think this is because I was willing to let it happen."

These descriptions provide insight as to how the participants may experience incongruent stimulation, or at least, how they might interpret the experience of self-touch when stimulation is incongruent. In a follow-up study (Experiment 1b), the experimental design was therefore refined to include a questionnaire for quantifying the perception of incongruent stimulation. In addition, we verified that the participant was aware of the stimulus congruence or incongruence, and we included asynchronous control trials to provide a baseline measure.

Experiment 1b

Method

Participants

Twenty-three right-handed participants were assessed following a protocol approved by the University of Oxford Research Ethics Committee, and in accordance with ethical standards laid down in the 2008 Helsinki Declaration. One participant was excluded due to failure to maintain eyes closed.[9] Data from 22 participants (aged 18–31 years; 16 female, 6 male) were analysed. All participants were naïve to the experimental objectives.

Materials and Procedure

The procedure was identical to Experiment 1a, with the following exception. In Experiment 1b, there were four stimulation trials. The Examiner guided the participant's right hand in administering stimulation to the index finger of the prosthetic hand, using the participant's index finger. At the same time, the Examiner administered stimulation to the index finger of the participant's left hand with an index finger (congruent stimulation – Trials 1 and 2) or with a paintbrush (incongruent stimulation – Trials 3 and 4). The Examiner's stimulation of the participant's left hand was timed to be either (a) synchronous (Trials 1 and 3) or (b) asynchronous (Trials 2 and 4) with the stimulation that the participant administered to the

[9] The participant repeatedly opened her eyes to check "what was going on". She couldn't make sense of the fact that one second she was touching a prosthetic hand, the next second she was touching her own hand, and when she opened her eyes she was back to touching the prosthetic hand!

prosthetic hand. The study by Ehrsson et al. (2005) found that the illusion of self-touch is elicited with synchronous stimulation; asynchronous trials were included as a baseline measure.

Self-Touch Illusion Questionnaire

Following each trial, the participant completed two short questionnaires. The first questionnaire comprised two statements as in Experiment 1:

(1) It felt as if I were touching my own hand.
(2) It felt as if my left hand were shrinking.

The second questionnaire comprised eight statements designed to measure the participant's perception of the stimuli used in the experimental trials. The statements were based on the experiences reported by participants in Experiment 1a:

(1) It felt as if I were administering touch with a finger.
(2) It felt as if I were administering touch with a brush.
(3) It felt as if I were administering touch with a finger and a brush simultaneously.
(4) My left index finger felt as if it were touched by a finger.
(5) My left index finger felt as if it were touched by a brush.
(6) My left index finger felt as if it were touched by a finger and a brush simultaneously.
(7) My right index finger felt like a finger.
(8) My right index finger felt like a brush.

The order of statements was randomised across trials, and a seven-point visual analogue scale (0 = *not at all*; 1 = *slightly agree*; 3 = *moderately agree*; 5 = *strongly agree*; 6 = *very strongly agree*) was used to rate agreement with the statements.

Once the participant had completed the questionnaire assessing her perception of the stimuli, she was asked to name both the stimulus used to administer stimulation to the prosthetic hand and the stimulus used to administer stimulation to her own hand. This question was designed to verify that the participant understood that the stimuli were incongruent on the critical trials. It was asked after the questionnaire was administered, so as to not bias participant's responses to each statement.

Proprioceptive Drift

Proprioceptive drift was assessed using the method presented in Experiment 1a.

Results

Self-Touch Illusion Questionnaire

Illusion. The first analysis investigated whether there was an effect for congruence. This analysis was conducted using individual Wilcoxon Signed-Rank Tests. The results for synchronous stimulation indicated that ratings for the illusion statement did not differ when stimulation was congruent (Md = 3) compared with incongruent (Md = 4)($z = -.569$, $p = .569$). Similarly, when stimulation was asynchronous, ratings for the illusion statement did not differ when stimulation was congruent (Md = 0) compared with incongruent (Md = 0)($z = -.917$, $p = .35$).

The second analysis investigated whether participants provided higher agreement ratings for synchronous compared with asynchronous stimulation. The analysis was conducted using individual Wilcoxon Signed-Rank Tests (and an adjusted alpha level of .025). Participants provided higher ratings for synchronous stimulation both when stimulation was congruent (z = -3.645, p < .001) and when stimulation was incongruent (z = -3.307, p < .001) (Figure 12). Visual inspection of Figure 12 reveals that the median ratings for the control statement were zero in all conditions.

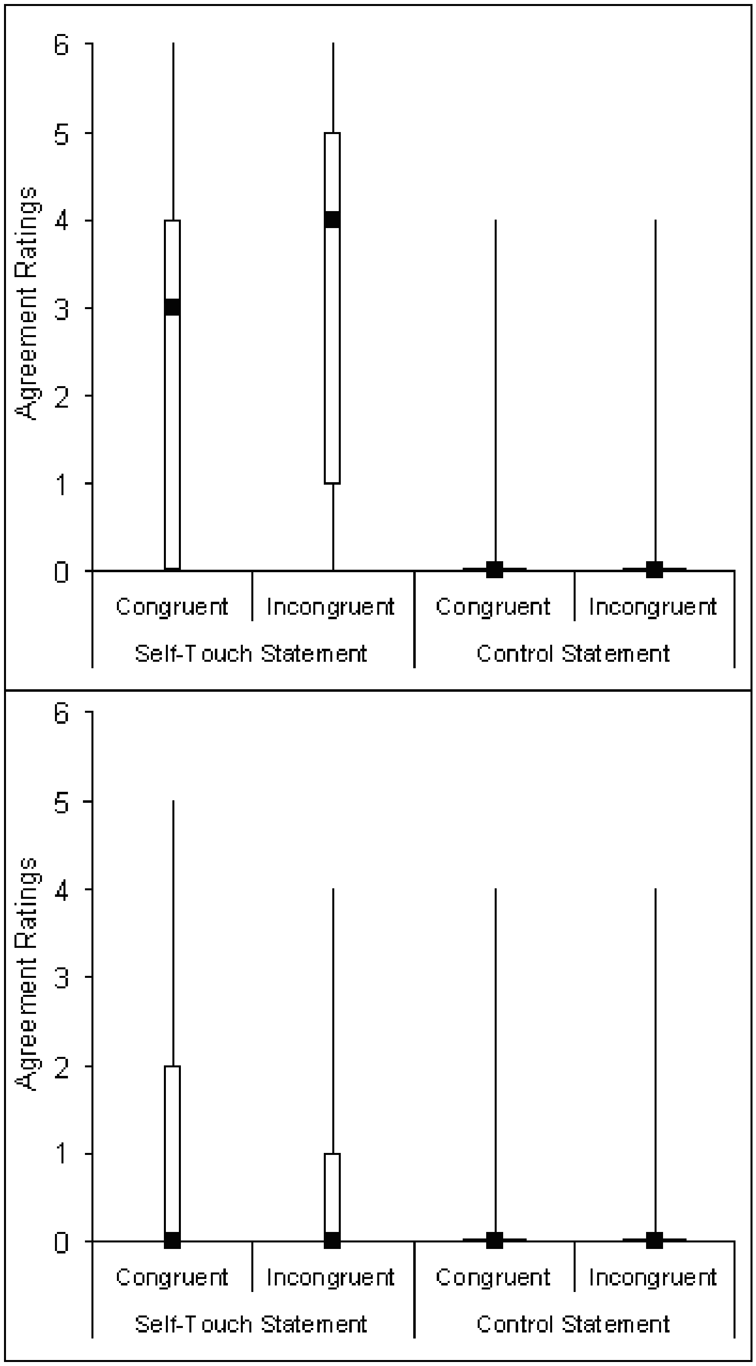

Figure 12. Median agreement ratings for the self-touch illusion questionnaire for synchronous (top panel) and asynchronous (bottom panel) stimulation. The black filled-in square indicates the median value, the box indicates the interquartile range, and the whiskers indicate the full range of responses.

Perception of the administering stimulus. Under conditions of incongruent stimulation, the participant may bind the tactile sensations from each hand when she experiences the illusion of self-touch. This may lead either to the perception that the receptive left hand is being simultaneously touched by two stimuli or, alternatively, to the perception that the index finger is brush-like. If the participant has these experiences, we would expect higher ratings for the incongruent stimulation trial (compared with the congruent stimulation trial) for the following statements:

(2) It felt as if I were administering touch with a brush.

(3) It felt as if I were administering touch with a finger and a brush simultaneously.

(6) My left index finger felt as if it were touched by a finger and a brush simultaneously.

(8) My right index finger felt like a brush.

Individual Wilcoxon Signed-Rank Tests confirmed this prediction. Participants provided higher ratings for these statements when assessed with incongruent stimulation: administering touch with a brush (Congruent $Md = 0$, Incongruent $Md = 2$, $z = -2.024$, $p = .043$); administering touch with a finger and a brush (Congruent $Md = 0$, Incongruent $Md = 0.5$, $z = -2.236$, $p = .025$); receiving touch from a finger and a brush (Congruent $Md = 0$, Incongruent $Md = 0.5$, $z = -2.214$, $p = .027$); right index finger feels like a brush (Congruent $Md = 0$, Incongruent $Md = 1.5$, $z = -3.170$, $p = .002$). However, when an adjusted alpha level of .0125 was used to control for Type 1 error, the only statement that produced a significant result was "My right index finger felt like a brush". This statement received a positive agreement rating from 14 of 22 participants.

Awareness of stimulus congruence and stimulus incongruence. On the congruent trial with synchronous stimulation, 20 of 22 participants correctly reported receiving stimulation from a finger. On the incongruent trial with synchronous stimulation, all 22 participants correctly reported receiving stimulation from a brush. (Not surprisingly, all participants correctly reported administering stimulation with an index finger on the congruent and incongruent stimulation trials.)

Proprioceptive Drift

Proprioceptive drift was analysed using a 2x2 ANOVA. The first factor was mode of stroking (synchronous, asynchronous) and the second factor was congruence (congruent, incongruent). There was a main effect for mode of stroking ($F(1, 21) = 16.220$, $p = .001$, partial eta squared = .436), with greater proprioceptive drift for synchronous ($M = 2.381$ cm) compared with asynchronous ($M = .034$ cm) stimulation. There was no main effect for congruence ($F(1, 21) = .020$, $p = .890$, multivariate partial eta-squared = .001). There was no interaction between mode of stroking and congruence ($F(1, 21) = .317$, $p = .579$, partial eta squared = .015)(Figure 13).

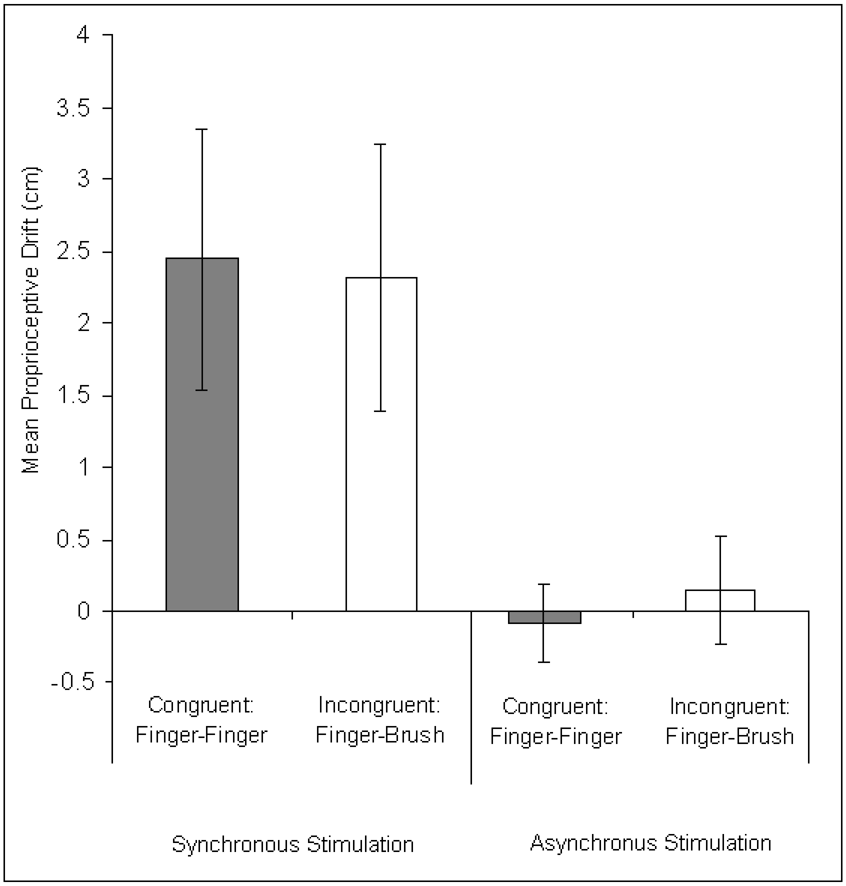

Figure 13. Mean proprioceptive drift (cm) under conditions of synchronous and asynchronous stimulation. Error bars indicate one standard error of the mean.

Experiment 2

The results of Experiments 1a and 1b indicate that the illusion of self-touch is not diminished by tactile incongruence. However, given that the paradigm is conducted with vision precluded, the participant may disregard the incongruent stimuli, perhaps by generating a visual mental image in which she is administering touch with, and receiving touch from, her finger. In Experiment 2, the procedure was carried out with vision permitted. This is the first study to investigate a visual version of the illusion of self-touch.

Method

Participants

Twelve participants (aged 19–27 years; 9 female, 3 male) took part in Experiment 2.

Experiment Overview

Experiment 2 comprised six trials. The baseline conditions (Trials 1 and 4) were conducted with vision precluded, and the remaining trials (Trials 2, 3, 5, 6) with vision permitted.

Baseline conditions

Materials and Procedure

Trials 1 and 4 were congruent (finger–finger) 60-s stimulation trials, conducted with vision precluded. The Examiner guided the participant's right index finger to administer stimulation to the prosthetic hand while the Examiner administered synchronous stimulation to the participant's left hand. The procedure for stimulation was as in Experiment 1 except that only strokes of the proximal phalanx of the index finger were used, rather than strokes and taps, and the strokes were always unidirectional toward the wrist, rather than toward the finger tip.

Self-Touch Illusion Questionnaire

Following each trial, the participant indicated her level of agreement with two statements as in Experiment 1:

(1) It felt as if I were touching my own hand.

(2) It felt as if my left hand were shrinking.

A seven-point scale (0 = *not at all*; 1 = *slightly agree*; 3 = *moderately agree*; 5 = *strongly agree*; 6 = *very strongly agree*) was used to rate agreement with the statements.

Vision conditions

Materials and Procedure

Trials 2, 3, 5 and 6 were conducted with vision permitted. Two examiners were required to conduct these trials. Examiner 1 sat to the left of the participant and Examiner 2 was positioned to the right.

Trials 2 and 5 comprised congruent stimulation: Examiner 1 used her right index finger to administer stimulation to the participant's left hand while Examiner 2 guided the participant's right index finger to administer stimulation to the prosthetic hand (Figure 14). Trials 3 and 6 comprised incongruent stimulation: Examiner 1 used a paintbrush to administer stimulation to the participant's left hand while Examiner 2 guided the participant's right index finger to administer stimulation to the prosthetic hand. Timing was guided by the stimulation administered by Examiner 1.

Six participants were permitted vision of their right hand on Trials 2 and 3 (view-right condition) and vision of their left hand on Trials 5 and 6 (view-left condition). The remaining six participants were permitted vision of their left hand on Trials 2 and 3 (view-left condition) and vision of their right hand on Trials 5 and 6 (view-right condition).

In the view-right condition, the participant had vision of her own right hand as it was guided by Examiner 2 to stroke the prosthetic hand. In the view-left condition, the participant had vision of her own left hand being stroked by Examiner 1. A partition was placed between the participant's left hand and the prosthetic hand to ensure that the participant could only see the hand(s) she was permitted to view. Once Examiner 1 and Examiner 2 had achieved synchronous stimulation, as determined by the participant and Examiner 2, the stopwatch was activated. Sixty seconds of synchronous stimulation followed.

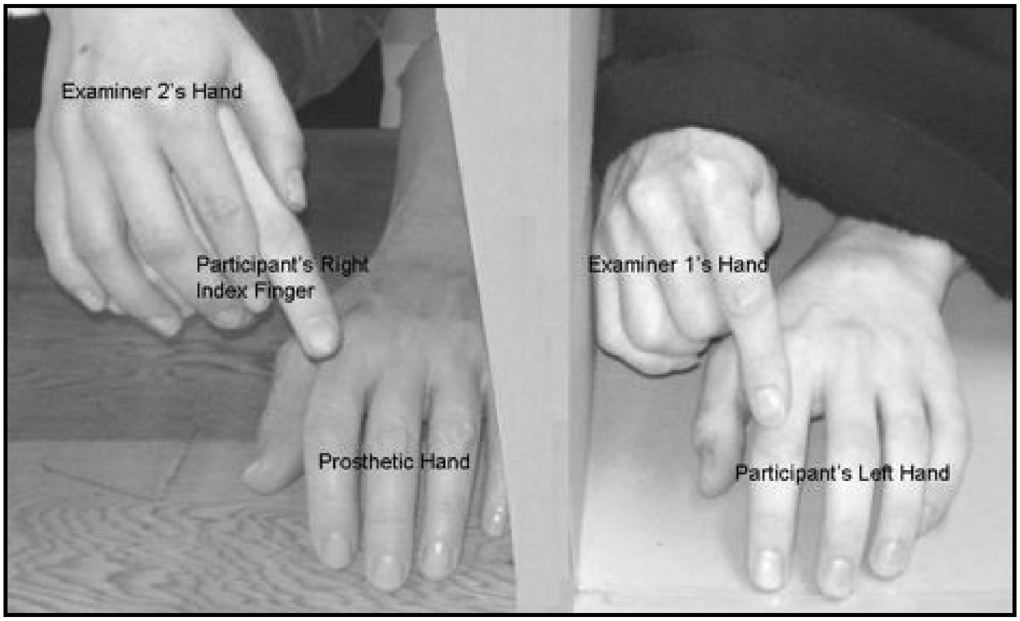

Figure 14. Experimental set-up in a congruent stimulation trial in which the participant was permitted vision of her own left hand as it was touched by Examiner 1. A black cloth was draped over the arms on the viewed side of space to prevent vision of irrelevant cues from clothing (view-left condition) or from the stump of the prosthetic hand (view-right condition).

Self-Touch Illusion Questionnaire

Following each trial, the participant indicated her level of agreement with three statements:

(1) It felt as if I were touching my own hand.

(2) It seemed as if I were observing my right hand stroking my left hand.

(3) It felt as if my left hand were shrinking.

The first statement was used to measure the participant's subjective experience of the illusion of self-touch. The second statement was used to measure whether the participant experienced ownership of the prosthetic hand (view-right condition) or the Examiner's administering hand (view-left condition). The third statement served as a control for suggestibility. A seven-point visual analogue scale (0 = *not at all*; 1 = *slightly agree*; 3 = *moderately agree*; 5 = *strongly agree*; 6 = *very strongly agree*) was used to rate agreement with the statements.

Results

Self-Touch Illusion Questionnaire: View-Right Condition

The first analysis investigated whether the illusion of self-touch was diminished by vision in the view-right condition. A Wilcoxon Signed-Rank Test was used to compare ratings for Statement 1 for the non-visual trial preceding the view-right trial (Md = 3.5) and the visual view-right trial (Md = 2). The results indicated a significant difference in illusion ratings for these two trials (z = -2.132, p = .033). Participants provided higher ratings for the self-touch statement when the paradigm was conducted with vision-precluded.

The second analysis investigated whether the *visual* illusion of self-touch was diminished by stimulus incongruence in the view-right condition. A Wilcoxon Signed-Rank Test was used to compare ratings for Statement 1 for the view-right trial conducted with congruent stimulation (Md = 2) and the view-right trial conducted with incongruent stimulation (Md = 2). The results indicated no difference in illusion ratings for these two trials (z = -.287, p = .774).

The third analysis investigated whether the illusion of ownership was diminished by stimulus incongruence in the view-right condition. A Wilcoxon Signed-Rank Test was used to compare ratings for Statement 2 for the view-right trial conducted with congruent stimulation (*Md* = 2) and the view-right trial conducted with incongruent stimulation (*Md* = 1). The results indicated a significant difference in illusion ratings for these two trials (z = -2.020, p = .043). Participants provided higher ratings for the ownership statement when the paradigm was conducted using congruent stimulation.

Visual inspection of Figure 15 reveals that the median ratings for the control statement were zero in both view-right conditions.

Self-Touch Illusion Questionnaire: View-Left Condition

The first analysis investigated whether the illusion of self-touch was diminished by vision in the view-left condition. A Wilcoxon Signed-Rank Test was used to compare ratings for Statement 1 for the non-visual trial preceding the view-left trial (*Md* = 3) and the visual view-left trial (*Md* = 3). The results indicated no difference in illusion ratings for these two trials (z = -.171, p = .864).

The second analysis investigated whether the *visual* illusion of self-touch was diminished by stimulus incongruence in the view-left condition. A Wilcoxon Signed-Rank Test was used to compare ratings for Statement 1 for the view-left trial conducted with congruent stimulation (*Md* = 3) and the view-left trial conducted with incongruent stimulation (*Md* = 3). The results indicated no difference in illusion ratings for these two trials (z = -1.529, p = .126).

The third analysis investigated whether the illusion of ownership was diminished by stimulus incongruence in the view-left condition. A Wilcoxon Signed-Rank Test was used to compare ratings for Statement 2 for the view-left trial conducted with congruent stimulation

(*Md* = 1) and the view-left trial conducted with incongruent stimulation (*Md* = 1). The results indicated no difference in illusion ratings for these two trials (z = -1.725, p = .084).

Visual inspection of Figure 15 reveals that the median ratings for the control statement were zero in both view-left conditions.

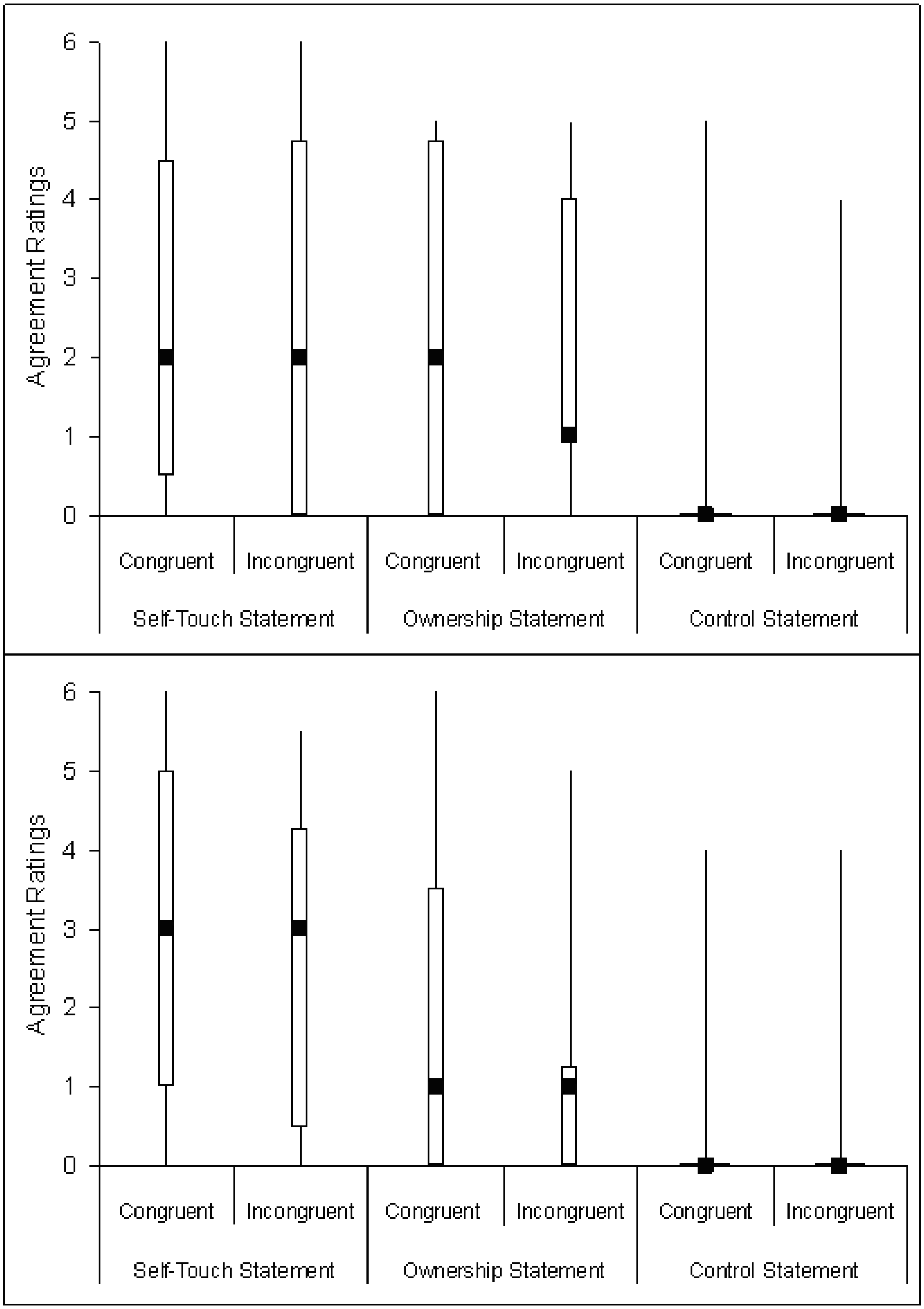

Figure 15. Median agreement ratings for the self-touch illusion questionnaire for the View-Right condition (top panel) and the View-Left condition (bottom panel). The black filled-in square indicates the median value, the box indicates the interquartile range, and the whiskers indicate the full range of responses.

General Discussion

We set out to investigate whether the illusion of self-touch is affected by violations of tactile expectation. We used the self-touch rubber hand paradigm devised by Ehrsson et al. (2005) to address this question. In this paradigm, the Examiner guides the participant to administer stimulation to a prosthetic hand while the Examiner administers synchronous stimulation to the participant's hand. If the participant experiences the illusion, she reports feeling as if she is touching her own hand. Three experiments were conducted. In Experiments 1a and 1b, we assessed whether the illusion of self-touch could be elicited when the participant administered stimulation to the prosthetic hand using her right index finger while her left hand was touched with – an incongruent stimulus – a paintbrush. In Experiment 2, we assessed whether the illusion of self-touch would be diminished when the participant had visual feedback indicating incongruent stimulation. This experiment combined the methodologies of the traditional visual (Botvinick & Cohen, 1998) and non-visual (Ehrsson et al.) rubber hand paradigms. The participants were involved in the administration of touch as they are in the non-visual paradigm but the paradigm was conducted with vision permitted.

Tactile Constraints on the 'Non-Visual' illusion of Self-Touch

In Experiment 1, participants were assessed under conditions of congruent and incongruent tactile stimulation. In the congruent stimulation condition, the participant used her index finger to administer stimulation to the prosthetic hand, and at the same time, the Examiner used her index finger to administer stimulation to the participant's receptive hand. In the incongruent stimulation condition, the participant used her index finger to administer stimulation to the prosthetic hand, and at the same time, the Examiner used a paintbrush to administer stimulation to the participant's receptive hand. Ratings for the illusion statement on the questionnaire did not differ between the congruent and incongruent stimulation trials, indicating that the subjective illusion of self-touch is equally compelling whether stimulation is congruent or incongruent. Similarly, there was no significant difference in proprioceptive drift when the participant administered touch with a finger and was synchronously touched with a finger compared with when the participant administered touch with a finger and was synchronously touched with a paintbrush. This finding indicates that participants experience mislocalisation in the proprioceptively perceived position of the receptive left hand, whether stimulation is congruent or incongruent. [10]

Schütz-Bosbach, Tausche, and Weiss (2009) demonstrated that the visual rubber hand illusion was resistant to violations of tactile expectation. In the incongruent trial of their study, the participant viewed a prosthetic hand being touched with either a soft or rough fabric while she received incongruent tactile stimulation on her hidden hand. We build on the results of Schütz-Bosbach et al. by demonstrating that the non-visual illusion of self-touch is also resistant to violations of tactile expectation. Participants experience the illusion of self-touch even under conditions of incongruent stimulation: the participant administers stimulation to the prosthetic hand using the index finger of her right hand while stimulation is administered to her left hand using a paintbrush.

In the only prior study using the (non-visual) self-touch rubber hand paradigm (Ehrsson et al., 2005), the 'incongruent-stimulation trial' took a different format. Specifically, the Examiner guided the participant to tap the bristles of a small dish brush while the Examiner synchronously

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[10] Earlier pilot experiments demonstrated that the illusion of self-touch could also be elicited when the participant administered stimulation with a paintbrush while her own hand was touched with a stick (and vice versa). However, in these conditions, the participant may have simply attended to administering touch with, and receiving touch from, an instrument; thus failing to register the stimulus incongruence. In the experiment proper, we used the finger-paintbrush incongruence condition, and so avoided this possible confound.

stimulated the participant's other hand. The illusion of self-touch was not typically elicited in this condition. There are some important differences between our Experiment 1 and the study by Ehrsson et al. In Experiment 1, the participant always administered stimulation to a prosthetic hand using her index finger but we manipulated the stimulus – index finger or paintbrush – the Examiner was using to touch the participant's other hand. In contrast, in the study by Ehrsson et al., the researchers manipulated the object to which the participant administered stimulation – prosthetic hand or dish brush, but the Examiner always used an index finger to touch the participant's other hand.

In short, we introduced incongruent stimulation by varying the instrument of stimulation while Ehrsson et al. (2005) introduced it by varying the object of stimulation. In our incongruent stimulation condition, the participant's tactile expectation was violated but there was no conflict with her higher-order body representation. In this condition, participants experienced the illusion of self-touch. We suggest that, in the study by Ehrsson et al., participants did not experience the illusion of self-touch in the incongruent stimulation condition because they were unable to incorporate a dish brush into their higher-order body representation, whereas the prosthetic hand was more easily incorporated.

One might question how the participant derives information that allows the prosthetic hand to be assimilated into her body image when vision of the hand is precluded. We believe that this information can be derived through stimulation of the prosthetic hand itself. The prosthetic hand used for the current experiments was exceptionally lifelike in shape and detail. When the participant administered stimulation, she was guided between the metacarpal phalangeal joint (the knuckle where the index finger meets the hand) and the proximal interphalangeal joint (the first knuckle of the index finger). The matching structure of the stimulated object would have been sufficient to indicate its correspondence with the participant's own stimulated hand.

The 'Visual' Illusion of Self-Touch

In Experiment 2, we introduced vision to assess whether visual feedback regarding stimulus incongruence would abolish the illusion of self-touch. There are two key differences in experimental design between the traditional visual rubber hand paradigm and the paradigm used in Experiment 2. First, in the traditional visual rubber hand paradigm, the participant is not involved in the administration of touch so there can be no illusion of self-touch, whereas in Experiment 2, the Examiner guided the participant to administer stimulation to the prosthetic hand. Second, in the traditional visual rubber hand paradigm, the participant is permitted vision of the prosthetic hand only, whereas in Experiment 2, the participant was permitted vision of either her right hand administering stimulation to the prosthetic hand or her left hand while it was being touched by the Examiner. Experiment 2 addressed two important questions: Can the illusion of self-touch be elicited when the participant has visual feedback? And, if the illusion can be elicited, will it persist when visual feedback indicates incongruent stimulation?

In the congruent stimulation condition, participants did experience the illusion of self-touch when vision was permitted. Five participants (42%) provided ratings in the top part of the scale (4 and above) in response to the statement "It felt as if I were touching my own hand" even when they had visual feedback indicating that this was not the case. Note though that the illusion of self-touch was diminished (but not abolished) by vision when the participant was looking at her right hand touching the prosthetic hand (view-right condition). It is possible that in the non-visual version of the paradigm, the participant did not experience the single event of self-touch as occurring at the location of the prosthetic hand. For example, the participant may have proprioceptively perceived her administering right hand as moving to the location of her receptive left hand. Thus when the paradigm was conducted with vision, it may have taken longer for the illusion to be elicited, because the visual feedback was contrary to the participant's non-visual experience of the illusion. Alternatively, visual feedback of a prosthetic hand, rather than a human hand, may have somewhat reduced the illusion of self-touch, or at least, the participant's subjective ratings. It is possible that the participant was less willing to provide a high rating for the statement "I felt as if I were touching my own hand" when visual feedback indicated the participant's right hand touching a non-human hand.

In the view-right condition, the participant observed touch on the prosthetic hand which corresponded to the touch on her (hidden) left hand. The viewing conditions were thus matched to the traditional visual rubber hand paradigm, in which the Examiner administers stimulation to the prosthetic hand, but now the Examiner guided the participant to administer the observed stimulation to the prosthetic hand. When the participant views touch on the prosthetic hand that corresponds to touch on her own hand, she may experience visual capture of touch – the illusion that she is experiencing tactile sensations in the location of the viewed prosthetic hand (Botvinick & Cohen, 1998). The novel finding is that participants can also experience a visual rubber hand illusion when they are not looking at a prosthetic hand. In the view-left condition, the participant observed touch being administered to her own left hand by the Examiner. The action of the Examiner's administering hand corresponded to the action of the participant's (hidden) right hand which was administering touch to the prosthetic hand. We propose that, to experience the illusion that her hands are in contact, the participant may experience visual capture of action – the illusion that the action of her administering hand is in the location of the Examiner's administering hand. Both types of displacement (touch and action) may lead to the visual illusion of self-touch. In the first case, tactile sensations are displaced to the location of the prosthetic hand and thus the location of the participant's administering hand. In the second case, action is displaced to the location of the Examiner's administering hand and thus the location of the participant's touched hand. This hypothesis will be investigated in Chapter 5.

Note that the concept of visual capture of action is not new. Nielsen (1963) conducted an elegant experiment in which the participant completed a simple line-drawing task. Unbeknownst to the participant, a mirror was inserted into the experimental set-up so that the participant was viewing another person's hand drawing the lines, rather than her own hand. Participants experienced the so-called alien hand as their own, making compensatory movements when the alien hand performed in an unpredictable manner. For example, when the task was to draw a straight line but the viewed hand veered rightward, most participants compensated for this error with a leftward adjustment of their own hand. Nielsen concluded that the "alien 'visual hand' dominate[d] the subject's 'kinesthetical/tactile hand'" (p. 230). He noted that most participants did not initially realise that they were viewing someone else's hand. In considering Nielsen's findings, we suggest that this pioneering study essentially elicited what would today be regarded as a visual rubber hand illusion, whereby participants took ownership of the actions of a viewed hand.

Tactile Constraints on the 'Visual' Illusion of Self-Touch

Having established that the illusion of self-touch can be elicited under congruent stimulation conditions which permit visual feedback, we next assessed whether the illusion was diminished under incongruent stimulation conditions which permit visual feedback. Specifically, we compared (1) the congruent trial in which the participant administered stimulation with, and received stimulation from, an index finger and (2) the incongruent trial in which the participant administered stimulation with an index finger, and received stimulation from a paintbrush. There was no difference in illusion ratings between the congruent and incongruent stimulation trials, and six participants (50%) provided ratings in the top part of the scale (4 and above) in response to the statement "It felt as if I were touching my own hand" even when they had visual feedback indicating incongruent stimulation. Experiment 2 shows that when vision is permitted in the 'non-visual' rubber hand paradigm (in which the participant is involved in administering stimulation), participants experience an equally compelling illusion of self-touch for congruent and incongruent stimulation.

A further question that we asked in Experiment 2 was whether participants would experience the illusion that they were observing their own right hand touching their own left hand, and whether this illusion would be affected by incongruent stimulation. The sense that one is observing one's two hands in contact may be taken to suggest that the participant is experiencing ownership of the 'alien' hand (i.e., the Examiner's hand in the view-left condition or the prosthetic hand in the view-right condition). The illusion that the participant was observing her right hand touching her left hand was diminished by stimulus incongruence in the View-Right condition. Participants indicated higher levels of agreement with the statement "It seemed as if I were observing my right hand stroking my left hand" in the congruent stimulation condition than in the incongruent stimulation condition. When the participant looked to her right hand, the visual image was of her right index finger being guided to touch the prosthetic hand. This visual image was inconsistent with the tactile perceptions of the hand. The results suggest that, although visual feedback of stimulus incongruence does not affect the felt illusion of self-touch, it can affect the illusion that the observed 'alien' hand is one's own.

Conclusion

In the current study, we investigated the role of tactile congruence in the illusion of self-touch, without confounding tactile congruence and higher-order body representation. This was achieved by manipulating tactile properties of the administering stimulus (as in Schütz-Bosbach, Tausche, & Weiss, 2009) rather than tactile properties of the object to which the participant administered stimulation. The illusion of self-touch was not diminished by incongruent stimulation, and this was true whether the procedure was conducted with vision precluded or permitted.

Armel and Ramachandran (2003) suggest that the traditional visual rubber hand illusion may be explained using a Bayesian model of perceptual learning, in which "two perceptions from different modalities are 'bound' when they co-occur with a high probability" (p. 1505). In the traditional visual rubber hand paradigm, the relevant modalities are vision (the observed touching of the prosthetic hand) and touch (the felt sensations in the participant's hand). Thus, "the seen and felt touch were bound because of their temporal synchrony" (p. 1505). A Bayesian model may likewise explain the illusion of self-touch, whereby the proprioceptive cues from the administering hand are bound with the tactile sensations of the receptive hand. Participants experience the illusion of self-touch when they administer touch to a prosthetic hand while receiving synchronous touch from the Examiner (see Ramachandran & Hirstein, 1997, 1998). According to Bayesian logic, there is a very low probability that the actions of the administering hand and the sensations on the receptive hand could correspond so precisely by chance; thus participants experience the illusion that the administering hand is touching the receptive hand. Self-as-active and self-as-receptive are experienced as participants in a single event of self-touch.

Using incongruent stimuli (and indeed introducing vision) does not change the temporal correspondence between the actions of the administering hand and the sensations of the receptive hand, and the improbability that this correspondence occurred by chance. Armel and Ramachandran (2003) note that the brain takes advantage of statistical correlations, "even when they do not 'make sense' from the cognitive point of view" (p. 1505).

In participants who experience the illusion of self-touch, information from multiple sensory sources is integrated into a single event file. Under conditions of incongruent stimulation, the dissonance between proprioceptive information from the administering right hand (I am administering touch with my finger) and tactile information from the receptive left hand (I am being touched with a brush) is apparent in participants' descriptions of their experience. They may agree with the statement "My right index finger felt like a brush".

CHAPTER 5: A NEW VISUAL ILLUSION OF SELF-TOUCH

A new paradigm elicits an illusion with three conceptually distinct components: (1) the participant experiences her hidden right hand as administering touch at the location of the Examiner's viewed administering hand (visual capture of action), (2) the participant experiences the Examiner's administering hand as being her own hand (experience of ownership), and (3) the participant experiences her two hands as being in contact, as if she were touching her own hand (illusion of self-touch). The presence of these illusory experiences was confirmed by questionnaire responses and proprioceptive drift data.

Over the past decade, the rubber hand paradigm has become an important tool for investigating body representation and the sense of embodiment. In the visual rubber hand paradigm (Botvinick & Cohen, 1998), the participant looks at a prosthetic hand being touched by the Examiner while the participant's own hand – hidden from view – is also touched by the Examiner. When touch on the prosthetic hand is synchronous with touch on the participant's hand, the participant may have the illusory experience of being touched at the location of the visible prosthetic hand. This *visual capture of touch* is said to occur because "vision may dominate the perception of body-part location" (Pavani et al., 2000, p. 353) and thus "can affect the localization of bodily sensations" (p. 358). In the original visual rubber hand paradigm, it may also seem to the participant that the prosthetic hand she is looking at is her own hand. These two components of the illusion elicited by the paradigm – visual capture of touch and the experience of ownership – are conceptually distinct and empirically dissociable (Longo, Schüür et al., 2008).

In another version of the rubber hand paradigm, with vision precluded (Ehrsson et al., 2005), the Examiner moves the participant's index finger so as to touch the prosthetic hand while at the same time administering touch to the participant's other (receptive) hand. When the participant's touch to the prosthetic hand is synchronous with the Examiner's touch to the participant's receptive hand, the participant may experience the illusion that her two hands are in contact, and that she is touching her own hand. The role of synchrony in this illusion of self-touch can be explained in Bayesian terms. There is a very low probability that the movements of the participant's index finger and the touches on her receptive hand could correspond so precisely by chance. Thus the participant experiences the illusion that her index finger is touching her receptive hand (Ramachandran & Hirstein, 1997, 1998).

In Chapter 4, we demonstrated the illusion of self-touch using a *visual* version of Ehrsson et al.'s (2005) paradigm. In this new rubber hand paradigm, as in the Ehrsson paradigm, the participant's two hands are involved: the participant's hand is guided by the Examiner to touch the prosthetic hand while her other hand is synchronously touched by the Examiner. The new paradigm is also matched as closely as possible to the original visual rubber hand paradigm (Botvinick & Cohen, 1998) in that one of the participant's two hands is hidden from view.

Two visual conditions can be tested. In Condition 1 (view-right), the participant looks at her administering right hand touching the prosthetic hand while her receptive left hand is hidden from view, and in Condition 2 (view-left), the participant looks at her receptive left hand receiving touch from the Examiner's hand while her administering right hand is hidden from view. Under conditions of synchronous stimulation, the participant may experience the illusion that her two hands are in contact and, if vision does dominate the perception of body-part location, the participant will experience her hidden hand as being at the viewed location. In Condition 1, the hidden receptive left hand will be experienced as being at the location of the viewed prosthetic hand and, in Condition 2, the hidden administering right hand will be experienced as being at the location of the Examiner's viewed administering hand.

Condition 1 of our paradigm provides the closest match to the original visual rubber hand paradigm (Botvinick & Cohen, 1998): the participant looks at the prosthetic hand being touched while her hidden left hand receives synchronous touch from the Examiner (Table 9). As in the original paradigm, the participant experiences visual capture of touch: the touch on her hidden receptive hand is experienced at the location of the viewed prosthetic hand. It may also seem to the participant that the prosthetic hand she is looking at is her own hand. The main difference between this condition and the original visual rubber hand paradigm is that the prosthetic hand is touched by the participant's own right hand (rather than by the Examiner's hand), and the participant experiences the illusion of self-touch.

Condition 2 in our new paradigm is the focus of the present Chapter. It is unique amongst rubber hand experiments in that the participant is not looking at the prosthetic hand but instead at her own hand being touched by the Examiner. How are we to understand the illusion that is elicited when a participant looks at her left hand being touched by the Examiner while her hidden right hand administers synchronous touch to the prosthetic hand? We propose that this new version of the rubber hand illusion has three conceptually distinct components. First, the participant experiences her hidden right hand as administering touch at the location of the Examiner's viewed administering hand. We call this *visual capture of action* by analogy with visual capture of touch. Second, it may also seem to the participant that the Examiner's administering hand is her own hand. Third, the participant experiences the illusion of self-touch.

There are more than fifty rubber hand studies documenting visual capture of touch; that is, the participant's experience of touch on her own hidden hand as occurring at the location of a viewed hand that is static (e.g., Armel & Ramachandran, 2003; Botvinick & Cohen, 1998; Capelari, Uribe, & Brasil-Neto, 2009; Costantini & Haggard, 2007; Ehrsson et al., 2004; Ehrsson, 2009; Folegatti et al., 2009; Haans et al., 2008; Lloyd, 2007; Longo, Schüür et al., 2008; Moseley et al., 2008; Pavani et al., 2000; Schütz-Bosbach, Tausche, & Weiss, 2009; Tsakiris et al., 2010; Tsakiris & Haggard, 2005). Many of these studies also find that the participant experiences ownership of the viewed static hand.

In contrast, only a few rubber hand studies provide evidence for visual capture of action; that is, the participant's experience of movement by her own hidden hand as occurring at the location of a viewed hand that is moving (Dummer, Picot-Annand, Neal, & Moore, 2009; Newport et al., 2010; Tsakiris, Prabhu, & Haggard, 2006). Similarly, few studies provide evidence that the participant experiences ownership of a viewed hand that is moving (see Petkova & Ehrsson, 2008). Here we set out a systematic empirical investigation of the proposal that the illusion elicited by our new rubber hand paradigm has three components: visual capture of action, the experience of ownership of the Examiner's administering hand, and the illusion of self-touch.

Table 9

Visuotactile rubber hand paradigm: Three versions

Rubber Hand Paradigm	Which hand is the participant looking at?	Who is touching the participant's hand?	Who is touching the prosthetic hand?	Where does the participant experience touch?	Where does the participant experience action?	Which hand is mislocalised to the viewed location?	Is touch or action mislocalised?
Original Visual Paradigm (Botvinick and Cohen 1998)	Prosthetic Hand	Examiner	Examiner	Prosthetic Hand	N/A	Participant's Receptive Hand	Touch
Adaptation of Ehrsson et al's (2005) Paradigm: Visual Condition 1 (Chapter 4)	Prosthetic Hand	Examiner	Participant (Examiner guided)	Prosthetic Hand	Participant's Administering Hand	Participant's Receptive Hand	Touch
Adaptation of Ehrsson et al's (2005) Paradigm: Visual Condition 2 (Chapter 4)	Participant's Receptive Hand	Examiner	Participant (Examiner guided)	Participant's Receptive Hand	Examiner's Administering Hand	Participant's Administering Hand	Action

Experiment

Method

Participants

Eight right-handed (Oldfield, 1971) participants (19-31 years; 6 female, 2 male) were assessed following a protocol approved by the University of Oxford Research Ethics Committee, and in accordance with ethical standards laid down in the 2008 Helsinki Declaration. All participants were naïve to the experimental objectives.

Materials and Procedure

The participant was seated at a testing table with her left hand positioned at body midline. The prosthetic left hand was positioned 15 cm to the right of the participant's left hand. Examiner 1 was seated on the left side of the participant and Examiner 2 was seated opposite and slightly to the right of the participant's body midline. Examiner 1 used a paintbrush, which she held in her right hand, to administered taps (approximately one per s) to the proximal phalanx of the participant's left index finger. The participant was guided by Examiner 2 to administer taps to the prosthetic hand using an identical paintbrush. The participant was asked to hold the paintbrush 5 cm above the bristles and to relax her hand. Examiner 2 held the same paintbrush 10 cm above the bristles and was in control of the movements of the paintbrush. This guided stimulation technique was practised until the participant's hand was relaxed so that she allowed the pattern of stimulation – and particularly the timing of the stimulation – to be controlled by Examiner 2. We note here that, although some studies have specifically investigated the contrast between active and passive participation in rubber hand paradigms (Dummer et al., 2009; Tsakiris et al., 2006), our guided stimulation technique seems to lie between these extremes: the participant yields control to the Examiner but is not inert.

The participant was asked to look at her left hand being touched by the paintbrush held in Examiner 1's right hand. A visual divider was situated so that the participant's left hand and Examiner 1's right hand were visible but the participant's right hand and the prosthetic hand were hidden from view. To hide irrelevant cues on the left side of the divider, black fabric was used to cover the left arm of the participant and the right arm of Examiner 1 (Figure 16). Care was taken to ensure that the posture of Examiner 1's right hand (as it administered touch to the participant's left hand) was matched to the exact posture of the participant's right hand (as it administered touch to the prosthetic left hand). (For studies manipulating postural compatibility using the original visual rubber hand paradigm, see Costantini and Haggard, 2005; Ehrsson et al., 2004; Pavani et al., 2000; Tsakiris and Haggard, 2005.)

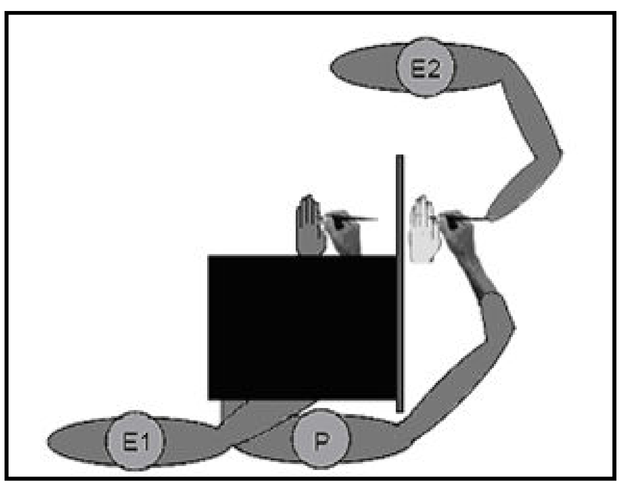

Figure 16. Experimental set-up: Examiner 1's hand administering touch to the participant's left hand (left side of the visual divider) and the participant's right hand administering touch to the prosthetic hand (right side of the visual divider). E1 = Examiner 1, E2 = Examiner 2, P = Participant.

Each participant took part in four 60-s stimulation trials – two synchronous and two asynchronous – and trial-order was randomised across participants. The rubber hand illusion is elicited with synchronous stimulation; asynchronous control trials were included as a baseline measure. Synchronous stimulation was achieved by having Examiner 2 follow the exact timing pattern established by Examiner 1. Stimulation was by 'tapping' as opposed to 'stroking' because pilot trials with five participants (none of whom participated in the Experiment reported here) indicated that this was the best method to achieve synchrony between Examiner 1 and Examiner 2.

Illusion Questionnaire

After each trial, the participant completed a questionnaire comprising nine statements, modeled on the questionnaire designed by Botvinick and Cohen (1998) to assess the original visual rubber hand illusion:

(1) It seemed as if I were feeling the tapping action of my right hand in the location where I saw the Examiner's hand (touching my own left hand).

(2) I felt as if the Examiner's hand were my hand.

(3) It felt as if the touch that I felt on my left hand was from the paintbrush that I held in my right hand.

(4) It felt as if my (right) hand were drifting towards the left (towards my left hand).

(5) It seemed as if I might have more than one right hand or arm.

(6) The Examiner's hand began to resemble my own (right) hand, in terms of shape, skin tone, freckles or some other visual feature.

(7) It seemed as if the tapping action I was performing came from somewhere between my own (right) hand and the Examiner's hand.

(8) It appeared (visually) as if the Examiner's hand were drifting towards my hand.

(9) My hands felt larger than normal.

The presentation order of statements was randomised across participants. Whereas Botvinick and Cohen investigated mislocalisation of *touch* to a viewed location and ownership of the *prosthetic* hand, we assessed mislocalisation of *action* to a viewed location (Statement 1) and ownership of the *Examiner's* hand (Statement 2). One statement was adapted from Ehrsson et al. (2005) to measure the illusion of self-touch, "It felt as if the touch that I felt on my left hand was from the paintbrush that I held in my right hand" (Statement 3). (The corresponding statement in Botvinick and Cohen's questionnaire was about causation: "It seemed as though the touch I felt was caused by the paintbrush touching the rubber hand". Self-touch requires not just causation but contact.)

Six statements served as controls for suggestibility and task demands. The participant indicated her level of agreement with each statement using a seven-point scale (0 = *not at all*; 1 = *slightly agree*; 3 = *moderately agree*; 5 = *strongly agree*; 6 = *very strongly agree*).

Proprioceptive Drift

To provide an additional measure of visual capture of action, we assessed whether the participant experienced proprioceptive drift. That is, whether the participant mislocalised her administering hand – hidden from view – leftward, towards the location of the Examiner's administering hand. Before and after each of the four stimulation trials, proprioceptive drift was assessed using the method developed by Ehrsson et al. (2005). The participant was instructed to maintain the position of her administering right hand and to extend her left arm, which the Examiner positioned at 45° to the left of the midsagittal plane of the participant's body. The participant was then asked to point quickly by sliding her left index finger along the table, in a single movement, until it was in line with the felt position of the paintbrush in her administering right hand. The participant's eyes were closed and the visual divider was removed from the table for these measurements. For each of the four 60-s stimulation trials, pre-stimulation (baseline) and post-stimulation measurements of proprioceptively perceived position were obtained. Proprioceptive drift was calculated as the change in felt position from baseline.

Results

Illusion Questionnaire

The three statements underlined in Figure 17 correspond to the three proposed components of this new version of the rubber hand illusion: visual capture of action, the experience of ownership of the Examiner's administering hand, and the illusion of self-touch. Wilcoxon Signed-Rank Tests indicated that participants gave significantly higher agreement ratings for these three statements following synchronous stimulation compared with asynchronous stimulation: visual capture of action ($z = 2.527$, $p = 0.012$); the experience of ownership of the Examiner's administering hand ($z = 2.379$, $p = 0.017$); the illusion of self-touch ($z = 2.375$, $p = 0.018$).

Agreement ratings for the control statements did not show a significant difference between synchronous and asynchronous stimulation, although there was a trend toward higher ratings for synchronous stimulation for the statement describing the experience of the

Examiner's hand beginning to visually resemble the participant's hand (z = -1.841, p = .066). (All other p values were > .285.)

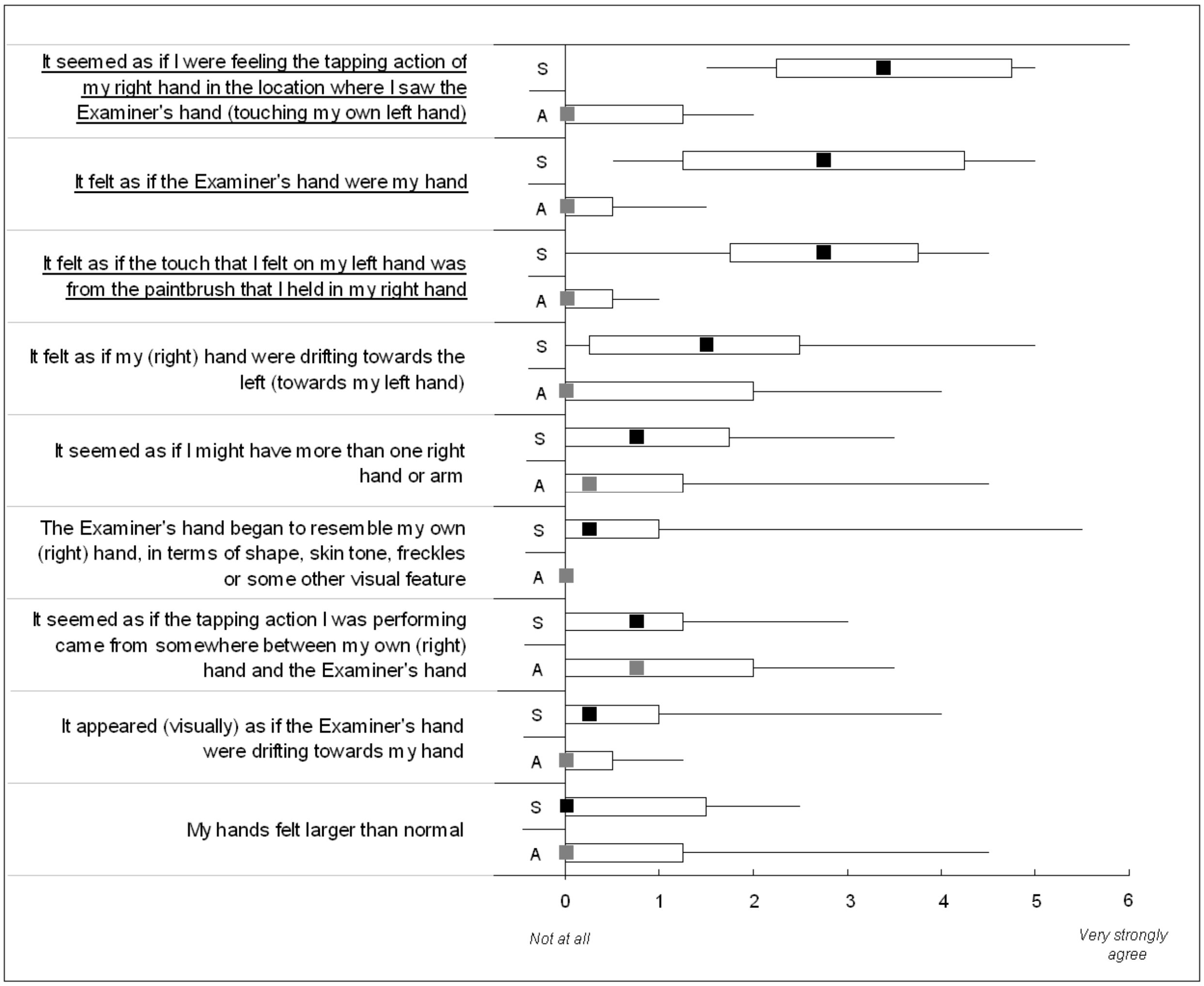

Figure 17. Median agreement ratings for the illusion questionnaire for the synchronous and asynchronous stimulation conditions, averaging across the two trials of each stimulation type. The black (synchronous) and grey (asynchronous) filled-in squares indicates the median value, the box indicates the interquartile range, and the whiskers indicate the full range of responses.

Proprioceptive Drift

The results in the synchronous stimulation condition indicated significant mislocalisation of the participant's administering hand leftward, toward the Examiner's administering hand ($t(7) = 3.381$, $p = .012$, two-tailed). In the asynchronous stimulation condition, mislocalisation was not significantly different from zero ($t(7) = 1.568$, $p = .161$, two-tailed) but mean drift was rightward, away from the Examiner's administering hand (Figure 18). This pattern of mislocalisation has previously been documented with the original visual rubber hand paradigm (Botvinick & Cohen, 1998; Tsakiris & Haggard, 2005: Figure 2, congruent posture condition).

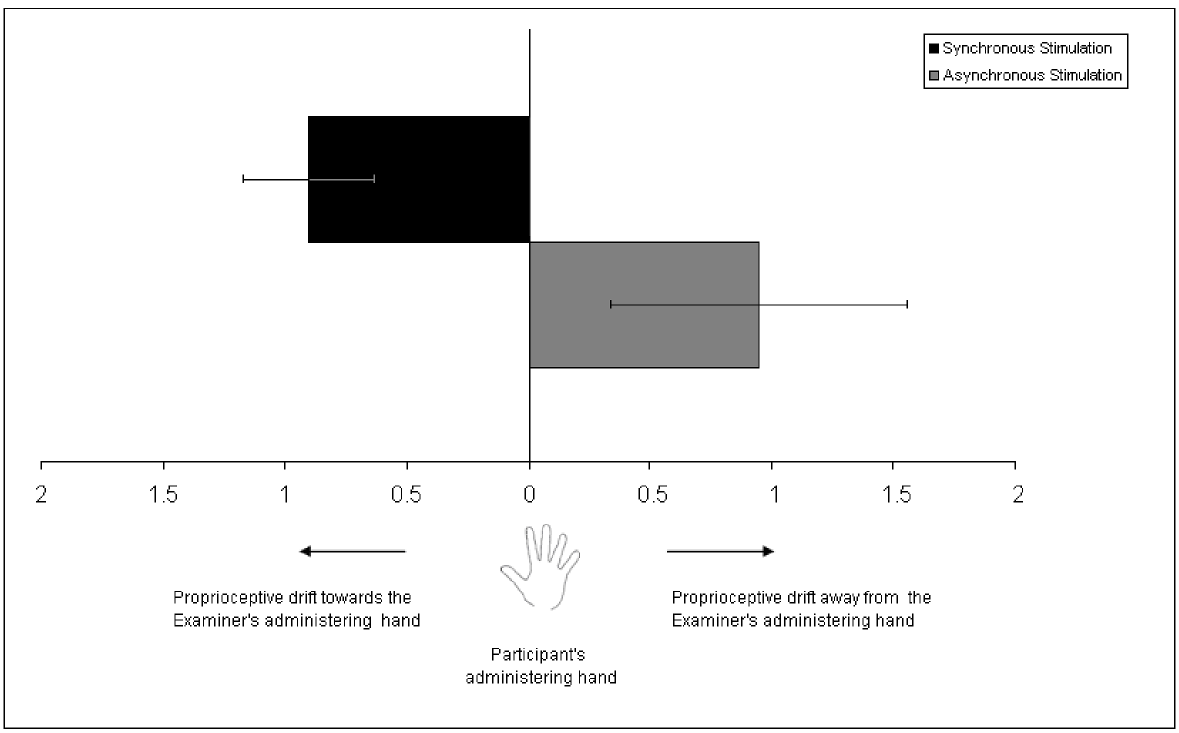

Figure 18. Mean proprioceptive drift (cm) in the synchronous (M = .91 cm leftward) and asynchronous (M = .95 cm rightward) stimulation conditions, averaging across the two trials of each stimulation type. Error bars indicate one standard error of the mean.

Discussion

Questionnaire responses and proprioceptive drift data confirmed that our new paradigm elicits an illusion with three components: (1) the participant experiences her hidden right hand as administering touch at the location of the Examiner's viewed administering hand (visual capture of action), (2) the participant experiences the Examiner's administering hand as being her own hand (experience of ownership), and (3) the participant experiences her two hands as being in contact, as if she were touching her own hand (illusion of self-touch).

Our new paradigm involves information from multiple sensory sources: visual, tactile and proprioceptive. The paradigm may also involve information about motor commands and predicted sensory feedback (Wolpert, 1997; see also Petkova & Ehrsson, 2008), to the extent that the participant – although guided by the Examiner – is herself involved in administering touch to the prosthetic hand. Participants who experience the illusion elicited by our paradigm integrate this information into a single event file. Sensory integration is most likely to occur when inputs are synchronous and there is no spatial discrepancy (Ernst & Bülthoff, 2004; Holmes & Spence, 2005).

The inputs in our paradigm are synchronous, and thus temporally consistent with a single-event interpretation. There is no spatial discrepancy between the visual and tactile inputs from the participant's receptive left hand: the participant sees her hand receiving touch in the location where she feels that touch. There is, however, a spatial discrepancy between the visual and tactile inputs from the left hand and the proprioceptive and tactile inputs from the participant's administering right hand. Since synchrony promotes a single-event interpretation, the visual and tactile information from the left hand may override the spatially discrepant information from the right hand. Thus the participant may experience the information in multiple modalities as originating from a single event of self-touch in a single location, and the source of the proprioceptive information may be mislocalised to the viewed location. The asynchronous condition of our paradigm, in contrast, may highlight the spatial separation between the event in which the participant is touched by the Examiner and the event in which the participant administers touch to the prosthetic hand.

The three components of the illusion elicited by our paradigm are conceptually distinct. First, visual capture of action is distinct from the participant's experience of ownership of the Examiner's administering hand. The phenomenon that we call visual capture of action is the participant's proprioceptive experience of her hidden right hand as displaced leftward, and administering touch at the location of the Examiner's viewed administering hand. Visual capture of action was assessed by agreement ratings for a statement on the questionnaire and by proprioceptive drift measurement. In studies using variants of the visual rubber hand paradigm, proprioceptive drift has been described as a behavioural measure of, or proxy for, the sense of ownership (Tsakiris & Haggard, 2005; Tsakiris et al., 2007; Tsakiris et al., 2010). But recently it has been shown that the location and ownership components of the visual rubber hand illusion are empirically dissociable and independent predictors of proprioceptive drift (Longo, Schüür et al. 2008; see also Makin et al., 2008).

Second, the experience of ownership is distinct from the illusion of self-touch. In our paradigm, the participant views her receptive left hand being touched by the Examiner's administering hand. The participant's sense that the Examiner's viewed hand is her own hand is clearly distinct from the participant's tactile-proprioceptive experience of self-touch. We have recently shown that these two components are not just conceptually but also empirically distinct, in that they may be affected differently by the same experimental manipulation. Incongruent stimulation (the participant administers stimulation with her index finger while receiving stimulation from a paintbrush) reduces the experience of ownership but not the illusion of self-touch (Chapter 4). While the ownership and self-touch components can be shown to be distinct in our paradigm where vision is permitted, it is not so clear that they can be separated in paradigms where vision is precluded (Ehrsson et al., 2005).

Third, visual capture of action is distinct from the illusion of self-touch. In principle, it is imaginable that the participant should experience her hidden right hand as displaced leftward but not experience her two hands as being in contact. Conversely, the participant could experience self-touch without experiencing leftward displacement of her right hand. She might, for example, experience rightward displacement of her left hand. It might be proposed that, despite this clear conceptual distinction, visual capture of action depends on the illusion of self-touch. But while the available evidence is limited, it does not support this proposal. At least three rubber hand studies provide evidence that visual capture of action (the participant's proprioceptive experience of her hidden hand as displaced, and moving at the location of a viewed synchronously moving hand) can occur without the illusion of self-touch (Dummer et al., 2009; Newport et al., 2010; Tsakiris et al., 2006).

There remain questions about the role of tactile sensations in the phenomenon that we call visual capture of action. Our paradigm was developed to investigate the illusion of self-touch and it involves tactile sensations in the participant's receptive and administering hands. Thus, vision and tactile sensations are associated: the participant both sees and feels touch being administered to her receptive left hand. Is the capture purely visual or rather visuotactile? The movement of the participant's administering hand is also associated with tactile sensations: the participant receives tactile feedback when she holds the paintbrush and administers touch to the prosthetic hand. Is the capture purely of action or rather of action combined with tactile feedback?

We have conducted pilot experiments to investigate whether tactile sensations are necessary to experience visual capture of action and ownership of the Examiner's hand. In all three conditions, the participant looked at her receptive left hand while her administering right hand was hidden from view. Tactile feedback was manipulated by controlling whether the participant's administering right hand made contact with the prosthetic hand and whether the Examiner's hand made contact with the participant's receptive left hand. In the first condition, the Examiner made contact with the participant's receptive left hand and the participant performed the same tapping action as the Examiner but without making contact with the prosthetic hand. The participant experienced: (1) visual capture of action, (2) ownership of the Examiner's hand and also, perhaps surprisingly, (3) the illusion of self-touch. In the second condition, the participant's administering right hand made contact with the prosthetic hand and the Examiner performed the same tapping action but without making contact with the participant's receptive left hand. The participant experienced (1) visual capture of action and (2) ownership of the Examiner's hand. In the final condition, the participant and the Examiner performed the same tapping action but no contact was made with either the prosthetic hand or the participant's receptive left hand, respectively. The participant nonetheless experienced (1) visual capture of action and (2) ownership of the Examiner's hand. These preliminary investigations suggest that tactile stimulation of the participant's receptive hand is necessary for the illusion of self-touch but that visual capture of action and the experience of ownership of the Examiner's hand may require neither tactile stimulation of the participant's receptive hand nor tactile feedback from the prosthetic hand.

CHAPTER 6: TWO HANDS ARE BETTER THAN ONE: A NEW ASSESSMENT METHOD AND A NEW INTERPRETATION OF THE NON-VISUAL ILLUSION OF SELF-TOUCH

A simple experimental paradigm creates the powerful illusion that one is touching one's own hand even when the two hands are separated by 15 cm. The participant uses her right hand to administer stimulation to a prosthetic hand while the Examiner provides identical stimulation to the participant's receptive left hand. Change in felt position of the receptive hand toward the prosthetic hand has previously led to the interpretation that the participant experiences self-touch at the location of the prosthetic hand, and experiences a sense of ownership of the prosthetic hand. Our results argue against this interpretation. We assessed change in felt position of the participant's receptive hand but we also assessed change in felt position of the participant's administering hand. Change in felt position of the administering hand was significantly greater than change in felt position of the receptive hand. Implications for theories of ownership are discussed.

The rubber hand paradigm creates an illusion that disrupts proprioception, the perception of the position (and movement) of our body, and thus sets up a conflict between what we know and what we feel about the location of our own body parts. There is a traditionally visual version (Botvinick & Cohen, 1998) and a traditionally non-visual version (Ehrsson et al., 2005) of this experimental paradigm. The purpose of this Chapter is to present a new interpretation of the illusion that is elicited using the non-visual paradigm. We demonstrate that the non-visual paradigm disrupts proprioception in a way that is distinct from the more widely investigated visual rubber hand paradigm.

In the traditional visual rubber hand paradigm (Botvinick & Cohen, 1998), the participant looks at a prosthetic hand being touched by the Examiner while the participant's own hand – hidden from view – is also touched by the Examiner. When touch on the prosthetic hand is synchronous with touch on the participant's receptive hand, it may seem to the participant that she is feeling touch at the location of the viewed prosthetic hand. The illusion involves "displacement of the felt location of the touch from the hidden real hand to the visible [prosthetic] hand" (Makin et al., 2008, p. 5). It may also seem to the participant that the prosthetic hand is the participant's hand. The illusion is commonly assessed using questionnaires and a measurement of proprioceptive drift. Proprioceptive drift refers to a change in the proprioceptively perceived position of the participant's hidden hand (see Paillard & Brouchon, 1968; Wann & Ibrahim, 1992). Numerous studies have shown that, subsequent to experiencing the rubber hand illusion, participants perceive the hidden hand (or, more specifically, the stimulated digit: see Tsakiris & Haggard, 2005) to be at a location that is shifted *toward* the location of the viewed prosthetic hand. Although the participant feels touch at the location of the prosthetic hand, she does not experience a complete adaptation in felt hand position. Following the experimental trial, the participant indicates that it feels as if her hidden hand is at a location that is about 15-30% of the full distance between the real hand and the prosthetic hand (see Makin et al., 2008). Proprioceptive drift is regarded as a behavioural proxy for the rubber hand illusion (Tsakiris et al., 2007; Tsakiris et al., 2010), but individuals can experience proprioceptive recalibration without experiencing the rubber hand illusion (see Holmes et al., 2006).[11]

In the *non-visual* (self-touch) rubber hand paradigm (Ehrsson et al., 2005), the Examiner guides the participant to touch a prosthetic hand, and at the same time, the Examiner administers touch to the participant's other hand (Figure 19, top panel). For example, the participant's right index finger strokes and taps the index finger of a prosthetic left hand, while the Examiner strokes and taps the index finger of the participant's left hand. When the participant's touch to the prosthetic hand is synchronous with the Examiner's touch to the participant's receptive hand, it may seem to the participant that she is touching her own hand. Previous studies have explained this illusion by drawing analogies with the widely investigated visual rubber hand illusion. The prevailing view is that there is a displacement of the proprioceptively perceived location of the

[11] Holmes et al. (2006) found that visual exposure to a prosthetic hand influenced the reaching movements of the participant's hidden left hand. However, a questionnaire indicated that this proprioceptive recalibration was not accompanied by a compelling illusion of ownership, prompting the researchers to suggest that "proprioception is recalibrated following visual exposure to prosthetic hands… recalibration is independent of the rubber hand illusion" (p. 685).

participant's receptive hand to the prosthetic hand, such that the participant experiences a "feeling of ownership of [the] touched rubber limb" (Ehrsson et al., p. 10569). On this view, it seems to the participant that she is touching her own hand because she experiences touch on her receptive hand as if it is occurring at the location where she is administering touch to the prosthetic hand. This view has led researchers to measure only the proprioceptive drift of the participant's receptive hand (Ehrsson et al., see also Chapter 4). Here, we propose an alternative explanation for what the participant experiences during the non-visual illusion of self-touch: it seems to the participant that she is touching her own hand because she experiences her *administering* hand as being at the location where the Examiner is administering touch to the participant's receptive hand. Thus, we are proposing that there may be more than one way for the participant to experience the non-visual illusion of self-touch (Figure 19).

To investigate these competing hypotheses, we present the first study to measure proprioceptive drift of both the participant's receptive and administering hand. If the participant experiences self-touch at (or toward) the location of the prosthetic hand, we predict greater proprioceptive drift of the receptive hand than of the administering hand. Alternatively, if the participant experiences self-touch at (or toward) the location of the Examiner's administering hand, we predict greater proprioceptive drift of the administering hand than of the receptive hand.

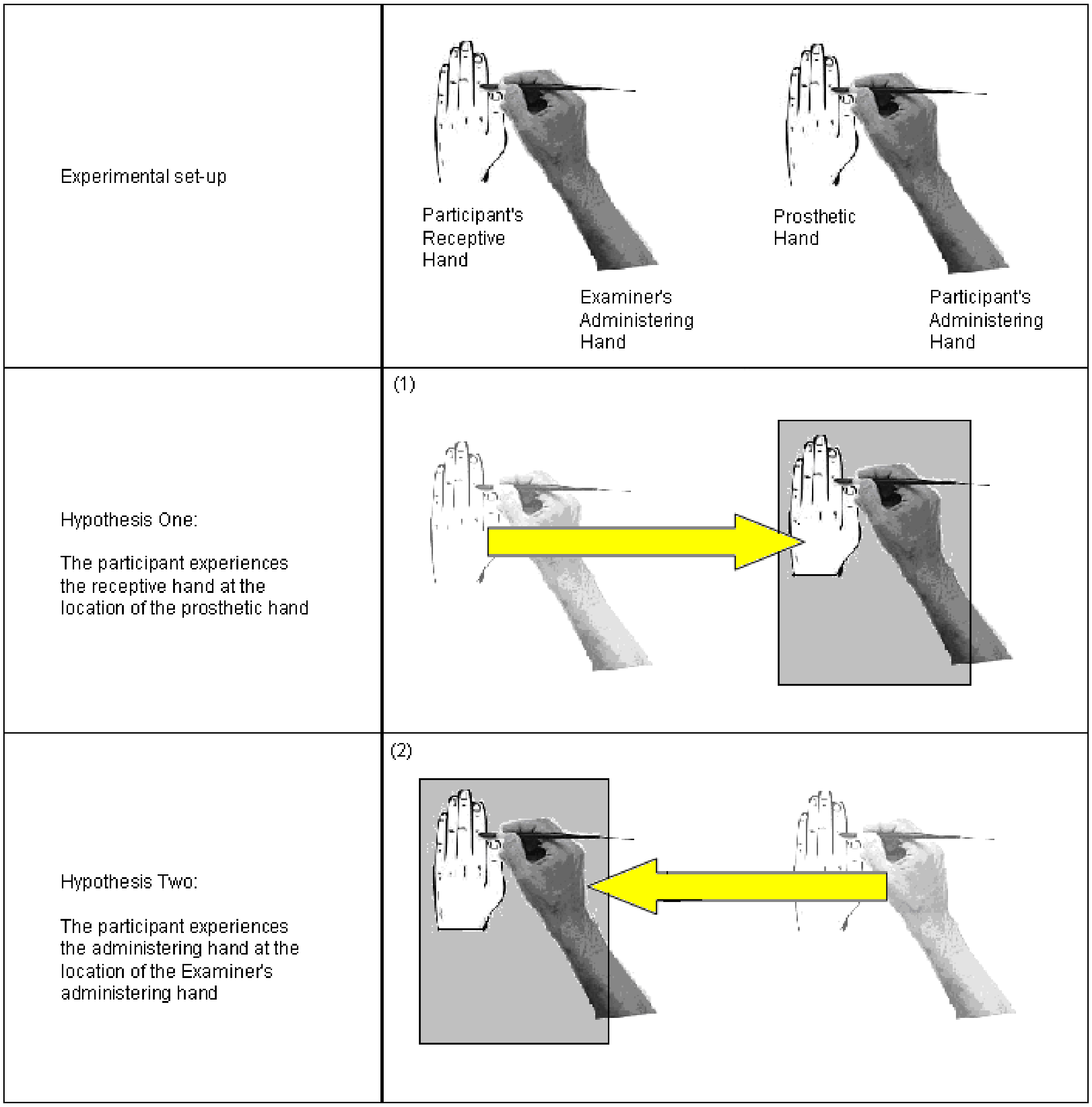

Figure 19. The top panel depicts the experimental set-up. Two hypotheses are proposed for the participant's experience of self-touch. The participant may experience (1) the receptive hand at the location of the prosthetic hand, or (2) the administering hand at the location of the Examiner's administering hand.

Experiment

Method

Participants

Forty participants (30 females and 10 males; aged 18–39 years, *M* = 23.4 years) were recruited from the University of Oxford community. The study was approved by the University of Oxford Research Ethics Committee, and conducted in accordance with the ethical standards laid down in the 2008 Declaration of Helsinki. Participants received course credits or £5 compensation for their time.

Apparatus and Procedure

The participant was seated at a testing table, opposite the Examiner. A prosthetic left hand was positioned on the table at the participant's body midline, and the participant's receptive left hand was positioned 15 cm to the left of the prosthetic hand. The Examiner used a paintbrush to administer strokes (unidirectional toward the fingertip) and taps to the proximal phalanx of the participant's left index finger. The participant was guided by the Examiner to administer strokes and taps to the index finger of the prosthetic hand using an identical paintbrush. The participant was asked to hold the paintbrush 5 cm above the bristles and to relax her hand. The Examiner held the same paintbrush 10 cm above the bristles and was in control of the movements of the paintbrush (Figure 20). This guided stimulation technique was practised until the participant relaxed her hand so that she allowed the pattern of the stimulation – and particularly the timing of the stimulation – to be controlled by the Examiner. The experimental set-up was concealed by a visual divider positioned above the hands.

Each participant took part in two 180-s trials – stimulation of the prosthetic hand by the participant was either *synchronous* or *asynchronous* with stimulation applied to the participant's receptive left hand by the Examiner. The order of trials (synchronous versus asynchronous) was randomised across participants. Previous studies have shown that the illusion of self-touch is elicited under conditions of synchronous stimulation; the asynchronous control trial was included as a baseline measure.

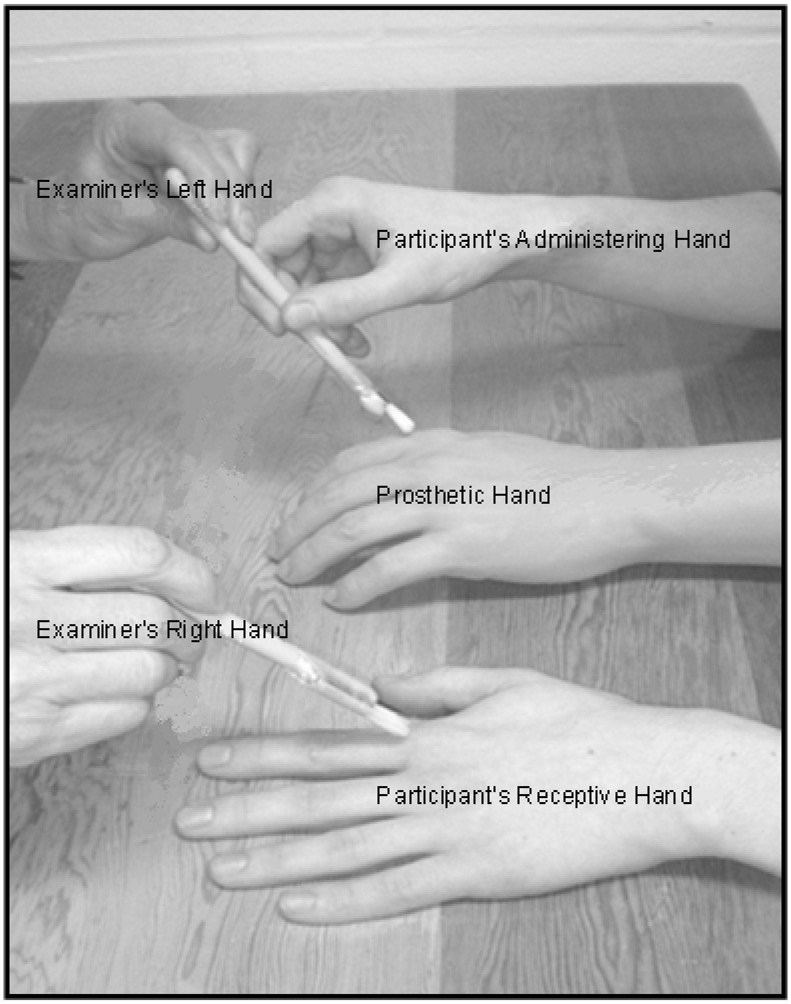

Figure 20. The basic procedure for eliciting the illusion of self-touch: the Examiner guides the participant to administer touch to a prosthetic hand while the Examiner administers touch to the participant's receptive hand.

Assessment

Self-Touch Illusion Questionnaire

At the end of each trial, the participant completed a questionnaire adapted from Ehrsson and colleagues (2005):

(1) It felt as if the touch that I felt on my left hand was from the paintbrush that I held in my right hand.

(2) I felt as if I had more than one left hand.

(3) I felt as if my left hand was larger than normal.

(4) I felt as if my left hand was moving.

(5) I could not feel my left hand.

The first statement assessed the illusion of self-touch. The participant should agree with this statement whether she experiences touch on her receptive hand as occurring at the location of the prosthetic hand, or the action of her administering hand as occurring at the location of the Examiner's administering hand. Subsequent statements (2-5) indicated experiences that the paradigm was not expected to elicit, and were used to control for suggestibility. Order of presentation was randomised across participants. A seven-point scale was used to rate agreement with each statement (0 = *not at all*; 1 = *slightly agree*; 3 = *moderately agree*; 5 = *strongly agree*; 6 = *very strongly agree*).

Proprioceptive Drift

Proprioceptively perceived hand position was assessed using a ruler placed on top of the visual divider that concealed the participant's hands below. (Previous studies using the ruler method to measure the proprioceptively perceived position of the hands include: Costantini & Haggard, 2007; Folegatti et al., 2009; Holmes, Crozier, & Spence, 2004; Longo, Schüür et al., 2008; Schütz-Bosbach, Tausche, & Weiss, 2009; Tsakiris & Haggard 2005; Tsakiris et al., 2006; Tsakiris et al., 2010.) The participant was asked to read the number on the ruler corresponding to (1) her administering right index finger (at the position of the paintbrush) and (2) her receptive left index finger. Half of the participants indicated the position of the administering right index finger before the receptive left index finger, and half of the participants were questioned in the reverse order.

A baseline measurement of proprioceptively perceived position was taken before stimulation began (0 s) and a post-trial measurement of proprioceptively perceived position was taken at the end of the trial (180 s). The post-trial measurement was compared to the baseline measurement for evidence of proprioceptive drift; that is, for evidence of a change in proprioceptively perceived hand position. Proprioceptive drift was signed positive if it was in the hypothesised direction: rightward drift for the receptive hand and leftward drift for the administering hand. To discourage the participant from simply reporting the same numbers, the ruler was removed from the testing unit during stimulation and it was repositioned with a different offset for each baseline and post-trial measurement. The participant was informed that the ruler would be offset each time it was repositioned on the testing unit.

Results

Self-Touch Illusion Questionnaire

Questionnaire responses were analysed with individual Wilcoxon Signed-Rank Tests. Agreement ratings for each statement were compared for synchronous and asynchronous stimulation. An alpha level of .01 was used to adjust for multiple comparisons. As predicted, there was a significant synchronous-asynchronous difference for the statement assessing the illusion of self-touch (synchronous: $Md = 5$, asynchronous: $Md = 0.5$; $z = -5.308$, $p < .001$). There was also a borderline significant difference for the statement "I felt as if my left hand was larger than normal" (synchronous: $Md = 1$, asynchronous: $Md = 0$; $z = -2.539$, $p = .011$). Although this statement was included to control for suggestibility, it is possible that the perception of a larger left hand is part of the participant's experience, or interpretation of the experience, of the illusion that she is touching her own hand. When the participant experiences the illusion of contact between her two hands (which are separated by 15 cm), she may perceive that her left hand has become larger, and that it fills the space between her two hands. There were no synchronous-asynchronous differences for any of the remaining three statements (all Medians = 0, all p values > .472).

Proprioceptive Drift

Proprioceptive drift was analysed with a mixed model ANOVA. The between-subjects factor was order of report for proprioceptively perceived position of each hand (receptive hand reported first, administering hand reported first). The within-subjects factors were hand (receptive hand, administering hand) and mode of stroking (synchronous, asynchronous).

There was no main effect for the between-subjects factor ($F(1, 38) = .136$, $p = .714$, partial eta squared = .004), and there were no interactions with the within-subjects factors (all p values > .175). Proprioceptive drift did not differ for participants who reported the proprioceptively perceived position of the receptive hand first compared with participants who reported the proprioceptively perceived position of the administering hand first.

There was a significant main effect for hand ($F(1, 38) = 10.808$, $p = .002$, partial eta squared = .221), and there was a significant main effect for mode of stroking ($F(1, 38) = 55.831$, $p < .001$, partial eta squared = .595). There was also a significant hand by mode of stroking interaction ($F(1, 38) = 7.210$, $p = .011$, partial eta squared = .159). To test this interaction, paired two-tailed *t*-tests were used to compare the amount of proprioceptive drift of the two hands from baseline, for both synchronous and asynchronous stimulation. An alpha level of .025 was used to adjust for multiple comparisons. With synchronous stimulation, there was more proprioceptive drift of the administering hand from baseline ($M = 3.58$ cm) than of the receptive hand ($M = 1.38$ cm) ($t(39) = 3.632$, $p = .001$). With asynchronous stimulation, there was no difference in proprioceptive drift of the administering hand from baseline ($M = -.01$ cm) compared with the receptive hand ($M = -.46$ cm) ($t(39) = 1.061$, $p = .295$).

One-sample two-tailed *t*-tests were used to investigate whether each proprioceptive drift value (synchronous stimulation of the receptive hand, synchronous stimulation of the administering hand, asynchronous stimulation of the receptive hand, asynchronous stimulation of the administering hand) was significantly different from zero; that is, whether each post-trial measurement was significantly different from its (respective) baseline measurement. An alpha level of .0125 was used to adjust for multiple comparisons. The results indicate that both hands showed significant proprioceptive drift from baseline with synchronous stimulation (synchronous stimulation of the receptive hand: $t(39) = 3.425$, $p = .001$; synchronous stimulation of the administering hand: $t(39) = 6.380$, $p < .001$), but that neither hand showed significant proprioceptive drift from baseline with asynchronous stimulation (asynchronous stimulation of the receptive hand: $t(39) = -1.432$, $p = .160$; asynchronous stimulation of the administering hand: $t(39) = -.046$, $p = .964$).

The scatter plot in Figure 21 presents the proprioceptive drift profile of each participant for the synchronous stimulation condition. There are two important points. First, the majority of participants (N = 25) demonstrate more proprioceptive drift of the administering hand (indicated with a red diamond), but some participants (N = 11) demonstrate more proprioceptive drift of the receptive hand (indicated with a blue triangle) and some participants (N = 4) demonstrate equal proprioceptive drift of the two hands (indicated with a yellow square). Second, for participants who demonstrate more proprioceptive drift of the administering hand, the magnitude of drift is large; 13 participants (out of 25) demonstrated at least 5 cm drift of the administering hand. In contrast, for participants who demonstrate more proprioceptive drift of the receptive hand, the magnitude of drift is smaller; only one participant (out of 11) demonstrated at least 5 cm drift of the receptive hand.

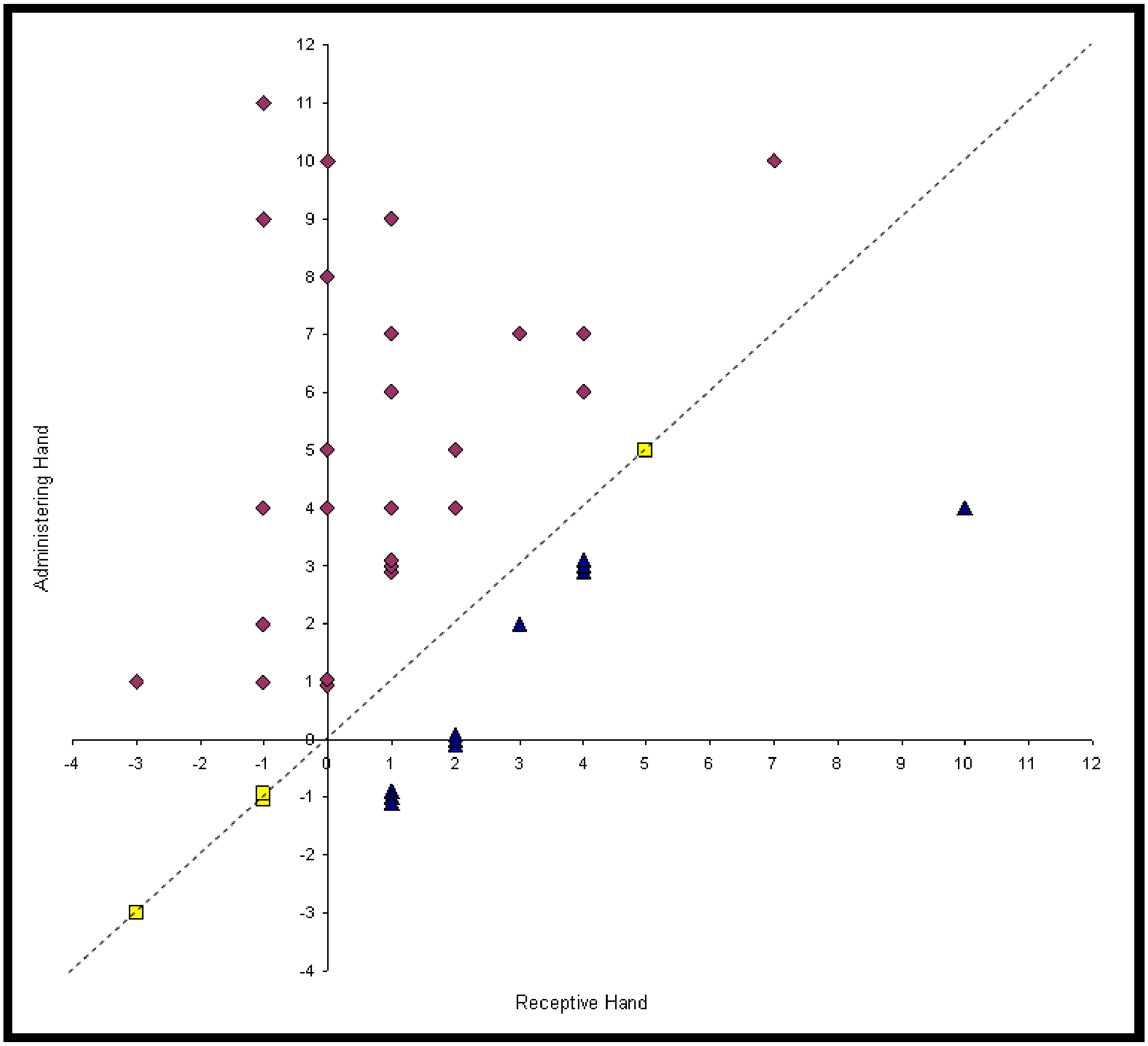

Figure 21. Proprioceptive drift (cm) of the administering hand and of the receptive hand under conditions of synchronous stimulation. Note that each data point represents a participant. Data points (yellow squares) on the diagonal line indicate equal drift of the administering hand and of the receptive hand. Data points (red diamonds) above the diagonal line indicate more drift of the administering hand than of the receptive hand. Data points (blue triangles) below the diagonal line indicate more drift of the receptive hand than of the administering hand.

Discussion

The compelling illusion that one is touching one's own hand, when the two hands are actually separated by 15 cm, provides a powerful illustration of the distinction between the on-line perception and the off-line representation of the body. Longo and colleagues state that "[I]t is important to distinguish between how we *perceive* our body to be, and how we *remember* or *believe* that it is" (Longo, Azañón, & Haggard, 2010, p. 655). A participant tested with the non-visual rubber hand paradigm perceives her two hands as being in contact; yet she knows that her hands are not in contact and that she is administering touch to a prosthetic hand. To further our understanding of what the participant experiences during this striking illusion, we assessed changes in the proprioceptively perceived position of the participant's two hands. Our results indicate that for some, or even most, participants there is more proprioceptive drift of the administering hand than of the receptive hand in the non-visual illusion of self-touch. Before offering an interpretation, we reflect on what proprioceptive drift tells us about the apparent location of an illusory event.

In the widely investigated visual rubber hand illusion, participants experience touch on the hidden receptive hand as occurring at the location of the viewed prosthetic hand. Questionnaire items that assess this experience include: "It seemed as if I were feeling the touch of the paintbrush in the location where I saw the rubber hand touched" (Botvinick & Cohen, 1998, p. 756) and "…it seemed like my hand was in the location where the rubber hand was" (Longo, Schüür, et al., 2008, p. 983). In these questionnaire items, the viewed prosthetic hand is specified as the location of the illusory event. Participants tested with the visual rubber hand paradigm demonstrate proprioceptive drift of the receptive hand toward the location of the viewed prosthetic hand; the receptive hand is experienced at a location that is displaced *toward* the location of the illusory event.

In the non-visual illusion, participants experience touch on the receptive hand as self-touch, even though it is the Examiner who is administering touch. Questionnaire items that assess this experience include: “I felt as if I were touching my right hand with my left index finger” (Ehrsson et al., 2005, p. 10565) and in our experiment, “It felt as if the touch that I felt on my left hand was from the paintbrush that I held in my right hand”. (Note that our participants touched a prosthetic *left* hand, whereas a prosthetic right hand was used in the pioneering study by Ehrsson and colleagues. Also, our participants used a paintbrush rather than their own index finger to administer stimulation to the prosthetic hand.) In contrast to the visual rubber hand illusion, the location of the illusory event is not specified in the questionnaire items for the non-visual illusion. The participant is asked whether she experienced the illusion of self-touch, but not *where* she experienced the illusion of self-touch. Given that the participant cannot see her hands in the non-visual version, we measured proprioceptive drift of the participant’s receptive and administering hand to determine the most likely location of the self-touch event. Our results indicate that some, or even most, participants demonstrate more proprioceptive drift of the administering hand (toward the location of the receptive hand) than proprioceptive drift of the receptive hand (toward the prosthetic hand). This leads us to suggest that for these participants the location of the illusory self-touch event is at, or close to, the participant’s receptive hand.

How are we to explain these differences in where the illusion is experienced in the visual and non-visual paradigms? Both the visual and the non-visual illusions involve sensory integration. The synchronous stimulation of the participant’s receptive hand and the prosthetic hand is consistent with there being a ‘single event’. When two events are close to one another in time, the individual tends to perceive a single underlying cause (Körding et al., 2007). Sensory integration obeys maximum-likelihood estimation. Each source of information is weighted according to its variance (specifically, the inverse of its variance). The perceived location of the sensory event is biased toward the location specified by the sensory information with the least variance; that is, the more reliable source of information (for an excellent review, see Ernst & Bülthoff, 2004).

A participant tested with the visual paradigm experiences the illusion that she is being touched at the location of the viewed prosthetic hand. To experience this illusion, the participant integrates information about the proprioceptively perceived position of the touched receptive hand and the visually-perceived position of the touched prosthetic hand into a single event interpretation. The single event is experienced as occurring at the location of the viewed prosthetic hand because visual information about limb position (usually) has less variance than proprioceptive information about limb position (see Ernst & Bülthoff, 2004; van Beers et al., 1999).

A participant tested with the non-visual paradigm experiences the illusion that she is touching her own hand. To experience this illusion, the participant integrates information about the proprioceptively perceived position of the touched receptive hand and the proprioceptively perceived position of the guided administering hand. We have shown that some, or even most, participants experience the single event of self-touch as occurring at a location displaced toward the participant's receptive hand. This finding suggests that there is less variance associated with locating the receptive hand compared with the administering hand. Although the Examiner never moves the administering hand leftward (toward the receptive hand), the very fact that it is being guided by another person may increase the variance associated with its location. Consistent with this point, previous research has shown that individuals are more accurate at locating a limb that is actively moving compared with a limb that is being moved by another person (Paillard &

Brouchon, 1968). It may be important that the participant administered stimulation with a paintbrush rather than with her own finger. The use of the paintbrush may increase the variance associated with locating the administering hand because this mode of stimulation is not as dynamic and informative as stimulation administered with the participant's own hand.

The findings we present here have important implications for how proprioceptive drift is assessed in future research. First, to capture the true magnitude of proprioceptive drift, proprioceptively perceived position of the participant's two hands – receptive and administering – needs to be assessed. When stimulation is synchronous, most participants demonstrate more proprioceptive drift of the administering hand than of the receptive hand. Nonetheless, for many participants who demonstrate this pattern of drift, the receptive hand is also experienced at a location that is displaced from proprioceptively perceived position at baseline (Figure 21). An interesting possibility is that the amount of proprioceptive drift demonstrated by each hand may depend on where the hands are positioned for the experiment; that is, the actual position of the hands relative to body midline. A decade before Botvinick and Cohen's (1998) pioneering use of the visual rubber hand paradigm, von Hofsten and Rösblad (1988) noted that "[t]he proprioceptors of the body are subject to drift and need to be continuously calibrated with vision" (p. 806). When an individual does not have vision of her arms there is proprioceptive drift toward the *body midline* (Paillard & Brouchon, 1968). The individual perceives her arms as being closer to body midline than is actually the case. In the current study, the participant's administering right hand was aligned with body midline as it stroked and tapped the prosthetic hand, and the participant's receptive left hand was positioned 15 cm to the left of body midline. Thus, the 3.58 cm proprioceptive drift of the administering hand is all the more striking given that it represents proprioceptive drift *away* from body midline. Different results might emerge if hand position was to be systematically manipulated. For example, if the participant's receptive hand was aligned with body midline and the participant's administering hand was 15 cm to the right of body midline. We predict that, in this condition, participants may demonstrate even more proprioceptive drift of the administering hand but less proprioceptive drift of the receptive hand than was found in the current study. This is an important avenue for future research, particularly given that it is customary to position the participant's receptive hand further from body midline than the prosthetic hand in rubber hand studies.

Second, to facilitate interpretation of proprioceptive drift, proprioceptively perceived position of the participant's two hands – receptive and administering – needs to be assessed using a method that does not require movement of either of the participant's hands. In previous studies using the non-visual rubber hand paradigm (Ehrsson et al., 2005; see also Chapter 4), proprioceptive drift has been measured by asking the blindfolded participant to slide her administering index finger along the table until it is in line with the perceived location of the receptive index finger. This method demonstrates approximately 3 cm proprioceptive drift of the receptive hand (Ehrsson et al.). The problem with this method is that the participant is using a potentially *mislocalised* body part (the administrating index finger) to indicate felt location of another potentially mislocalised body part (the receptive hand). As a result, the interpretation of displacement is not straightforward. (For a study demonstrating that the visual rubber hand paradigm affects pointing movements of the 'mislocalised' hand, see Newport et al., 2010; but see also Kammers, de Vignemont, Verhagen, and Dijkerman, 2009).

Let us consider two hypothetical participants, tested with the receptive left hand positioned 15 cm to the left of the prosthetic hand at body midline (as in the current study). Following the synchronous stimulation trial, Participant 1's experience is that her receptive left hand has shifted 3 cm (rightward) toward the prosthetic hand but Participant 2's experience is that her administering right hand has shifted 3 cm (leftward) toward the receptive hand. They both experience the receptive and administering hands as separated by 12 cm. Next, the participant uses the administering index finger to point to the felt position of the receptive index finger. Participant 1 points to a location that is 3 cm rightward of the receptive left hand, as does Participant 2. The Examiner concludes that both participants experience the receptive hand at a location that is displaced toward the prosthetic hand. This interpretation is correct for Participant 1 who experienced her receptive left hand as shifted 3 cm (rightward) toward the prosthetic hand. But Participant 2 experienced her receptive left hand in its veridical location as it was not shifted toward the prosthetic hand. Therefore, the pointing error for Participant 2 occurred because she experienced her administering right hand as being 3 cm leftward of its true location. These different experiences are more accurately assessed when the participant indicates felt position without moving either of her two hands, such as by reporting the numbers corresponding to felt position on a ruler.[12]

Conclusion

Over the past five years, the illusion of self-touch has been regarded as a non-visual analogue of the traditional visual rubber hand illusion in which the participant experiences ownership of a viewed prosthetic hand. For example, Ehrsson et al. (2005) suggested that "blindfolded persons felt that a rubber hand they touched was their own hand" thus indicating that "the rubber-hand illusion is not simply generated by the dominance of vision over

[12] We acknowledge that self-report of felt hand position is not bias-free. It is possible that the participant does not report the actual perceived position of her hands. She may be biased toward reporting numbers that are consistent with the subjectively-perceived position of the hands during the stimulation trial, rather than numbers that are consistent with the subjectively-perceived position of the hands post-stimulation. Or the participant may wish to please the Examiner by reporting numbers that indicate the paradigm has had 'an effect'. Although it is important to bear these limitations in mind, we note that our participants were completely naïve to the experimental objectives. Moreover, if left to chance, it is just as likely that the participant would demonstrate greater proprioceptive drift of the receptive hand compared with the administering hand.

somesthesis, but that temporally correlated and matching tactile and proprioceptive signals from two body parts is sufficient to change the feeling of ownership of a touched rubber limb" (p. 10569). This conclusion was based on the view that the participant displaces touch to the location of the prosthetic hand, as in the visual rubber hand illusion. But the current results demonstrate that this is not the experience of the majority of participants.

In fact, describing the non-visual illusion as a rubber hand illusion may be misleading. The participant does not have vision of the prosthetic hand during the experiment and, particularly when she administers touch with a paintbrush, there are few cues (apart from memory) as to the nature of the object to which the participant administers touch. If the participant administered stimulation to the tabletop, another person's leg, or a block of wood (while she received synchronous stimulation on her hand from the Examiner), she would experience the illusion of self-touch. (Indeed we have experimented with each of these and find that, when the participant administers stimulation with a paintbrush, there is a compelling illusion of self-touch irrespective of the stimulated object.) In contrast, in the visual rubber hand paradigm, it is important that the viewed hand fits with the participant's higher-order body representation, and that it has the same left-right laterality as the participant's hidden hand (Tsakiris & Haggard, 2005; Tsakiris et al., 2007). When the paradigm is conducted using a non-hand-object (e.g., a stick: Tsakiris & Haggard, 2005; a block of wood with a hand-like structure: Tsakiris et al., 2010; a tabletop: Haans et al., 2008), the participant does not experience the rubber hand illusion (but see Armel & Ramachandran, 2003; Hohwy & Paton, 2010). Thus, a realistic hand is crucial for the visual rubber hand illusion whereas the nature of the object that is touched may not be crucial for the non-visual illusion of self-touch.

We conclude by suggesting that the non-visual illusion of self-touch should not be conflated with the illusion of ownership; although it may seem counterintuitive, one can feel as if one is touching one's own hand without feeling as if the touched hand is one's own. We propose that when the participant's stimulation of the prosthetic hand is synchronous with the Examiner's stimulation of the participant's hand, the prosthetic hand and the Examiner's administering hand cease to be a part of the participant's phenomenology: all that remains is the participant's experience of her own two hands.

CHAPTER 7: SPATIAL CONSTRAINTS ON THE ILLUSION OF SELF-TOUCH

The self-touch rubber hand paradigm elicits the compelling illusion that one is touching one's own hand even though the two hands are not in contact. In this non-visual paradigm, the individual administers touch to a prosthetic hand while the Examiner administers synchronous touch to the individual's other hand. In previous investigations, the prosthetic hand and the individual's receptive hand have been separated by 15 cm and positioned palm downward on the table with the fingers pointing straight ahead. We manipulated distance and alignment of the prosthetic hand relative to the participant's receptive hand. The illusion of self-touch was diminished when the distance between the hands increased and when the two hands were misaligned. Drift of proprioceptively perceived hand position was also diminished by an increase in distance between the hands but it was abolished by misalignment. Implications of this dissociation between illusion ratings and proprioceptive drift extend to visual rubber hand experiments.

In studies that use Botvinick and Cohen's (1998) visual rubber hand paradigm, the participant looks at a prosthetic hand as it is stroked with a paintbrush by the Examiner while at the same time the Examiner administers strokes to the participant's hidden hand with an identical paintbrush. When timing of stimulation on the prosthetic hand is matched to timing of stimulation on the participant's hidden receptive hand, the participant feels "the touch not of the hidden brush but that of the viewed brush, as if the rubber hand had sensed the touch" (Botvinick & Cohen, 1998, p. 756). It may also seem to the participant that the viewed prosthetic hand is her own hand. These two components of the rubber hand illusion elicited by the *visual* rubber hand paradigm – visual capture of touch and the experience of ownership of the viewed prosthetic hand – are commonly assessed with questionnaire ratings of the intensity of the illusion and with a measure of proprioceptive drift. Proprioceptive drift is a shift in the proprioceptively perceived position of the hand. In most rubber hand studies, it is a shift in the proprioceptively perceived position of the hidden receptive hand toward the location of the viewed prosthetic hand. The magnitude of the shift is typically about 15-30% of the full distance between the receptive hand and the prosthetic hand (Makin et al., 2008).

Spatial discrepancies in distance, or in alignment, between the viewed prosthetic hand and the participant's hidden hand have been shown to diminish, and sometimes to abolish, the visual rubber hand illusion. The illusion is diminished by increasing the distance between the two hands (Lloyd, 2007) and it is abolished by misaligning the two hands (Costantini & Haggard, 2007; Ehrsson et al., 2004; Pavani et al., 2000; Tsakiris & Haggard, 2005). Here our interest is in conducting a systematic investigation (questionnaire ratings, proprioceptive drift, and time of illusion onset) of the spatial limits on the illusion of self-touch using the *non-visual* self-touch rubber hand paradigm (Ehrsson et al., 2005).

In previous studies of the illusion of self-touch (Ehrsson et al., 2005; see also Chapters 4, 5, and 6), the prosthetic hand and the participant's receptive hand have been separated by 15 cm and positioned palm downward on the table with the fingers pointing straight ahead. By varying distance and alignment of the prosthetic hand relative to the participant's receptive hand, we investigate the impact of these spatial manipulations when vision is not involved. One possibility is that the illusion of self-touch will be sensitive to spatial manipulations in the same way as the visual rubber hand illusion. Alternatively, the illusion of self-touch might be more robust than the visual rubber hand illusion because the paradigm is conducted without vision of either the prosthetic hand or the receptive hand. Without vision, information about spatial discrepancy must be derived from proprioceptive information about the participant's two hands.

In the non-visual self-touch rubber hand paradigm, the participant – guided by the Examiner – administers stimulation with a paintbrush to a prosthetic hand while at the same time the Examiner administers stimulation with an identical paintbrush to the participant's other hand. When timing of stimulation on the prosthetic hand is matched to timing of stimulation on the participant's receptive hand, the participant experiences the illusion that she is touching her own hand. It may seem to the participant that her receptive hand has moved to the location of the prosthetic hand, where she herself is administering stimulation to the prosthetic hand, or alternatively, that her administering hand has moved to the location of her receptive hand, which is receiving stimulation from the Examiner (Chapter 6).

Before presenting our current experiments, which examine the spatial limits on the non-visual self-touch rubber hand paradigm, we review methodological differences in previous studies that have manipulated distance and alignment in the visual rubber hand paradigm. Two visual studies that have manipulated distance are compared: Lloyd (2007), in which the visual rubber hand illusion was assessed with questionnaire ratings of the participant's subjective experience along with time of illusion onset, and Zopf et al. (2010), who used questionnaire ratings along with proprioceptive drift in a crossmodal congruency task.[13] Four visual studies that have manipulated alignment are compared: Pavani et al. (2000), in which the visual rubber hand illusion was assessed with questionnaire ratings of the participant's subjective experience in a crossmodal congruency task; Ehrsson et al. (2004), who used questionnaire ratings in an fMRI study of the visual rubber hand illusion; and two studies by Tsakiris and Haggard (2005) and Costantini and Haggard (2007), in which the visual rubber hand illusion was assessed by measuring proprioceptive drift.[14]

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[13] In the crossmodal congruency task, the participant makes a speeded decision as to which finger of her hidden hand is receiving vibrotactile stimulation. The task is made more difficult by visual distractors on a viewed prosthetic hand; that is, lights which are activated at a location that is either congruent or incongruent with vibrotactile stimulation on the hidden hand. Participants are faster to report which finger of the hidden hand has been stimulated on congruent trials. The difference in reaction time between the congruent and incongruent trials is referred to as the *crossmodal congruency effect*. This effect provides information about the "influence of the visual distracter on discriminating the tactile target location" (Zopf et al., p. 714).

[14] Armel and Ramachandran (2003) have also examined the effects of manipulating distance in the visual rubber hand illusion and two further studies (Durgin, Evans, Dunphy, & Klostermann, 2007; Petkova & Ehrsson, 2009) have examined the effects of manipulating alignment, with a 180° rotation of the viewed prosthetic hand. The Armel and Ramachandran study is not discussed more fully because the authors did not specify the distance between the viewed prosthetic hand and the participant's hidden hand. The information provided was that the viewed prosthetic hand was positioned either at a realistic location relative to the participant's body or that it was positioned 91 cm in front of the participant's body. The studies manipulating alignment are not discussed further because the participant's hidden hand did not receive tactile stimulation.

Distance Manipulation

Lloyd (2007) systematically manipulated the distance between the prosthetic hand and the participant's hidden receptive hand. She set out to "quantify the spatial boundaries over which referred tactile sensations can be felt on a rubber hand" (p. 104). The prosthetic hand was positioned at one of six distances (17.5 cm, 27.5 cm, 37.5 cm, 47.5 cm, 57.5 cm, 67.5 cm) from the participant's receptive hand, with the order of hand-placement conditions randomised. The strength of the illusion was assessed by asking participants to provide a rating of agreement from +3 (*strongly agree*) to -3 (*strongly disagree*) with the statement "It seemed as though the touch I felt was caused by the experimenter touching the rubber hand" (p. 106). Participants provided higher agreement ratings with the hands separated by 17.5 cm than in any of the other five hand-placement conditions. Participants also provided higher agreement ratings with the hands separated by 27.5 cm than with the hands separated by 47.5 cm, 57.5 cm or 67.5 cm. Time of illusion onset was also assessed, by asking the participant to *stop* the trial when there was agreement (or disagreement) with the illusion statement. Among participants who did agree with the illusion statement, there was only one significant finding: time of illusion onset was faster with the hands separated by 27.5 cm than with the hands separated by 37.5 cm.

Lloyd's (2007) results indicate that the visual rubber hand illusion is diminished by increasing the distance between the viewed prosthetic hand and the participant's hidden receptive hand. Lloyd explains these effects for distance with reference to visuo-tactile bimodal cells in the premotor and parietal cortices. These cells code peripersonal space around the hand and "respond to both the visual and tactile characteristics of objects approaching and touching the hand" (p. 104). Visual receptive fields are larger than tactile receptive fields, to allow for incorporation of tools into the body schema (see Iriki, Tanaka, & Iwamura, 1996). Lloyd's view is that the visual rubber hand illusion occurs when the viewed prosthetic hand falls within the region of space coded by bimodal visuo-tactile cells; that is, within the visual receptive field surrounding the tactile receptive field of the participant's stimulated hand. Thus, the fact that the visual rubber hand illusion was strongest at the 17.5 cm and 27.5 cm hand-placement conditions, and "declined significantly once the rubber hand was placed more than 27.5 cm away from the participant's own right hand" (Lloyd, p. 108), is broadly consistent with findings regarding the size of the visual receptive fields that surround the tactile receptive fields (Fogassi & Gallese, 2004; Fogassi, Gallese, Fadiga, Luppino, Matelli, & Rizzolatti, 1996).

It has been suggested (Makin et al., 2008; Zopf et al., 2010) that Lloyd's (2007) findings – a diminished visual rubber hand illusion with increasing distance between the hands – may be better explained by the mismatch in alignment between the prosthetic hand and the participant's hidden hand. Lloyd set out to manipulate distance while also controlling for anatomical plausibility, but in doing so she may have introduced a possible confound. Throughout the experiment, the participant's hidden right hand was palm downward and pointing forward, positioned 17.5 cm to the right of the line of the right shoulder. The viewed prosthetic right hand was positioned to the left of the participant's hidden right hand. In the 17.5 cm hand-placement condition, the viewed prosthetic right hand was aligned with the participant's hidden right hand. But as the distance between the hands increased (27.5 cm, 37.5 cm, 47.5 cm, 57.5 cm, 67.5 cm), the viewed prosthetic hand was rotated progressively further leftward, so that the fingers of the prosthetic hand pointed to the left rather than straight ahead. Lloyd believed that this rotation would keep the viewed prosthetic right hand in an anatomically plausible orientation relative to the participant's right shoulder. Thus, alignment was matched when the prosthetic hand and the participant's hidden hand were close to one another (17.5 cm prosthetic hand-placement condition) but alignment was increasingly mismatched as the distance between the two hands increased. This potential problem has been addressed by Zopf et al. (2010; Experiment 2): they increased the distance between the prosthetic hand (positioned near the participant's body midline) and the participant's hidden hand but held alignment constant. Their findings do not support Lloyd's because the visual rubber hand illusion was not diminished when the participant's hand was 45 cm from the prosthetic hand, as compared with 15 cm.

Lloyd (2007) and Zopf et al. (2010) arrived at different conclusions about the impact of distance manipulation on the visual rubber hand illusion but there are methodological differences that need to be taken into account before drawing conclusions about whether Lloyd's effects for distance were actually effects for a mismatch in alignment. Lloyd used a traditional method for eliciting the visual rubber hand illusion. Each distance condition comprised a maximum of 60 s of synchronous stimulation of the viewed prosthetic hand and the participant's hidden hand followed by questionnaire ratings of the perceived intensity of the rubber hand illusion. In contrast, Zopf et al. interleaved the stimulation of the hands with a crossmodal congruency task, in which the participant reported the location of vibrotactile stimulation on her hidden hand. Each distance condition comprised a 16 min block of 216 trials (Zopf, personal communication), with each trial consisting of a brush stroke of the viewed prosthetic hand and of the participant's hidden hand, and the crossmodal congruency task. The participant indicated proprioceptively perceived hand position before and after the 16 min block, and provided questionnaire ratings after the 16 min block. The statements in the questionnaire were chosen from previous rubber hand experiments. For example, "It seemed as if I were feeling the touch of the brush in the location where I saw the rubber hand touched" and "I felt as if the rubber hand was my hand" (see Botvinick & Cohen, 1998). In the crossmodal congruency task, timing of the light and of the vibrotactile stimulation was offset by 150 ms, to "reduce the potential for the crossmodal congruency task to generate the rubber hand illusion" (p. 720). Zopf et al. wanted the illusion to be generated by the synchronous brushstrokes and not by the interleaved crossmodal congruency task. But Shimada et al. (2009) have shown that the rubber hand illusion is diminished only when the timing of stimulation administered to the viewed prosthetic hand and to the participant's hidden hand is offset by more than 300 ms. Therefore, it may be that the crossmodal task did facilitate the rubber hand illusion, and that the rubber hand illusion was not diminished by distance because the experiment involved a longer period of stimulation.

Although the focus of the current paper is on distance and alignment manipulations in the *non-visual* illusion of self-touch, this brief review highlights the fact that there is also scope for future work to investigate further the effect of distance on the visual rubber hand illusion.

Alignment Manipulation

Pavani et al. (2000) were the first to report that subjective ratings of intensity for the visual rubber hand illusion were diminished by a mismatch in alignment of the hands. Unlike most visual rubber hand studies, participants viewed two prosthetic hands instead of one, and the experiment did not involve synchronous stroking. The participant viewed a left and a right prosthetic hand while the participant's two hands were hidden from view. The viewed prosthetic hands were either aligned with the participant's hands (with the fingers pointing straight ahead), or they were misaligned by 90° (with the fingers of the two prosthetic hands pointing toward one another). A light was activated on one of the two prosthetic hands (left or right) while either the participant's hidden left hand or the participant's hidden right hand received vibrotactile stimulation. The location of the light was either congruent or incongruent with the location of vibrotactile stimulation. The participant was asked to report the location of vibrotactile stimulation on her own hand. Participants demonstrated a larger crossmodal congruency effect in the aligned hand-placement condition. Pavani et al. used a five-item questionnaire to assess whether the temporal correspondence between the viewed light on the prosthetic hand and the vibrotactile stimulation on the participant's hidden hand elicited the visual rubber hand illusion. The strength of the illusion was assessed by asking participants to provide a rating of agreement from 1 (*totally disagree*) to 7 (*totally agree*) with the statements assessing visual capture of touch "It seemed as if I was feeling the vibration in the location where I saw the rubber hands" and the experience of ownership "I felt as if the rubber hands were my hands" p. 357). Participants provided higher agreement ratings for statements in the aligned hand-placement condition, as compared with the misaligned hand-placement condition. The ratings indicated that participants did not experience the visual rubber hand illusion in the misaligned condition, but these findings did not preclude the possibility that the illusion could be elicited in the misaligned condition with a more traditional method that included synchronous strokes to the viewed and hidden hand(s).

Questionnaire ratings were also used by Ehrsson et al. (2004) in a study that did use a traditional method for eliciting the visual rubber hand illusion and included a misaligned control condition. In this study, the viewed prosthetic hand was misaligned with the participant's hand by 180° (the fingers of the prosthetic hand pointed toward the participant's body). Thus, the prosthetic hand was not only misaligned but also in an anatomically implausible position. The strength of the illusion was assessed by asking participants to provide a rating of agreement on a seven-point scale (– – –, – –, –, 0, +, ++, +++) with statements assessing visual capture of touch "touch feeling is located on rubber hand" and the experience of ownership "feeling that the rubber hand is my hand" (p. 16 of supplementary online material). Participants provided higher agreement ratings for statements in the synchronous-aligned condition, as compared with three control conditions: synchronous-misaligned; asynchronous-aligned; asynchronous-misaligned. As predicted, the ratings for the synchronous-misaligned condition indicated that participants did not experience a subjective visual rubber hand illusion.

Two further studies (Costantini & Haggard, 2007; Tsakiris & Haggard, 2005) that manipulated the alignment of the prosthetic hand used proprioceptive drift rather than questionnaire ratings to assess the visual rubber hand illusion. In both studies, the prosthetic hand was always positioned at the participant's body midline. In the study by Tsakiris and Haggard (Experiment 1), the participant's hidden hand was palm downward with the fingers pointing straight ahead, and positioned 17.5 cm to the left of the prosthetic hand. The prosthetic hand was either aligned with the participant's hand or rotated by 90°. In the aligned hand-placement condition (but not in the misaligned condition), participants demonstrated significantly greater proprioceptive drift toward the prosthetic hand with synchronous stimulation, as compared with asynchronous stimulation. To obtain a more specific measure of the rubber hand illusion the researchers subtracted asynchronous proprioceptive drift from synchronous proprioceptive drift. In the aligned hand-placement condition, the resulting value was positive, which indicated proprioceptive drift toward the viewed prosthetic hand; in the misaligned condition, the resulting value was negative (see Tsakiris & Haggard, p. 82, Figure 2). The researchers suggested, that "for the RHI [rubber hand illusion] to occur, the rubber hand had to be in a congruent position with respect to the participant's hand" (p. 83).

In the study by Costantini and Haggard (2007), the participant's hidden hand was positioned 30 cm to the right of the prosthetic hand. Two refinements in the approach to alignment manipulation were investigated. In the first, the participant's hidden hand was palm downward with the fingers pointing straight ahead while the viewed prosthetic hand was either aligned with the participant's hidden hand (0°) or rotated by 10°, 20°, or 30°. In the second refinement, the prosthetic hand was palm downward with the fingers pointing straight ahead while the participant's hidden hand was either aligned with the prosthetic hand (0°) or rotated by 10°, 20°, or 30°. As expected, in the aligned hand-placement condition, participants demonstrated significant proprioceptive drift toward the prosthetic hand. Given that visual acuity is higher than proprioceptive acuity, Costantini and Haggard predicted that small mismatches in what the participant views (orientation of the prosthetic hand) would reduce the illusion more than equivalent mismatches in what the participant feels (orientation of the participant's hidden hand). Consistent with this, there was no proprioceptive drift in any of the conditions in which the viewed prosthetic hand was rotated. In contrast, participants demonstrated proprioceptive drift when the hidden hand was rotated by 10°, although there was no drift with either a 20° or 30° rotation.[15] Costantini and Haggard concluded "the RHI [rubber hand illusion] was abolished by mismatches due to changed posture of the rubber hand…but survived equivalent small mismatches due to changes in posture of the subject's hand" (p. 235).

Taken together, these findings indicate that the visual rubber hand illusion can be abolished by misalignment of the prosthetic and receptive hands. This was confirmed by subjective ratings of the illusion (Ehrsson et al., 2004; Pavani et al., 2000) and by proprioceptive drift (Costantini & Haggard, 2007; Tsakiris & Haggard, 2005).

[15] Note that in the two conditions with a 10° rotation, mismatch between what the participant viewed and felt was 10° regardless of which hand – viewed or hidden – was rotated. The finding that the illusion was abolished only when the viewed prosthetic hand was rotated, suggests that participants were sensitive to the viewed hand being misaligned with the *straight-ahead* position, rather than sensitive to it being misaligned with the participant's hidden hand. Interestingly, if we follow through with this logic, the prediction is that the visual rubber hand illusion will be abolished if both hands – viewed and hidden –are rotated by 10° in the same direction so that neither hand is pointing straight ahead, but both hands are indeed aligned.

Overview of Experiments

Two experiments were conducted to investigate systematically the spatial limits on the illusion of self-touch using the *non-visual* self-touch rubber hand paradigm. In Experiment 1, the *distance* between the prosthetic hand and the participant's receptive hand was manipulated, while the alignment of the two hands was held constant. In Experiment 2, the *alignment* of the prosthetic hand relative to the participant's receptive hand was manipulated, while the distance between the two hands was held constant. The self-touch rubber hand paradigm was conducted with vision of the hands precluded. Thus, a distance or an alignment manipulation of the prosthetic hand was experienced as a change in the proprioceptively perceived position of the administering hand relative to the proprioceptively perceived position of the receptive hand.

General Methods

Participants

There were 28 participants in Experiment 1 (20 females and 8 males; 18–28 years, *M* = 20.2 years) and 16 participants in Experiment 2 (15 females and 1 male; 16-32 years, *M* = 20.1 years). The participants were recruited from the University of Oxford community and they provided informed written consent. The protocol was approved by the University of Oxford Research Ethics Committee, and was in accordance with the ethical standards laid down in the 2008 Declaration of Helsinki. Participants received course credits or £5 compensation for their time.

Apparatus and Procedure

The participant was seated at a table, opposite the Examiner. A prosthetic left hand was positioned at the participant's body midline. The participant's receptive left hand was positioned palm downward on the table with the fingers pointing straight ahead. Hand placement was manipulated in Experiment 1 (distance between the prosthetic hand and the participant's receptive left hand) and in Experiment 2 (alignment of the prosthetic hand relative to the participant's receptive left hand), and will be described in more detail at the beginning of each experiment. The participant – guided by the Examiner – administered stimulation with a paintbrush to the index finger of the prosthetic hand while at the same time the Examiner administered stimulation with an identical paintbrush to the proximal phalanx of the participant's left index finger. The participant was asked to hold the paintbrush 5 cm above the bristles and to relax her administering right hand. The Examiner held the same paintbrush 10 cm above the bristles and was in control of the movements of the paintbrush (see Figure 20). This guided stimulation technique was practised until the participant relaxed her hand so that she allowed the pattern of stimulation – and particularly the timing of stimulation – to be controlled by the Examiner. The experimental set-up was concealed from the participant by a testing unit (width: 100 cm; depth: 100 cm; height: 30 cm) positioned above the hands.

Stimulation of the prosthetic hand by the participant was either *synchronous* or *asynchronous* with stimulation administered to the participant's receptive left hand by the Examiner. Previous studies have shown that the illusion of self-touch is elicited with synchronous stimulation. Asynchronous control trials were included as a baseline measure. Three methods were used to assess the illusion of self-touch: (1) self-touch illusion questionnaire, (2) proprioceptive drift, and (3) time of illusion onset.

Self-Touch Illusion Questionnaire

Following each trial, the participant completed a questionnaire adapted from Ehrsson et al. (2005):

(1) It felt as if the touch that I felt on my left hand was from the paintbrush that I held in my right hand.
(2) I felt as if I had more than one left hand.
(3) I felt as if my left hand was larger than normal.
(4) I felt as if my left hand was moving.
(5) I could not feel my left hand.

Statement 1 assessed the illusion of self-touch. Statements 2-5 indicated experiences that the paradigm was not expected to elicit, and were thus used to control for suggestibility. Order of presenting the five statements was randomised across participants and trials. The strength of the illusion was assessed by asking participants to provide a rating of agreement to these five statements on a seven-point scale (0 = *not at all*; 1 = *slightly agree*; 3 = *moderately agree*; 5 = *strongly agree*; 6 = *very strongly agree*).

Proprioceptive Drift

Proprioceptive drift was assessed immediately before and after each trial, using a ruler positioned on top of the testing unit directly above the participant's hands. The findings presented in Chapter 6 indicate that the participant may proprioceptively perceive her administering hand as displaced toward the location of her receptive hand and/or proprioceptively perceive her receptive hand as displaced toward the location of her administering hand. Therefore, the participant was asked to read the number on the ruler corresponding to her administering right index finger (at the position of the brush) *and* the number corresponding to her receptive left index finger. A baseline measurement of proprioceptively perceived hand position was taken before stimulation began (0 s) and a post-trial measurement of proprioceptively perceived hand position was taken at the end of the trial (60 s). To discourage the participant from reporting the same numbers each time, the ruler was offset each time it was repositioned on top of the testing unit, with a different offset for each baseline and post-trial measurement.

The post-trial measurement was compared to the baseline measurement for evidence of a change in proprioceptively perceived hand position. Proprioceptive drift was signed positive if it was in the hypothesised direction: leftward drift of the administering hand toward the receptive hand and rightward drift of the receptive hand toward the administering hand. A proprioceptive drift value was derived for each participant by summing drift of the administering hand and drift of the receptive hand.

Time of Illusion Onset

The onset of the illusion was timed. The participant was asked to inform the Examiner when she *agreed* with the statement "It feels as if my left hand is being touched by the paintbrush in my right hand". The participant was reassured that she should not feel 'pressure' to report this experience. Regardless of the point in time at which the participant indicated the onset of the illusion, the trial continued until the participant had received the full 60 s of stimulation. The methodology of the current study thus differs from the methodology of the study by Lloyd (2007). In Lloyd's study, participants were instructed to stop the trial when they agreed or disagreed with the illusion statement. Therefore trial length (and thus the amount of stimulation received) will have been different for each participant.[16]

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[16] One could argue that stopping the trial when the participant agreed or disagreed with the illusion statement may have had an effect on the questionnaire ratings in the study by Lloyd (2007). For example, some participants may have waited until they experienced a compelling illusion before stopping the trial. It is likely that these participants will have provided a high rating of agreement for the illusion statement. Conversely, other participants may have stopped the trial as soon as they experienced even a mild illusion. It is likely that these participants will have provided lower ratings of agreement for the illusion statement. Furthermore, a participant may have stopped the trial prematurely because she disagreed with the illusion statement, even though further stimulation may have led to the onset of the illusion.

Experiment 1

There were four hand-placement conditions for the participant's receptive left hand in Experiment 1. The participant's receptive left hand was positioned palm downward on the table with the fingers pointing straight ahead, and at one of four distances – 15 cm, 30 cm, 45 cm, 60 cm – to the left of the prosthetic hand. The prosthetic hand was always positioned at the participant's body midline with the fingers pointing straight ahead (see Figure 22). Stimulation consisted of strokes and taps. The strokes were unidirectional from the knuckle (where the index finger meets the hand) toward the fingertip, taking in the full-length of the index finger from knuckle to fingertip.

Each participant took part in eight trials – one synchronous trial and one asynchronous trial in each of the four hand-placement conditions. The order of the four hand-placement conditions was randomised across participants.

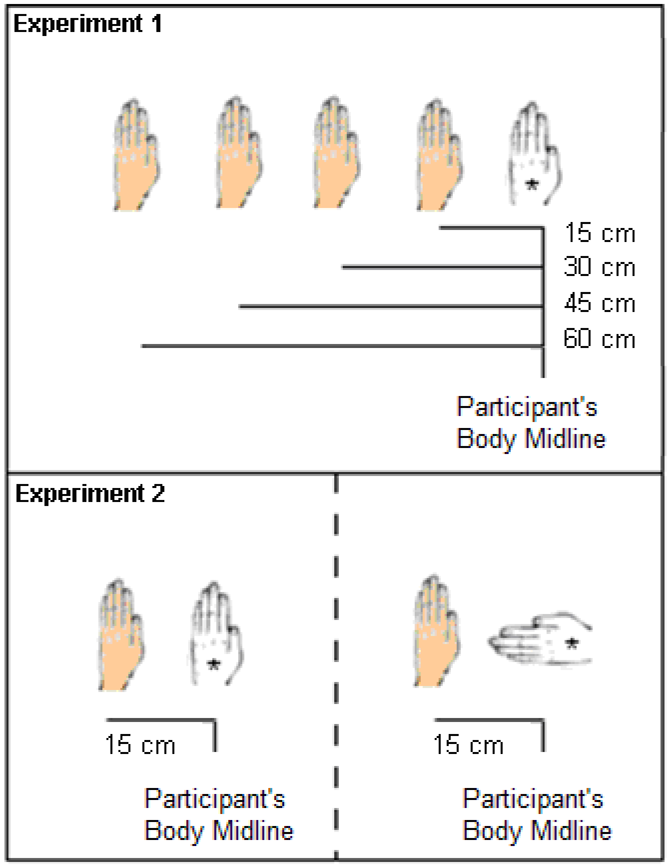

Figure 22. Hand-placement conditions for Experiment 1 and Experiment 2. The * indicates the prosthetic hand.

Results

Self-Touch Illusion Questionnaire

The first analysis investigated whether there was an *effect for synchrony*. The analysis was conducted using individual Wilcoxon Signed-Rank Tests (the non-parametric alternative to a paired-samples *t*-test), with an adjusted alpha level of .0125. Participants provided higher agreement ratings for the illusion statement (Statement 1) following synchronous compared with asynchronous stimulation in all four hand-placement conditions: hands separated by

15 cm (*Md* = 5 vs *Md* = 0; z = -4.490, p < .001); 30 cm (*Md* = 4 vs *Md* = 0; z = -4.404, p < .001); 45 cm (*Md* = 4 vs *Md* = 0; z = -4.131, p < .001); 60 cm (*Md* = 3 vs *Md* = 0; z = -4.039, p < .001).

The second analysis investigated whether there was an overall *effect for distance*. This analysis was conducted using the Friedman Test (the non-parametric alternative to a one-way repeated measures ANOVA), with an adjusted alpha level of .025. The results for *synchronous* stimulation (Figure 23, top panel) indicated that there was a significant difference in the ratings provided for the illusion statement (Statement 1) across the four hand-placement conditions, χ^2(3, n = 28) = 32.360, p < .001. Inspection of the median values indicated that the decrease in illusion ratings corresponded with an increase in distance between the participant's hand and the prosthetic hand: 15 cm (*Md* = 5); 30 cm (*Md* = 4); 45 cm (*Md* = 4); and 60 cm (*Md* = 3). This was confirmed in a follow-up analysis using individual Wilcoxon Signed-Rank Tests, with an adjusted alpha level of .008. Median illusion ratings were significantly higher at 15 cm than at all other distances: 30 cm (z = -3.288, p = .001); 45 cm (z = -3.891, p < .001); 60 cm (z = -4.039, p < .001). Median illusion ratings were also significantly higher at 30 cm than at 60 cm (z = -2.883, p = .004) but there was no significant difference in illusion ratings between 30 cm and 45 cm (z = -1.592, p = .111) or between 45 cm and 60 cm (z = -1.999, p = .046). The results for *asynchronous* stimulation (Figure 23, bottom panel) indicated that there was no significant difference in median ratings provided for the illusion statement (Statement 1) across the four hand-placement conditions, χ^2(3, n = 28) = 1.735, p = .629. The median value was zero for all conditions.

Visual inspection of Figure 23 reveals that participants provided low agreement ratings for the control statements (Statements 2-5). The median agreement rating was zero for all statements with the exception of Statement 3 "I felt as if my left hand was larger than normal". Statement 3 produced marginally higher agreement ratings (*Md* = 1 with synchronous stimulation in all hand-placement conditions) than the other control statements. This finding is consistent with results presented in Chapter 6. Although the statement was intended as a control statement, it is possible that the perception of a larger left hand is a part of the participant's experience, or interpretation of the experience, of the illusion that she is touching her own hand. When the participant experiences the illusion of contact between her two hands, she may perceive her left hand as having become larger, and as filling the space between her two hands.

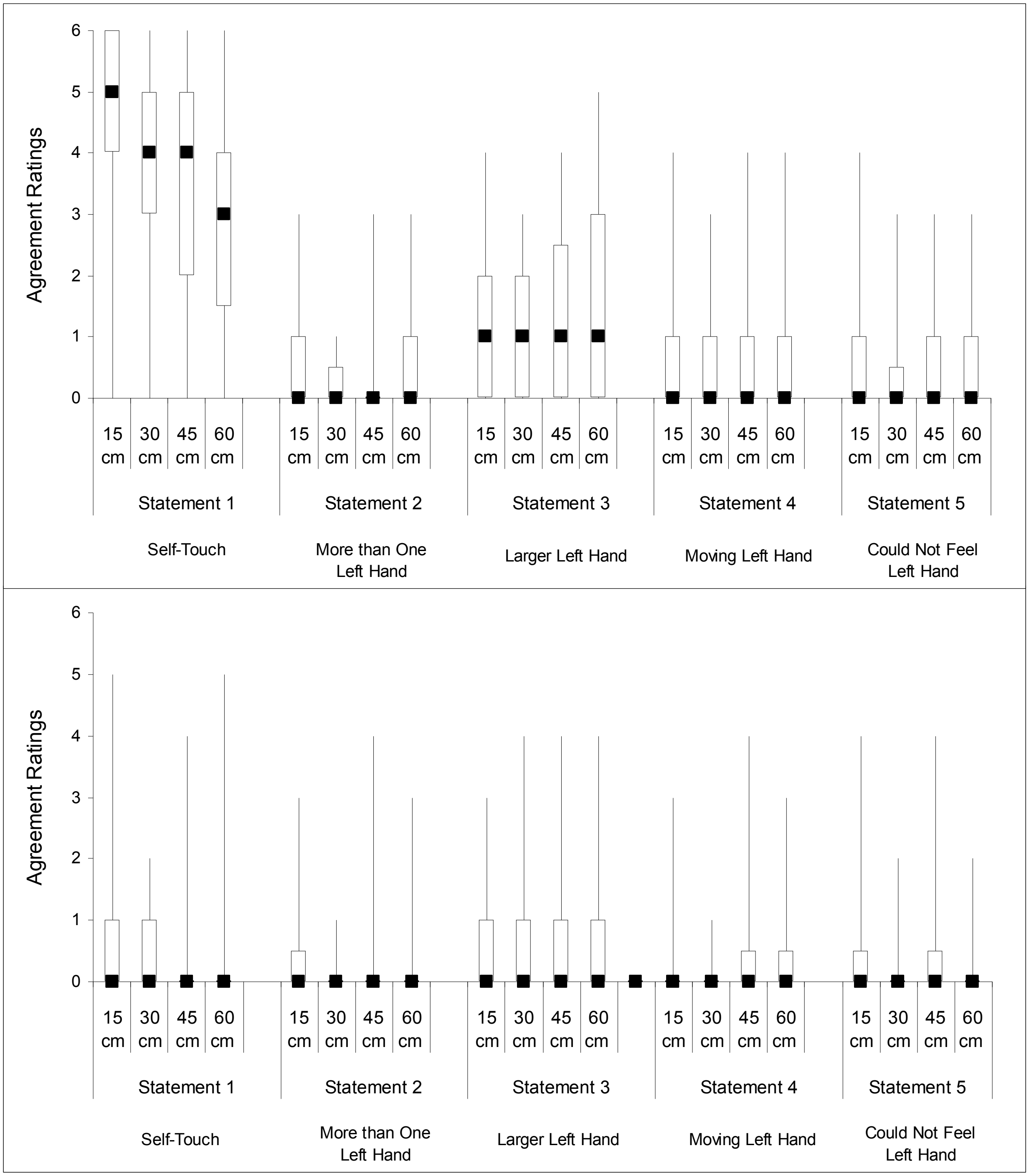

Figure 23. Median agreement ratings for the self-touch illusion questionnaire for synchronous (top panel) and asynchronous (bottom panel) stimulation. The black filled-in square indicates the median value, the box indicates the interquartile range, and the whiskers indicate the full range of responses.

Proprioceptive Drift

A 2x4 within-subjects ANOVA was conducted for proprioceptive drift. The factors were mode of stroking (synchronous, asynchronous) and hand-placement condition (15 cm, 30 cm, 45 cm, 60 cm). There was a main effect for mode of stroking ($F(1, 27) = 27.094$, $p < .001$, multivariate partial eta-squared = .501), with greater proprioceptive drift in the synchronous ($M = 6.99$ cm) compared with the asynchronous ($M = 2.55$ cm) stimulation condition. There was a main effect for hand-placement condition ($F(3, 25) = 6.108$, $p = .003$, multivariate partial eta-squared = .423), with less proprioceptive drift when the hands were separated by 15 cm ($M = 2.59$ cm) compared with 30 cm ($M = 4.70$ cm; $p = .009$) or 45 cm ($M = 6.48$ cm; $p = .006$). There was also a trend toward less proprioceptive drift when the hands were separated by 15 cm ($M = 2.59$ cm) compared with 60 cm ($M = 5.82$ cm; $p = .059$). There was no significant mode of stroking by hand-placement condition interaction ($F(3, 25) = .241$, $p = .867$, multivariate partial eta-squared = .028).

The finding of less proprioceptive drift at 15 cm requires interpretation. Proprioceptive drift "generally increase[s] the further the real hand is placed away from the stroked object and/or the body midline" (Zopf et al., 2010, pp. 721-722). Moreover, when the hands are separated by 15 cm, the maximum proprioceptive drift possible is ~15 cm, whereas there is potential for greater proprioceptive drift as the distance between the hands increases to 30 cm, 45 cm, or 60 cm. Thus, following Zopf et al., a second analysis was conducted in which proprioceptive drift was calculated as a proportion of the actual distance between the hands. With this method, a 1.5 cm proprioceptive drift at 15 cm is equivalent to a 4.5 cm proprioceptive drift at 45 cm (i.e., 10% of the actual distance between the hands).

A 2x4 within-subjects ANOVA was conducted using the corrected values. There was a main effect for mode of stroking ($F(1, 27) = 37.014$, $p < .001$, multivariate partial eta-squared = .578), a main effect for hand-placement condition ($F(3, 25) = 3.529$, $p = .029$, multivariate partial eta-squared = .298), and a mode of stroking by hand-placement condition interaction ($F(3, 25) = 8.336$, $p = .001$, multivariate partial eta-squared = .500). To investigate this interaction, we conducted separate one-way ANOVAs for synchronous and asynchronous stimulation. When stimulation was synchronous, there was a significant main effect for hand-placement condition ($F(3, 25) = 6.970$, $p = .001$, multivariate partial eta-squared = .455). Pairwise comparisons, adjusted for multiple comparisons, indicated that participants demonstrated proportionally greater proprioceptive drift when the hands were separated by 15 cm ($M = .333$) compared with 45 cm ($M = .198$; $p = .016$) or 60 cm ($M = .121$; $p = .001$), and when the hands were separated by 30 cm ($M = .225$) compared with 60 cm ($M = .121$; $p = .004$). None of the other comparisons between the different hand-placement conditions reached statistical significance (all p values > .113). When stimulation was asynchronous, there was no main effect for hand-placement condition ($F(3, 25) = 1.520$, $p = .234$, multivariate partial eta-squared = .154).

The reader may be interested to note that one-sample two-tailed *t*-tests (using an adjusted alpha level of .006) showed that proprioceptive drift, whether measured in centimeters or as a proportion of the actual distance between the hands, was not significantly different from zero *only* in the 15 cm asynchronous-stimulation condition ($t(27) = .364$, $p = .719$). In all other synchronous and asynchronous conditions, there was significant proprioceptive drift from proprioceptively perceived position at baseline (all p values < .003). See Figure 24.

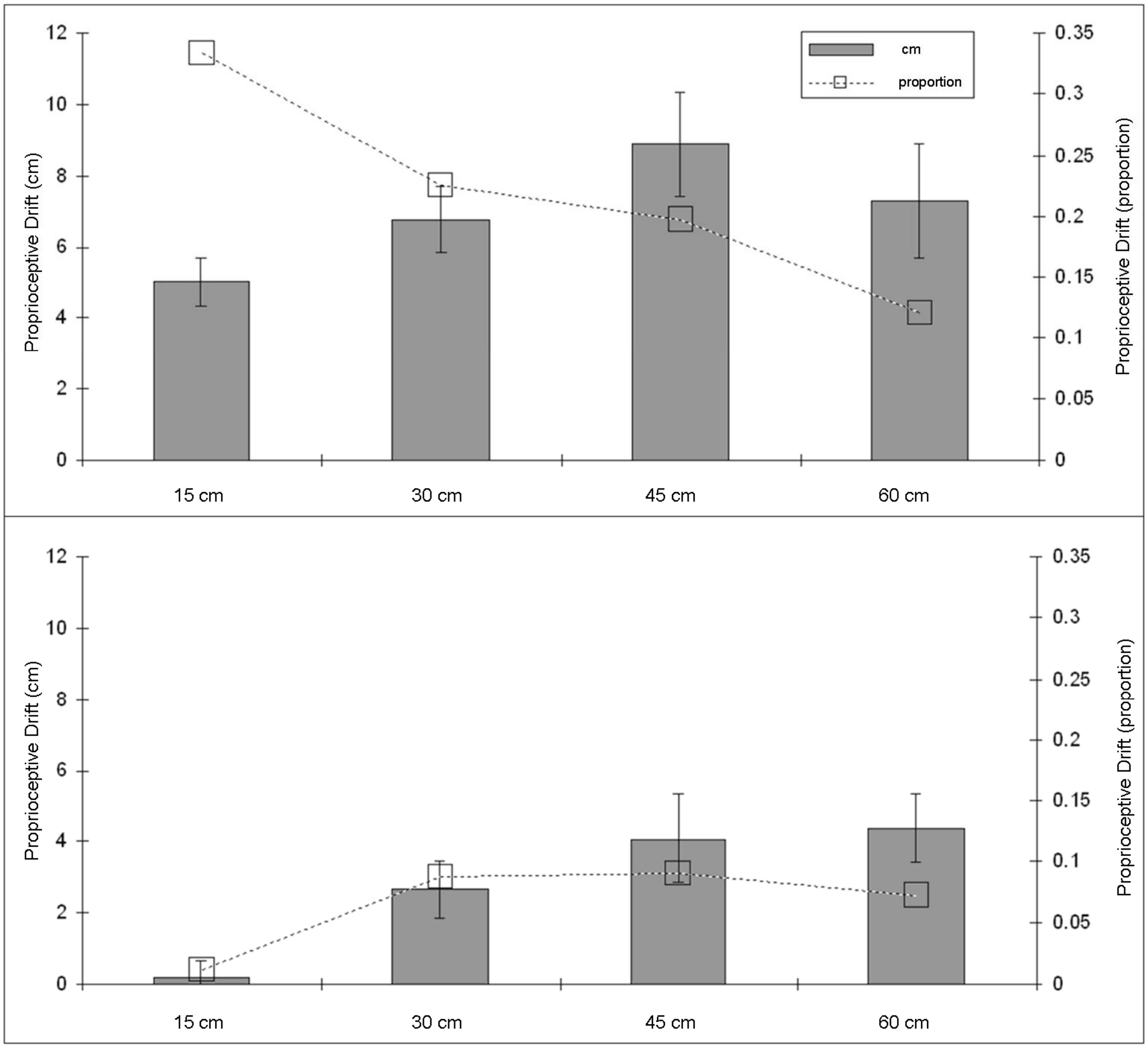

Figure 24. Mean proprioceptive drift in centimetres (Y-axis 1) and as a proportion of the actual distance between the participant's hands (Y-axis 2). The top panel presents proprioceptive drift for synchronous stimulation and the bottom panel presents proprioceptive drift for asynchronous stimulation. Error bars indicate one standard error of the mean.

Time of Illusion Onset

Time of illusion onset provided information about the *number* of participants who reported the onset of the illusion, and it also provided information about *when* in the trial the participant reported the subjective experience of self-touch. Different numbers of participants reported the onset of the illusion in the four hand-placement conditions with synchronous stimulation: 15 cm (n = 26, $M = 13.39$ s); 30 cm (n = 24, $M = 20.67$ s); 45 cm (n = 21, $M = 23.48$ s); 60 cm (n = 19, $M = 28.37$ s). With asynchronous stimulation, the onset of the illusion was reported on only 8 of 112 trials.

Time of illusion onset was analysed using a repeated-measures ANOVA. Sixteen of twenty-eight participants reported the onset of the illusion in all four hand-placement conditions with synchronous stimulation, and these sixteen were included in the analysis. There was a significant effect for hand-placement condition ($F(3, 13) = 13.911$, $p < .001$, multivariate partial-eta squared = .762). Pairwise comparisons (adjusted for multiple comparisons) indicated that participants were quicker to report the onset of the illusion when the hands were separated by 15 cm ($M = 10.31$ s) compared with 45 cm ($M = 21.25$ s; $p < .001$) and 60 cm ($M = 29.31$ s; $p = .001$), and they were also quicker when the hands were separated by 30 cm ($M = 17.69$ s) compared with 60 cm ($M = 29.31$ s; $p = .045$)(Figure 25).

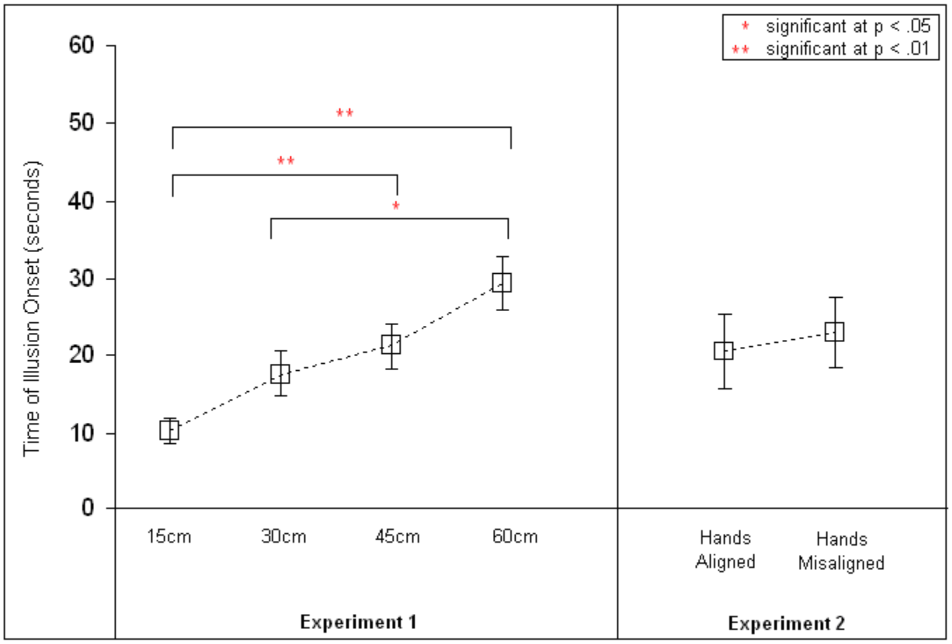

Figure 25. Mean time of illusion onset for Experiment 1 and Experiment 2. Error bars represent one standard error of the mean.

Experiment 2

There were two hand-placement conditions for the prosthetic hand in Experiment 2. The prosthetic hand was positioned at the participant's body midline, either with the fingers pointing straight ahead (*aligned* with the participant's receptive hand) or with the fingers pointing 90° anti-clockwise from straight ahead (*misaligned*, and pointing toward the participant's receptive hand). The participant's receptive left hand was always positioned 15 cm to the left of the prosthetic hand (measured at the knuckle where the index finger meets the hand), with the fingers pointing straight ahead (Figure 22). Stimulation consisted of strokes only (and not taps). With the hands concealed from view, it was the direction of the guided strokes that provided information to the participant about alignment or misalignment of the two hands.

The distance between the prosthetic hand and the participant's receptive hand was 15 cm always, but the distance between the participant's *administering* hand and receptive hand varied somewhat in the misaligned condition because of the length and direction of the administered strokes. With the prosthetic hand rotated anti-clockwise by 90º, the (stimulated) index finger of the prosthetic hand pointed toward the participant's receptive hand. Therefore, at the end of each stroke (at the fingertip of the index finger of the prosthetic hand), the participant's administering hand was approximately 8 cm closer to the receptive hand. The Examiner ensured that each 60-s trial was terminated at the beginning of a stroke, so that the paintbrush in the participant's administering hand was positioned at the knuckle where the index finger meets the prosthetic hand when proprioceptive drift was assessed.

Each participant took part in four trials – one synchronous trial and one asynchronous trial in each of the two hand-placement conditions. The order of the two hand-placement conditions and the order of the synchronous and asynchronous trials within each condition were randomised across participants.

Results

Self-Touch Illusion Questionnaire

The first analysis investigated whether there was an *effect for synchrony*. The analysis was conducted using individual Wilcoxon Signed-Rank Tests, with an adjusted alpha level of .025. Participants provided higher agreement ratings for the illusion statement (Statement 1) following synchronous compared with asynchronous stimulation in both hand-placement conditions: hands aligned ($Md = 5$ vs $Md = 0$; $z = -3.355$, $p = .001$) and hands misaligned ($Md = 3.5$ vs $Md = 0$; $z = -3.020$, $p = .003$).

The second analysis investigated whether there was an *effect for alignment*. This analysis was conducted using individual Wilcoxon Signed-Rank Tests, with an adjusted alpha level of .025. The results for *synchronous* stimulation (Figure 26, top panel) indicated that median ratings provided for the illusion statement (Statement 1) were significantly higher when the prosthetic hand and the participant's hidden hand were aligned ($Md = 5$) than when the prosthetic hand and the participant's hidden hand were misaligned ($Md = 3.5$)($z = -2.715$, $p = .007$). The results for *asynchronous* stimulation (Figure 26, bottom panel) indicated that there was no significant difference in median ratings provided for the illusion statement (Statement 1) when the hands were aligned compared with misaligned ($z = -.073$, $p = .942$). The median value was zero for both conditions.

Visual inspection of Figure 26 reveals that participants provided low agreement ratings for the control statements (Statements 2-5). The median agreement rating was zero for all statements.

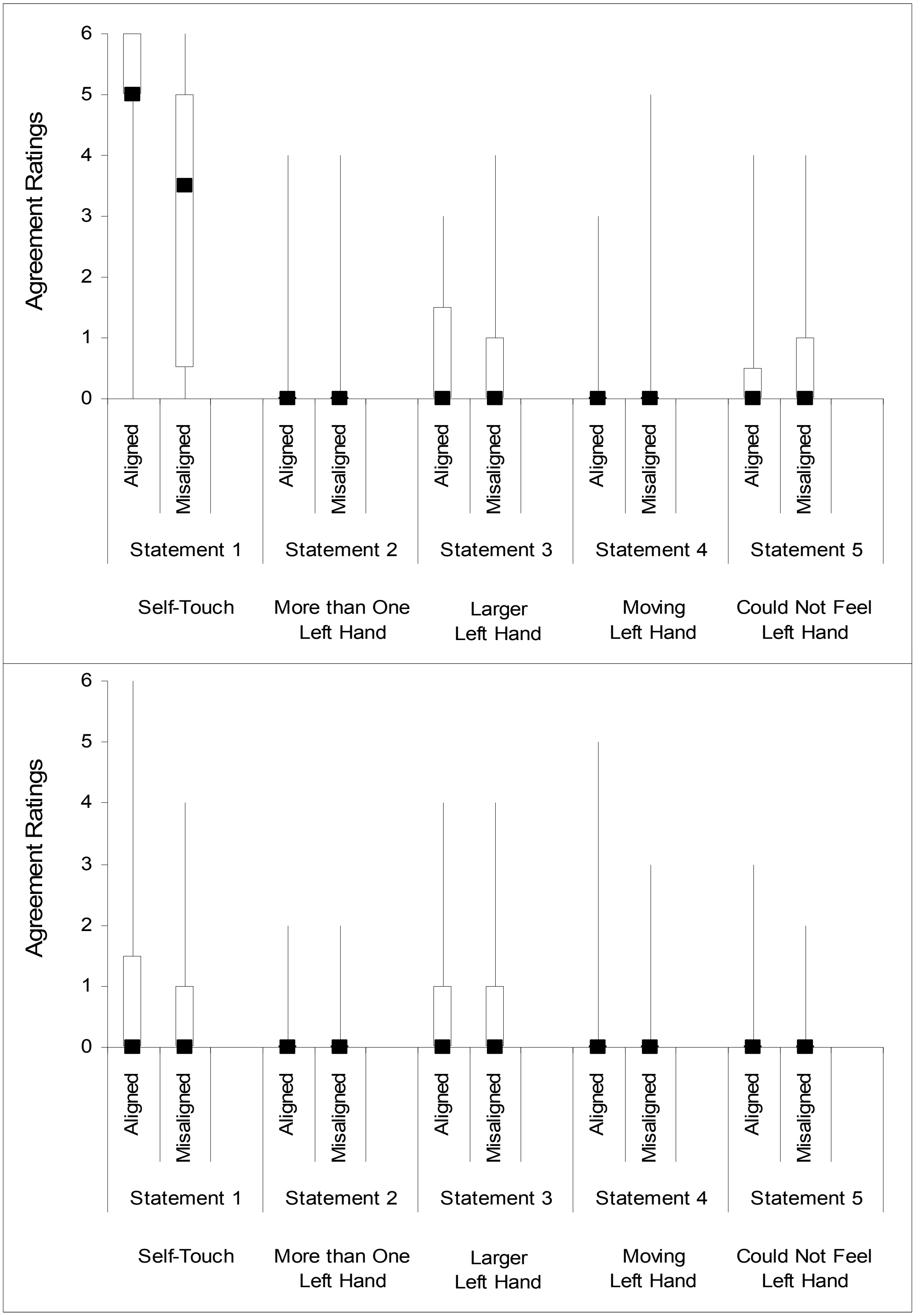

Figure 26. Median agreement ratings for the self-touch illusion questionnaire for synchronous (top panel) and asynchronous (bottom panel) stimulation. The black filled-in square indicates the median value, the box indicates the interquartile range, and the whiskers indicate the full range of responses.

Proprioceptive Drift

A 2x2 within-subjects ANOVA was conducted for proprioceptive drift. The factors were mode of stroking (synchronous, asynchronous) and hand-placement condition (aligned, misaligned). There was a main effect for mode of stroking ($F(1, 15) = 23.282$, $p < .001$, multivariate partial eta-squared = .608) and a main effect for hand-placement condition ($F(1, 15) = 14.115$. $p = .002$, multivariate partial eta-squared = .485), and a mode of stroking by hand-placement condition interaction ($F(1, 15) = 13.189$, $p = .002$, multivariate partial eta-squared = .468). To investigate this interaction, separate two-tailed paired *t*-tests were conducted for synchronous and asynchronous stimulation, with an adjusted alpha level of .025. The results for synchronous stimulation ($t(15) = 4.633$, $p <.001$) indicated that there was greater proprioceptive drift when the hands were aligned compared with misaligned (Aligned $M = 5.81$ cm; Misaligned $M = .94$ cm) (Figure 27, top panel). The results for asynchronous stimulation ($t(15) = 1.409$, $p = .179$) indicated that there was no significant difference in proprioceptive drift in the two hand-placement conditions (Aligned $M = .69$ cm; Misaligned $M = -.50$ cm) (Figure 27, bottom panel).

One-sample two-tailed *t*-tests were used to investigate whether each proprioceptive drift value (synchronous-aligned, synchronous-misaligned, asynchronous-aligned, asynchronous-misaligned) was significantly different from zero; that is, whether each post-trial measurement was significantly different from its (respective) baseline measurement. An alpha level of .0125 was used to adjust for multiple comparisons. The results indicated significant proprioceptive drift from baseline for the synchronous-aligned trial ($t(15) = 6.267$, $p < .001$). The results for the other three trials indicated that there was no significant difference in proprioceptive drift compared to baseline: synchronous-misaligned ($t(15) = 1.431$, $p = .173$); asynchronous-aligned ($t(15) = 1.210$, $p = .245$); asynchronous-misaligned ($t(15) = -.760$, $p = .459$).

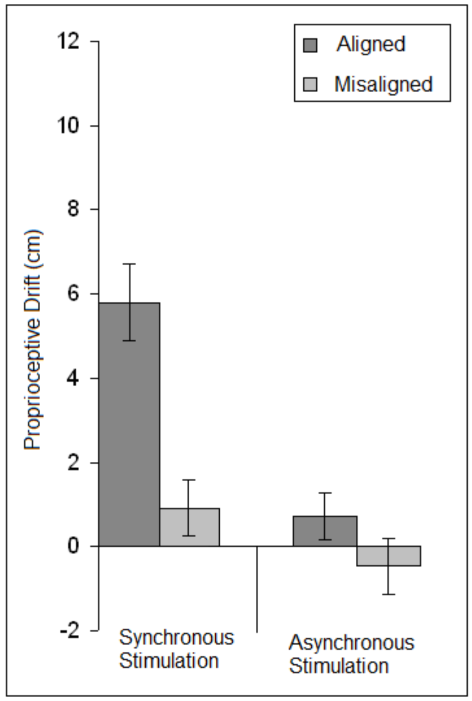

Figure 27. Mean proprioceptive drift (cm) for the aligned hand-placement condition and for the misaligned hand-placement condition, for both synchronous and asynchronous stimulation. Error bars indicate one standard error of the mean.

Time of Illusion Onset

Different numbers of participants reported the onset of the illusion in the two hand-placement conditions with synchronous stimulation: aligned hand-placement condition (n = 15, $M = 20.73$ s); misaligned hand-placement condition (n = 7, $M = 23.00$ s). With asynchronous stimulation, the onset of the illusion was reported in zero of 32 trials. Time of illusion onset was analysed using a two-tailed paired *t*-test. Seven of sixteen participants reported the onset of the illusion in both hand-placement conditions with synchronous stimulation, and these seven were included in the analysis. There was no significant difference in the time of onset between the aligned (*M* = 20.57 s) and the misaligned (*M* = 23.00 s) hand-placement conditions ($t(6) = -.789$, $p = .460$)(Figure 25).

It is interesting to consider time of illusion onset in the hand-placement condition that was common to Experiments 1 and 2; that is, the condition in which the prosthetic hand and the participant's receptive hand were aligned and separated by 15 cm. Visual inspection of Figure 25 indicates that participants were faster to report the illusion of self-touch in the aligned 15 cm condition of Experiment 1 (*M* = 10.31 s) than in the aligned 15 cm condition of Experiment 2 (*M* = 20.57 s) even though the distance between the hands was identical. This is most likely explained by the more predictable stimulation sequence in Experiment 2: stimulation comprised taps and unidirectional strokes to the index finger in Experiment 1 but it comprised only unidirectional strokes in Experiment 2. This view is supported by findings from a study by Armel and Ramachandran (2003), in which participants tested with the visual rubber hand paradigm reported that "the more random and unpredictable the touch (if synchronized), the more vivid the illusion" and that "having their fingers lifted and knuckles pushed was extremely effective in enhancing the illusion, while stroking of the fingers was less effective" (p. 1504). Our reason for using only strokes in Experiment 2 was that the stroke direction provided the best information to the participant about alignment or misalignment of the hands. With vision precluded, taps would not have provided information about alignment.

Discussion

This study provides the first investigation of the effects of distance (15 cm, 30 cm, 45 cm, 60 cm) and alignment (0°, 90°) manipulations on the non-visual illusion of self-touch. We used three methods to assess the illusion of self-touch and our findings demonstrate that the subjective ratings of intensity, and time of onset, of the illusion dissociate from proprioceptive drift. In Experiment 1, with increasing distance between the hands in the *asynchronous*-stimulation condition, participants did not experience the illusion of self-touch but there was proprioceptive drift toward the prosthetic hand. And, in the misaligned synchronous-stimulation condition of Experiment 2, participants did experience the illusion but *without* proprioceptive drift. Given that the assessment methods in this research programme are also widely used in studies investigating the visual rubber hand illusion, the implications of our findings extend beyond the non-visual illusion of self-touch.

In Experiment 1, we manipulated the distance between the prosthetic hand and the participant's receptive hand or, considered differently, the distance between the participant's administering hand and receptive hand. With increasing distance between the hands and synchronous stimulation: (1) illusion ratings diminished, (2) participants demonstrated less proprioceptive drift (as a proportion of the actual distance between the hands), (3) fewer participants reported the onset of the illusion and, among participants who did report onset, greater distance resulted in slower onset of the illusion. The results for the three methods of assessment lead us to conclude that the non-visual illusion of self-touch is sensitive to distance – as was shown for the visual rubber hand illusion by Lloyd (2007).

In Experiment 2, we manipulated the alignment of the prosthetic hand relative to the participant's receptive hand. With misalignment of the two hands and synchronous stimulation:

(1) illusion ratings diminished, (2) proprioceptive drift was abolished, (3) fewer participants reported the onset of the illusion but, among participants who did report onset, misalignment did not result in slower onset of the illusion. The results for the three methods of assessment lead us to conclude that the non-visual illusion of self-touch is sensitive to alignment – as was shown for the visual rubber hand illusion by Pavani et al. (2000), Ehrsson et al. (2004), Tsakiris and Haggard (2005), and Costantini and Haggard (2007). Specifically, our proprioceptive drift results are consonant with previous findings demonstrating that, in the visual rubber hand paradigm, proprioceptive drift is abolished by misalignment between the prosthetic hand and the participant's receptive hand (Costantini & Haggard).

Distance Manipulation

The effects of the distance manipulation in our study are broadly similar to the effects that Lloyd (2007) has shown for the visual rubber hand illusion (although Lloyd did not report proprioceptive drift). Lloyd explains the effects for distance with reference to visuo-tactile bimodal cells in the premotor and parietal cortices. These cells code peripersonal space around the hand, and respond to both visual and tactile characteristics of objects that approach and touch the hand. Lloyd suggests that the visual rubber hand illusion is diminished when the viewed prosthetic hand is positioned outside the visual receptive field surrounding the tactile receptive field of the participant's stimulated hand (beyond approximately 30 cm). The agreement ratings for the illusion statement in our study pattern quite closely with those reported by Lloyd, and with our own additional measure of proprioceptive drift; yet the illusion of self-touch is elicited without vision of the hands. Thus, it is unlikely that our findings can be explained by appeal to *visuo*-tactile bimodal cells.

A possible explanation of the effects of the distance manipulation in our study involves proprioception. When the participant's two hands are separated by only 15cm, a small rotation of the elbow joint would be sufficient to bring the hands into contact. Thus, if the illusion of self-touch involves proprioceptive recalibration, it would require recalibration of the proprioceptively perceived position of just the forearms and hands. But, as the distance between the hands is increased, a large rotation of the shoulder joint (as well as the elbow joint) would be necessary to bring the hands into contact. Thus, the illusion of self-touch would require proprioceptive recalibration of the perceived position of the upper arms, forearms and hands.

Even if the illusion of self-touch does not require full proprioceptive recalibration, the reason why the illusion is diminished with increasing distance between the receptive and administering hands may be that, with the arms outstretched, a substantial amount of proprioceptive information about the actual position of the hands and arms needs to be overridden if a compelling illusion is to emerge.

In our study, the administering right hand and the prosthetic hand are both located at body midline. As the receptive left hand is positioned increasingly far to the left of midline, the shoulder is rotated (abducted in the horizontal plane) and the elbow is more extended. Fuentes and Bastian (2010) reported that, as the elbow approaches the limit of its range (of extension or flexion), estimates of the elbow angle based on proprioception are biased toward the limit; and this effect is greater when the shoulder is abducted. So, when the shoulder is abducted and the elbow extended, proprioceptive evidence against the self-touch hypothesis may even be amplified. We note that Fuentes and Bastian found that elbow angle estimates were less precise when tested directly than when tested with a fingertip-location task (see also van Beers, Sittig, & Denier van der Gon, 1998).

In summary, with increasing distance between the hands, there is stronger proprioceptive evidence against the self-touch hypothesis and this may account for the reduced ratings for the illusion of self-touch.[17]

Alignment Manipulation

The effects of the alignment manipulation on proprioceptive drift in our study are broadly similar to the effects reported by Haggard and colleagues (Costantini & Haggard, 2007; Tsakiris & Haggard, 2005) for the visual rubber hand illusion. But the effects of the manipulation on subjective illusion ratings in our study differ from the effects for the visual rubber hand illusion reported by Pavani et al. (2000) and Ehrsson et al. (2004). The visual rubber hand illusion was not elicited when there was a 90° misalignment between the prosthetic hand and the participant's receptive hand (Pavani et al) or a 180° misalignment (Ehrsson et al.). In contrast, in our study the illusion of self-touch was elicited with a 90° misalignment, although illusion ratings were lower than in the aligned condition. This difference is perhaps not surprising since, in the non-visual self-touch rubber hand paradigm, all mismatches need to be detected using proprioception, which does not share the spatial acuity of vision.

Our dissociation between assessment methods for the illusion of self-touch – agreement ratings *versus* proprioceptive drift – complements the recent finding by Rohde, Di Luca, and Ernst (2011), that subjective ratings of the visual rubber hand illusion dissociate from proprioceptive drift (see also Holmes et al., 2006). Whereas Rohde et al. demonstrated

[17] An explanation of reduced illusion ratings in terms of proprioception may seem to draw additional support from findings that the resolution of joint position sense is better for proximal joints (e.g., shoulder) than for distal joints (Jones, 2000). However, apparently superior resolution (e.g. for the elbow over the thumb) when accuracy is assessed directly in terms of rotation of the joint may be reversed (for the same data) when accuracy is assessed in terms of the consequences of joint rotation for displacement of an extremity (e.g., the tip of the thumb) (De Domenico & McCloskey, 1987).

proprioceptive drift toward a viewed hand in two conditions (asynchronous stimulation, no stroking: vision-only condition) in which participants did not experience ownership of the viewed prosthetic hand, we demonstrate the reverse dissociation using the non-visual paradigm – the illusion of self-touch in the absence of significant proprioceptive drift. (Indeed, we actually show a double dissociation, because in three of the asynchronous-stimulation conditions of Experiment 1 [30 cm, 45 cm, 60 cm], participants demonstrated significant proprioceptive drift without the accompanying illusion of self-touch.)

It may be possible to achieve a better understanding of the illusion of self-touch and its robustness against the alignment manipulation if we consider the illusion alongside the phenomenon of self-touch attenuation: self-touch is experienced as being less intense than identical stimulation that is externally produced (e.g., Bays, Flanagan, & Wolpert, 2006; Bays, Wolpert, & Flanagan, 2005; Blakemore, Wolpert, & Frith, 1998; Blakemore, Frith, & Wolpert, 1999; Blakemore, Wolpert, & Frith, 2000; Claxton, 1975; Weiskrantz, Elliot, & Darlington, 1971). Self-touch attenuation is explained in terms of motor prediction (Wolpert & Flanagan, 2001) and the cancellation or attenuation of predicted components of sensory input. Any unpredicted residue provides information about events in the external environment.

Self-touch attenuation occurs when the individual is fully in control of the movement and also when the individual is being guided to administer stimulation (Weiskrantz et al., 1971) as was the case in the current experiments. In some studies, self-touch attenuation has been investigated using a set-up that is very closely matched to the self-touch rubber hand paradigm. In a study by Blakemore et al. (1999), the participant's administering and receptive hands were not in direct contact. The participant held a cylindrical object in her administering hand and, as she moved the cylindrical object, information was transmitted to a robotic device, which administered stimulation to the participant's receptive hand. We can think of the cylindrical object as being similar to the paintbrush in the participant's administering hand (in our study), and the robotic device as being similar to the paintbrush that the Examiner used to administer stimulation to the participant's receptive hand.

In the Blakemore et al. (1999) study, as in ours, movements of the participant's administering hand coincided in timing and alignment with stimulation on the participant's receptive hand. The participant rated touch on her receptive hand on the dimensions of tickliness, intensity, and pleasantness, and self-produced touch was perceived as less tickly, less intense, and less pleasant than externally-produced touch. (In the externally-produced condition, the robotic device was programmed to administer touch to the participant's receptive hand but the participant did not move the cylindrical object in her administering hand.)

In a highly relevant manipulation, Blakemore et al. (1999) varied the direction of stimulation: trajectory rotations of 30°, 60°, and 90° were introduced between the movement made by the participant's administering hand and the movement made by the robotic device. The condition using the 90° trajectory rotation is most similar to the misaligned condition of our Experiment 2. In this condition, ratings for tickliness were significantly higher than in the aligned condition and not significantly different from the externally-produced condition. For intensity and pleasantness there was only a non-significant trend to higher ratings as misalignment increased.

It would potentially be illuminating to explore whether the sensation of touch on the participant's receptive hand is experienced as less intense, for example, in various conditions in which the illusion of self-touch is elicited and, specifically, in the misaligned condition. If sensory attenuation reliably co-occurs with the illusion of self-touch then we should investigate the causal relationship between the two phenomena and the role, in each, of the predictability – on the basis of the participant's actions with her administering hand – of the otherwise fairly unpredictable stimulation on her receptive hand. One apparent possibility, for example, would be that predictability of the felt touches leads directly to sensory attenuation and that this, in turn, functions as evidence in support of the self-touch hypothesis, outweighing the evidence against the hypothesis provided by misalignment (or distance).

CHAPTER 8: ANATOMICAL CONSTRAINTS ON THE ILLUSION OF SELF-TOUCH

A self-touch paradigm is used to create the illusion that one is touching one's own left elbow when one is actually touching the Examiner's arm. Our new illusion of self-touch is sensitive to the anatomical structure of the body: you can touch your left elbow with your right index finger but not with your left index finger. Illusion onset was faster and illusion ratings were higher when participants administered touch using the plausible right index finger compared with the implausible left index finger.

There is a simple experimental procedure that can be used to create the illusion that one is touching one's body when one is actually touching another person. The Examiner guides the blindfolded participant to touch another person while the Examiner administers corresponding touch to the participant's body. Previous studies have used this elegant paradigm to create (1) the illusion that the individual is touching her nose when she is touching another person's nose (Ramachandran & Hirstein, 1997), and (2) the illusion that the individual is touching her hand when she is touching a prosthetic hand (Ehrsson et al., 2005). Here we investigate whether the illusion of self-touch is sensitive to the anatomical structure of the body. It is physically impossible to touch one's left elbow with one's left index finger but will this have an impact on the illusion that the individual is touching her left elbow?

Experiment

Method

Participants

Sixteen participants (14 females and 2 males; 18-30 years, *M* = 21.19 years) were assessed following a protocol approved by the University of Oxford Research Ethics Committee and in accordance with the ethical standards laid down in the 2008 Declaration of Helsinki.

Procedure

The participant was seated at a table with her *eyes closed*, her forearms resting on a testing unit (30 cm length x 25 cm width x 13 cm height) and her hands extended in front of her body. The Examiner positioned her left forearm so that it extended horizontally in front of the participant's two hands. The Examiner administered unidirectional strokes to the inner part of the participant's left elbow. In the anatomical-plausible condition the participant used her right index finger to administer strokes to the Examiner's forearm (Figure 28a), and in the anatomical-implausible condition the participant used her left index finger (Figure 28b). The participant's arms and hands were in an identical position in the two conditions; the only difference was whether it was the participant's right or left index finger that was moving. The stimulation administered by the Examiner to the participant's elbow was either *synchronous* or *asynchronous* with stimulation administered by the participant to the Examiner's forearm. Each trial was 60 s in duration, and the order of the trials was randomised across participants.

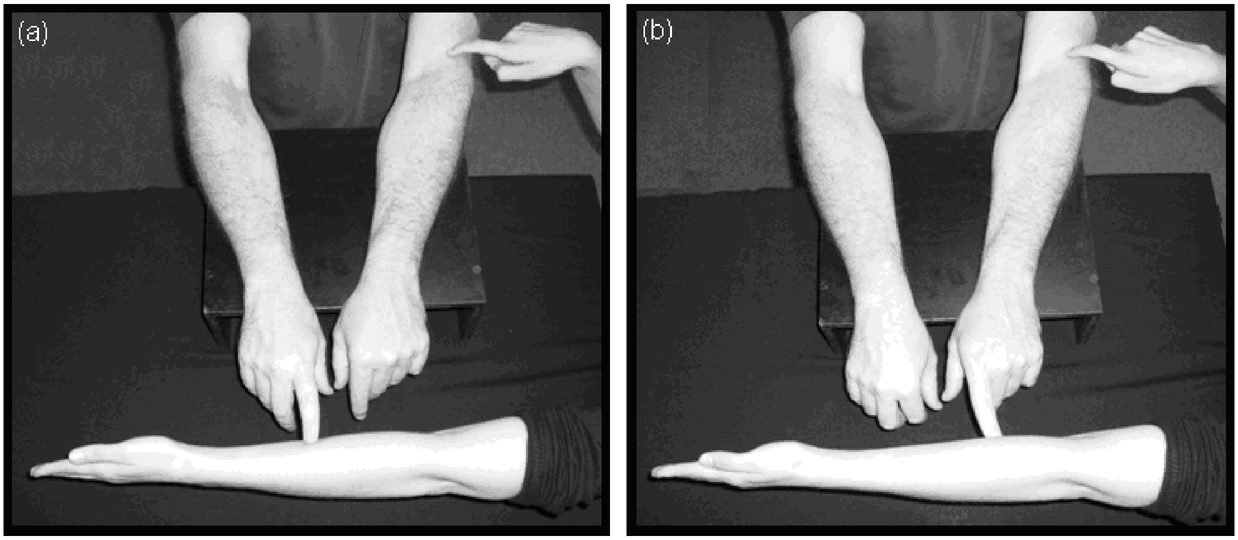

Figure 28. Experimental set-up for (a) the plausible right-index-finger condition and (b) the implausible left-index-finger condition. Note that both arms are outstretched, which makes (finger-to-elbow) self-touch physically impossible in both conditions. Therefore, the plausibility being tested concerns the anatomical structure of the body rather than the position of the participant's arms and hands in this experiment.

Results

Time of Illusion Onset

We timed the onset of the illusion by asking the participant to inform the Examiner when she agreed with the statement "It feels as if the touch on my left elbow is from my own index finger". The participant was reassured that she should not feel any pressure to report this experience. With one exception, participants did not report the onset of the illusion with asynchronous stimulation. A paired *t*-test was conducted for the 11 participants who reported the onset of the illusion in both the plausible- and the implausible-synchronous conditions.[18]

[18] Illusion onset was reported by 13 participants in the plausible-synchronous (right-index-finger) condition (M = 21.38 s) and 12 participants in the implausible-synchronous (left-index-finger) condition (M = 31.08 s).

Participants were quicker to report the illusion in the plausible right-index-finger condition (*M* = 20.36 s, SEM = 3.803) compared with the implausible left-index-finger condition (*M* = 30.09 s, SEM = 4.00 s) ($t(10) = 2.854$, $p = .017$, two tailed).

Illusion Questionnaire

Following each trial, the participant indicated agreement (0 = *not at all*; 1 = *slightly agree*; 3 = *moderately agree*; 5 = *strongly agree*; 6 = *very strongly agree*) with the five statements listed in Figure 29. The order of the five statements was randomised across participants and trials. Statement 1 assessed the illusion of self-touch and Statements 2 to 5 were control statements. (Visual inspection of Figure 29 confirms that there were low agreement ratings for the control statements.) Ratings for Statement 1 were analysed using individual Wilcoxon Signed-Rank Tests. With synchronous stimulation, participants provided higher agreement ratings in the plausible right-index-finger condition (*Md* = 4.5) compared with the implausible left-index-finger condition (*Md* = 1.5); (Comparison 1: $z = -2.286$, $p = .022$).

Two further comparisons indicated that agreement ratings were higher for synchronous compared with asynchronous stimulation, both in the plausible right-index-finger condition (*Md* = 4.5 versus *Md* = .0; Comparison 2: $z = -3.420$, $p = .001$) and in the implausible left-index-finger condition (*Md* = 1.5 versus *Md* = 0; Comparison 3: $z = -3.331$, $p = .001$). (Asynchronous-stimulation conditions were included as a baseline for the illusion of self-touch.)

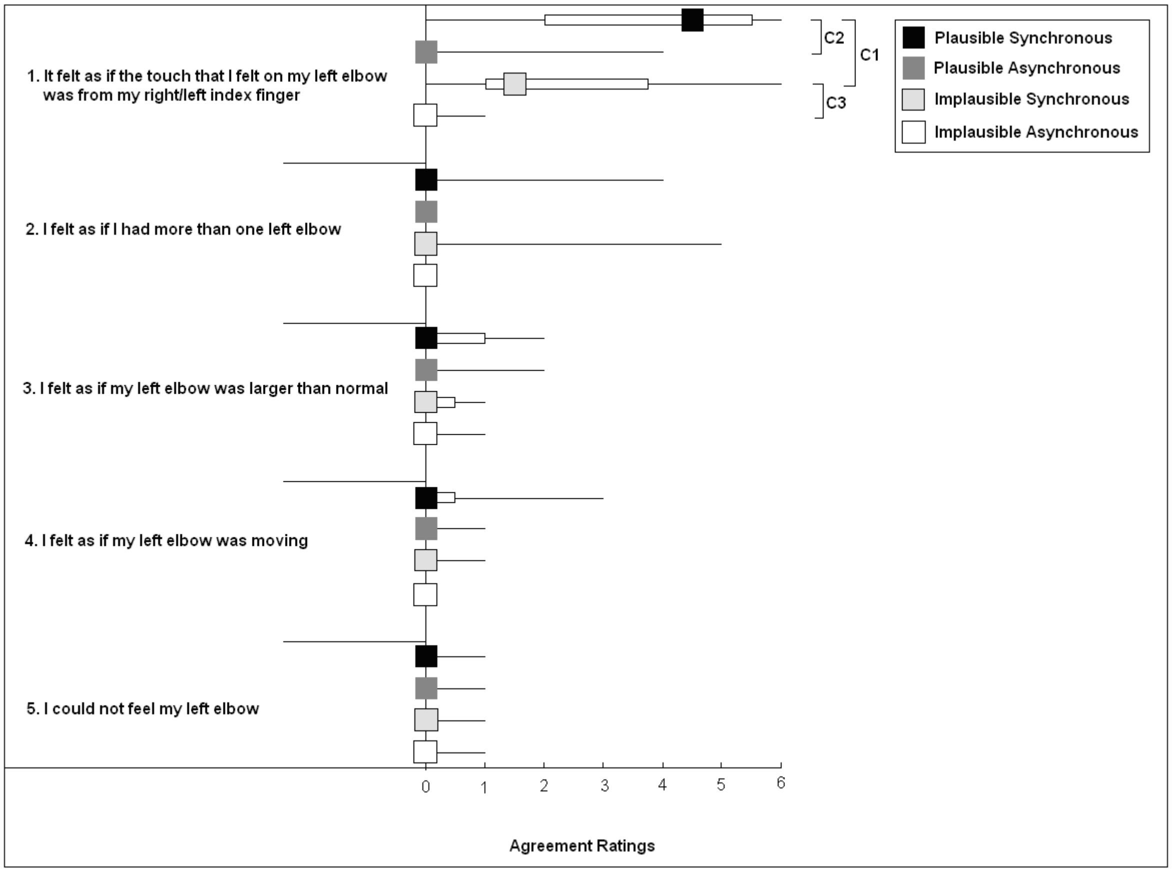

Figure 29. Median agreement ratings for the self-touch illusion questionnaire. The square (black, dark grey, light grey, white) indicates the median value, the box indicates the interquartile range, and the whiskers indicate the full range of responses.

C1: Comparison of plausible and implausible conditions for synchronous stimulation;

C2: Comparison of synchronous and asynchronous stimulation in the plausible conditions;

C3: Comparison of synchronous and asynchronous stimulation in the implausible conditions.

Discussion

Our new illusion of self-touch is sensitive to the anatomical structure of the body. The participant was faster to report the illusion that she was touching her own left elbow when she was administering touch with the right index finger compared with when she was administering touch with the left index finger. Similarly, administering touch with the right index finger resulted in higher agreement ratings for the illusion statement on the questionnaire. But while the illusion was diminished by anatomical implausibility, it was not abolished. The participant experienced the illusion that there was contact between her left index finger and her left elbow despite the fact that these body parts had never (and could never) come into contact in real life (for other implausible illusions see Lackner, 1988; Ramachandran & Rogers-Ramachandran, 1996).

To elicit this novel illusion, the Examiner touched the participant's elbow as the participant touched the Examiner's forearm. The Examiner kept time with the participant's unidirectional stroke, and withdrew her finger from the participant's skin at the moment that the participant withdrew her finger from the Examiner's skin. We can explain the illusion and its sensitivity to the anatomical structure of the body in Bayesian terms. The temporal correspondence between the action of the participant's administering index finger and the sensation on the participant's receptive left elbow was consistent with the participant's index finger and elbow being in the same location. In Bayesian terms, the *likelihood* – the probability of the sensory input given the hypothesised state (index finger and left elbow in the same location) – was high for both the right index finger and the left index finger. However, the *prior* probability of the hypothesised state (index finger and left elbow in the same location) independent of sensory input was higher for the right index finger than for the left index finger.

Bayes rule estimates the posterior probability of a hypothesis by multiplying the likelihood by the prior probability of the hypothesis (and normalising). The percept is the hypothesised state of the perceptual system that has the highest posterior probability. Within a Bayesian framework, the illusion of self-touch was elicited because, given the sensory input, the probability that the index finger (right or left) and the left elbow were in the same location was higher than the probability that they were in different locations. The illusion of self-touch was attenuated when the *left* index finger was used because of the low prior probability of the left index finger and the left elbow being in the same location. The fact that the illusion was experienced at all in the implausible condition indicates that this prior probability was not zero, and moreover, that the likelihood was sufficiently high to compensate for the low prior probability of self-touch.

CHAPTER 9: GENERAL DISCUSSION

The thesis had two main aims. The first aim was to use the self-touch rubber hand paradigm to investigate self-touch enhancement in patients following stroke. The second aim was to provide a systematic investigation of the constraints on the illusion of self-touch. The thesis achieved these two main aims, and during the course of the project, unexpected findings inspired additional experiments and new lines of enquiry. Most notably, during the investigation of the constraints on the illusion of self-touch, a new interpretation for how the participant experiences the illusion came to light. This interpretation was followed up in two experiments that were not anticipated in the original plan of research. The General Discussion is divided into two main sections. Part One considers the experiments investigating self-touch enhancement following stroke (Chapters 2 and 3). Part Two considers the experiments investigating the illusion of self-touch, first the chapters that provided a new interpretation of the illusion of self-touch (Chapters 4, 5, and 6), and second, the chapters that investigated the constraints on the illusion of self-touch (Chapters 4, 7, and 8). The General Discussion concludes with a summary of the contributions of this thesis and a brief prospectus for further research.

Part One: Self-Touch Enhancement Following Stroke

In the first two empirical chapters of the thesis (Chapters 2 and 3), the self-touch rubber hand paradigm (Ehrsson et al., 2005) was used to investigate self-touch enhancement in patients following right-hemisphere stroke. To recap briefly, two previous research programmes (Valentini et al., 2008; Weiskrantz & Zhang, 1987) had demonstrated that, following stroke (particularly right-hemisphere stroke: Valentini et al.), some patients who are unable to detect stimulation on the affected hand when it is administered by the Examiner, are able to detect stimulation of the same intensity when it is self-administered. The first objective of this thesis was to distinguish explanations for self-touch enhancement based on feeling from explanations based on knowledge. It was important to establish whether patients have residual sensation that is evident under conditions of self-touch, or alternatively, whether patients use information about the relative position of their two hands – proprioceptive information – to infer that they are being touched.

The results of the experiments presented in Chapter 2 (and Chapter 3) allow us to discount an interpretation for self-touch enhancement based on knowledge. Patients demonstrated self-touch enhancement under conditions of the self-touch rubber hand paradigm; when they were administering touch to a prosthetic hand and receiving synchronous touch from the Examiner (Chapter 2: Experiment 3). With this set-up, patients could not infer touch based on the relative position of their two hands (administering and receptive), because they were administering touch and receiving touch in two distinct spatial locations. Patients did not report touch on sham trials in which they were guided to administer touch to the prosthetic hand, but no touch was administered (by the Examiner) to the patient's affected hand. And patients continued to show self-touch enhancement when the movements of the administering hand were held to a minimum so that the patient could not use subtle movements of the administering hand (relative to the prosthetic hand) to deduce the digit of his or her own hand that was receiving stimulation (Chapter 2: Experiment 4). The results thus suggest that patients have residual sensation that is evident under conditions of self-touch. Having discounted an explanation for self-touch enhancement in terms of patients using proprioceptive information to *infer* touch, the experiments moved to investigating alternative explanations for the effect.

Valentini et al. (2008) suggested that self-touch enhancement may represent a type of attentional modulation: the administering hand may act like an *attentional wand* directing the patient's attention to the affected hand. The metaphor of the hand as an attentional wand garners support from empirical work investigating the role of the body in spatial attention. Reed et al. (2007) reported that when the hand is in action – as is the case when a patient self-administers touch – attention shifts to the "functional spatial range of the action" (p. 51). But, patients in the current experimental series continued to demonstrate self-touch enhancement when the prosthetic hand was positioned in the right hemispace, and the patient's affected hand was positioned in the left hemispace (and vice versa), so that the patient's administering hand-action was in the opposite hemispace to the touch on her affected hand (Chapter 2: Experiment 5).

The reader may wonder whether the self-touch rubber hand paradigm elicited *mislocalisation* of either one or both of the patient's two hands, with the result that it seemed to the patient that her receptive hand *was* located within the functional spatial range of the administering hand action. Although it is possible that patients experienced proprioceptive mislocalisation, this would not explain self-touch enhancement in Experiment 5. To experience this type of proprioceptive mislocalisation, the patient would need to be experiencing the illusion of self-touch, and to experience this illusion the patient would need to feel the stimulation on the affected hand. Stated differently, the patient would need to feel the stimulation on her affected hand before she could possibly mislocalise either one or both hands, so as to perceive the receptive hand as falling within the functional spatial range of the administering hand action. Notably, all four patients detected the first stimulation in the left and right hemispace conditions of Experiment 5, before proprioceptive mislocalisation could possibly have occurred. Thus, we believe that the findings of Experiment 5 argue against an explanation for self-touch enhancement in terms of the administering hand acting like an attentional wand and directing attention to the functional spatial range of the action. However, a subsequent experiment conducted with one of our four patients indicated that the administering hand action modulated attention in other (non-spatial) ways.

The final experiment in Chapter 2 (Experiment 6) highlighted a role for temporal expectation in self-touch enhancement. When Patient NG's stimulation of the prosthetic hand preceded the Examiner's stimulation of Patient NG's receptive hand (by approximately 1 s), she no longer demonstrated self-touch enhancement. One possible interpretation is that patients are better at detecting self-administered touch (compared with Examiner-administered touch) because they use the action of the administering hand to focus attention at a precise moment in time. On this interpretation, the patient's involvement transforms the testing conditions. Whereas the Examiner-administered sensory assessment requires patients to sustain attention over a long time window, the self-administered sensory assessment comprises cues indicating the precise moment at which maximal attention is required. This is important because uncertainty about the temporal occurrence of a stimulus diminishes perceptual processing (Rolke & Hofmann, 2007) and temporal cues improve perceptual processing (e.g., Correa, Lupiáñez, & Tudela, 2005).

For patients with right-hemisphere damage, temporal cues may be particularly valuable, given that the right hemisphere is thought to have a special role in tasks involving *sustained* somatosensory attention. The role of the right hemisphere in tasks involving sustained somatosensory attention was first demonstrated in a positron emission tomographic (PET) study by Pardo et al. (1991). Participants focused attention on either their right big toe or their left big toe. Over a period of 40 s, the toe was repeatedly stimulated with a von Frey filament at 3-5 Hz. Approximately every 10 s, there was a period of 1 to 3 s, in which no stimulations were administered. The participant's task was to report how many times there was a pause in stimulation. Regardless of whether the participant was monitoring the right or the left big toe, the task resulted in increased blood flow in the *right* prefrontal and right superior parietal cortices. The same activation was apparent when participants performed a visual sustained attention task. Pardo et al. suggested that these patterns of activation were consistent with there being a right frontal and parietal network involved in "sustained attention to sensory input" (p. 63). In support of this proposal, several researchers have demonstrated sustained attention deficits in patients with damage to the right hemisphere (e.g., Rueckert & Grafman, 1996; Sturm & Willmes, 2001; Wilkins, Shallice, & McCarthy, 1987, for a review see Husain & Rorden, 2003). Perhaps most relevant is work by Wilkins et al. showing that patients with damage to the right frontal lobe (in this case unilateral neocortical removal for intractable epilepsy) are impaired at tasks requiring sustained attention to tactile events on the body.

We have proposed that temporal expectation provides a possible explanation for self-touch enhancement. It may also help to explain Valentini et al.'s (2008) finding that self-touch enhancement is more common following right-hemisphere stroke. Patients who have had a right-hemisphere stroke may be impaired on the Examiner-administered sensory assessment specifically because it requires that they sustain attention to unpredictably-timed stimulation occurring on the body. By involving the patient in the administration of stimulation, the task becomes less about sustaining attention and more about orienting attention to precise moments in time. In effect, the patient's involvement changes the attentional demands of the task, and this change may benefit patients with deficits of sustained somatosensory attention, which is more common following right-hemisphere stroke.[19]

It will be interesting for future studies systematically to investigate temporal expectation as an explanation for self-touch enhancement; first to replicate the finding in a larger group of patients, and second to vary the patient's involvement in generating the temporal cues. One possibility is that patients will demonstrate self-touch enhancement irrespective of whether their own action generates the temporal cue; for example, if the Examiner were to signal impending

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[19] On this view, self-touch enhancement is infrequent following left-hemisphere stroke because, among left-hemisphere stroke patients, the failure to report Examiner-administered stimulation is generally not accounted for by problems with sustained somatosensory attention. Thus, the patient does not benefit from the reduced attentional demands of the self-administered stimulation condition.

stimulation with a bell, the patient may use this auditory cue to focus attention to a precise time point. An alternative possibility is that patients will only demonstrate self-touch enhancement when the temporal cue is bound up in a *motor command*. It will be important to identify the types of cues that are effective, as these will no doubt have an important role in sensory rehabilitation following stroke. It will also be valuable to collect independent evidence demonstrating that patients who show self-touch enhancement have impaired sustained somatosensory attention. This evidence will provide further support for the temporal expectation hypothesis.

An Unexpected Finding: Improved Localisation in Patient NG

Part One of the thesis was primarily concerned with tactile *detection* following stroke; the patient's report of self-administered compared with Examiner-administered stimulations. But we also collected information about tactile *localisation*; the patient's capacity to localise sensation to the digit that received stimulation. During one patient's sensory assessment, a surprising pattern of sensory mislocalisations came to light. Chapter 3 reported an intensive series of experiments evaluating Patient NG. Under standard conditions of Examiner-administered touch, Patient NG detected 9 of 40 stimulations administered to the little and ring finger of her affected left hand (Chapter 3: Experiment 1a). Under standard conditions of self-administered touch, Patient NG detected significantly more stimulations, 29 of 40, on these affected fingers (i.e., self-touch enhancement), but she systematically mislocalised this touch and reported feeling it on the neighbouring rightward finger (Chapter 3: Experiment 1b). Systematic sensory mislocalisations are proposed to result from a compressed perceptual representation of the affected body part (see Rapp et al., 2002), and Patient NG's results were consistent with an impaired and compressed representation of the left side of her affected left hand.

Patient NG exhibited a significant improvement in stimulus localisation in some of the conditions using the self-touch rubber hand paradigm, specifically when she was required to reach (leftward) over and beyond the impaired region (i.e., the ring and little finger) of her affected left hand to administer touch to the prosthetic hand (Chapter 2: Experiments 2a, 2b, 3, and 4). This was true whether the patient's affected left hand was positioned in the left hemispace or in the right hemispace, and similarly, whether NG reached into the left or into the right hemispace to administer touch to the prosthetic hand. This was an unanticipated, yet important, finding. Although patients who systematically mislocalise touch have been described in the literature (e.g., Rapp et al., 2002), the current thesis presented the first instance of a temporary remission in this particular sensory deficit.

To account for the improvement in performance, two possible explanations were put forward. Patient NG may have experienced a *subjective leftward elongation* of her affected hand when she reached leftward over her affected hand to administer touch to the prosthetic hand. This subjective leftward elongation would make sense of Patient NG's experience of self-touch when her right hand was reaching beyond the spatial position occupied by her receptive left hand. In turn, the subjective leftward elongation of the affected hand may have prompted an expansion of the compressed left side of Patient NG's perceptual representation of her hand, which would explain the improvement in stimulus localisation.

This interpretation was purely speculative. One limitation of the current work is that I did not collect information about how the patient perceived her body during the assessment; for example, whether it seemed to the patient that she *was* touching her own hand, and whether it seemed to the patient that her left hand was elongated. In one of the conditions using the self-touch rubber hand paradigm, Patient NG remarked that the condition was easier (than the Examiner-administered stimulation condition) because "when I am touching my own hand I find it easier to concentrate". That Patient NG referred to the experience of touching her own hand suggests that she was experiencing the illusion of self-touch, but it would have been valuable to verify this using a systematic questionnaire. Patient NG did not allude to a subjective experience of having an elongated hand. However, it is noteworthy that the Experiments presented in Chapters 6 and 7 demonstrated that neurologically healthy participants perceived that the receptive left hand was "larger than normal" when they experienced the illusion of self-touch[20]. This finding fits with the account that we are putting forward. Also of relevance is a prior study by Schaefer et al. (2007) in which the illusory elongation of the participant's arm was associated with dynamic modulations to the topography of the primary somatosensory cortex. The study by Schaefer et al. is important because it confirms that the illusory elongation of a body part can have an immediate effect on the way that the body is represented in the brain.

A second possible explanation for Patient NG's improvement aligns the self-touch rubber hand paradigm with *prism adaptation*. Prismatic lenses displace the visual field to the left or to the right. As the participant adapts to the lenses, she is required to point to objects. When the participant is wearing rightward-displacing prismatic lenses, the object will appear to be further to the right than is the case. Therefore, the participant will initially make rightward pointing errors (Phase 1: Pre-adaptation). However, the participant rapidly adjusts to this displacement, 'learning' that she must point to the left of where she perceives the object in order to touch it. Thus, there is a realignment of the participant's visual and proprioceptive-motor spatial coordinate systems (Phase 2: adaptation). When the prismatic lenses are removed, the participant's pointing errors are in the opposite direction; that is, to the left of the object (Phase 3: Post-adaptation). And, when asked to point to the 'subjective straight ahead' without vision, the participant points

[20] A positive agreement rating for this statement was provided by more than half of all participants (54%) who took part in the experiment presented in Chapter 6, and nearly all participants (82.14%) who took part in Experiment 1 of Chapter 7.

toward the left (e.g., Berberovic, Pisella, Morris, & Mattingley, 2004). A particularly relevant study by Maravita et al. (2003) has shown that prism adaptation can reduce tactile inattention in patients following right-hemisphere stroke. Four patients took part in a sensory assessment. Prior to prism adaptation, all four patients demonstrated tactile extinction: they were impaired at detecting touch on the index finger of the left hand when the index finger of the right hand was also being stimulated (i.e., under conditions of bilateral stimulation). After prism adaptation, all four patients demonstrated a significant improvement in their detection of touch on the left index finger under conditions of bilateral stimulation. The researchers suggested that prism adaptation may have "influence[ed] the high-level, multimodal representations associated with spatial attention" (p. 1831).

The self-touch rubber hand paradigm may have influenced Patient NG's representation of her affected left hand in a similar way. To touch her own hand, or more correctly, to experience the illusion that she was touching her own hand, the patient reached to the left of its proprioceptively perceived position. There are important parallels with Phase 2 (adaptation) in the prisms example presented above. In the adaptation phase with prisms, there is a realignment of the participant's visual and proprioceptive-motor spatial coordinate systems: the participant learns to point to the left of where she perceives the visual object in order to touch it. We suggest that in the adaptation phase of the self-touch rubber hand paradigm, there is realignment of the patient's tactile and motor-proprioceptive coordinate systems: the patient points to the left of where she perceives her hand to in order to 'touch it', or at least, to experience the illusion that she is touching her own hand. This realignment may be sufficient to improve sensory localisation. As noted in Chapter 3, this is a finding with potential clinical implications. The self-touch rubber hand paradigm may provide an alternative to prism adaptation for use in rehabilitation following stroke, and given that the paradigm does not require the specialist equipment of prism adaptation, it is perhaps more likely to be implemented.

Implications for Rehabilitation

Together, the results from Chapter 2 (the group study) and Chapter 3 (the case study) highlight the usefulness of the self-touch rubber hand paradigm in the assessment of sensation, understanding of self-touch enhancement, and potentially, the rehabilitation of sensation following stroke. The paradigm creates an experience that is closely matched to the conditions of actual self-touch. But, because the patient is administering and receiving touch in distinct locations, it is possible to manipulate different aspects of the self-touch experience; that is, to deconstruct systematically the different elements of self-touch that may account for self-touch enhancement. For example, the Examiner can manipulate the location of the patient's two hands, the Examiner can hold potentially-informative movements of the patient's administering hand to a minimum, and the Examiner can disambiguate the timing of stimulation that the patient administers and receives. An exciting twist is that the paradigm is not only useful for answering questions about the conditions in which self-touch enhancement occurs, it may also have a role in sensory rehabilitation following stroke. The intensive case study with Patient NG highlights the fact that, for some patients, it may be possible to use the paradigm to improve aspects of the patient's sensory performance (e.g., localisation).

The confirmation that patients *feel* rather than infer self-administered touch has important clinical implications. Patients have residual sensation that should be targeted in post-stroke sensory rehabilitation. In general, sensory rehabilitation does not receive much attention in the post-stroke recovery period (Connell, 2007). Motor rehabilitation is prioritised in formal rehabilitation programmes, and in many cases, patients do not receive any rehabilitation for their sensory impairments. This is surprising given that sensory impairments have a negative impact on motor recovery (see Kusoffsky, Wadell, & Nilsson, 1982; Smania, Montagnana, Faccioli, Fiaschi, & Aglioti, 2003). It has been suggested that patients with impaired sensation may "lack the urge to move" or "not know how to move limbs or segments of limbs which they do not feel properly" (Bobath, 1990, p. 25). Thus, the importance of directing attention to sensory rehabilitation following stroke cannot be underestimated. It will be interesting for future work systematically to build self-touch into sensory rehabilitation for patients following stroke. At the very least, self-touch may lead to improved sensory function; ideally, it may also enhance motor recovery following stroke.

Implications for Theory: Anosognosia for Somatosensory Impairments

At first glance, self-touch enhancement seems like a wholly positive phenomenon; the patient has residual sensory function and this may be targeted in the rehabilitation setting. The flip side is that the patient may *underestimate* her sensory impairment because sensation is adequate when the patient self-administers stimulation. As a result, the patient may be at risk of sustaining an injury. This potential problem has not been discussed in the literature on self-touch enhancement. However, its consideration flags a second literature base that is relevant to the current discussion; namely, the literature on anosognosia for somatosensory impairments.

The term *anosognosia* translates as lack (a-) of knowledge (-gnosia) of disease (-noso-). Anosognosia is most commonly investigated in the context of post-stroke motor impairments; for example, a patient who has anosognosia for hemiplegia may claim that she can move her left arm when in reality her left side is completely paralysed as a result of her right-hemisphere stroke.

In recent years, researchers have also turned their attention to anosognosia for somatosensory impairments. A patient with this type of anosognosia may claim that she does not have problems detecting touch administered to her affected limb, and yet, on subsequent testing the patient may fail to detect touch administered by the Examiner (Marcel, Tegnér, & Nimmo-Smith, 2005; Spinazzola, Pia, Folegatti, Marchetti, & Berti, 2008). Here I propose that the patient may claim that she does not have problems detecting touch, quite simply, because she experiences self-touch enhancement (or visual enhancement of touch), precluding the straightforward discovery of the somatosensory impairment.

In a structured interview to assess awareness or unawareness of somatosensory impairment, a patient may be asked "How is the sensation in your arms and legs?"; "Do you have any problems feeling things touching you on either of your arms (or legs) (Marcel et al., 2004, p. 40)?" With vision of the limbs precluded, the patient is then asked to detect and report light touch administered to the hands or to the feet. A diagnosis of anosognosia is given if the patient's prior belief about her capacity to detect light touch substantially overstates her performance on the assessment. In a study conducted by Marcel et al., this interview format was used to demonstrate (1) unawareness of impaired touch sensation in the hands of 66% of right-hemisphere patients and 38% of left-hemisphere patients, and (2) unawareness of impaired touch sensation in the feet of 66% of right-hemisphere patients and 19% of left-hemisphere patients.

Marcel et al. (2004) suggested that "long-term knowledge of having a problem in sensation… can be derived from visually monitoring one's performance" (p. 32). They note that there is no single explanation that accounts for all cases of anosognosia, but in some cases, there may be "an impairment of body-specific self-monitoring" (p. 37). A failure of self-monitoring may provide one possible explanation of anosognosia for somatosensory impairments but, as this thesis demonstrates, self-monitoring itself may lead the patient to the incorrect conclusion about her sensory impairment. Some patients demonstrate enhanced tactile detection under conditions permitting visual feedback (Halligan et al., 1996, 1997; Rorden et al., 1999; Serino et al., 2007), which means that visual self-monitoring will not aid the patient in discovering her somatosensory impairment. Similarly, some patients are better at detecting self-administered touch (compared with Examiner-administered touch), which means that checking sensation through self-touch will also lead the patient to the incorrect conclusion.

In a second recent study investigating anosognosia for somatosensory impairments, Spinazzola et al. (2008) assessed four right-hemisphere stroke patients. Awareness of somatosensory impairments was assessed by asking the patients the following questions: "How is sensation in your arm (leg)?; Are you able to perceive a light touch on your left hand (foot)?" (p. 924). Sensation was assessed following these questions. With eyes closed, the patient received forty randomised stimulations (10 to the left hand; 10 to the right hand; 10 to the left foot; 10 to the right foot). Patients were required to report when they were touched, and they were also required to indicate whether the touch was on the left or the right side of the body. Patients were classified as having a severe *sensory impairment* if they detected fewer than five stimulations to either the contralesional hand or the contralesional foot. Patients were classified as having *anosognosia* if their original response to the Examiner's questions about sensation (e.g., Are you able to perceive a light touch on your left hand [foot]?) overestimated the actual performance on the assessment of sensation. Using this method, Spinazzola et al. found that three of the four right-hemisphere patients demonstrated anosognosia for their somatosensory impairment.

In their discussion of anosognosia for somatosensory impairment, Spinazzola et al. (2008) suggest that patients fail to distinguish "between an imagined sensation and a real, physical one" (p. 919). Here it is assumed that a patient's capacity to report unwatched Examiner-administered stimulation is representative of that patient's capacity to detect stimulation under *all* conditions.

But if patients *can* feel touch under certain testing conditions (e.g., with vision permitted or when they self-administer touch), they presumably report that they are able to perceive light touch based on experience in these conditions, and not because they are unable to distinguish "between an imagined sensation and a real, physical one" (p. 919). To demonstrate that a patient was indeed unable to distinguish imagined and real sensation, Spinazzola et al.'s experiment would need to take a different format. Rather than asking the patient whether she is able to feel touch *prior* to administering the stimulation, the Examiner would need to ask the patient whether she is feeling touch *as* the patient receives stimulation (or sham stimulation). A patient who reports that she is feeling touch under conditions in which no stimulation is administered *may* be imagining the touch, although there are other possible explanations (e.g., motivation to be well) that would need to be discounted.

It will be interesting for future work to investigate anosognosia for somatosensory impairments alongside visual enhancement of touch and self-touch enhancement. Here it is proposed that patients who present with anosognosia (as determined by an awareness interview) will likely also demonstrate visual enhancement of touch or self-touch enhancement.[21] Certainly the fact that anosognosia for somatosensory impairments occurs more frequently in right-hemisphere patients (Marcel et al., 2004) is consistent with the finding that self-touch enhancement occurs more frequently in right-hemisphere patients (Valentini et al., 2008). Future

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[21] An anecdote from one of the patients assessed as part of the experimental series presented in Chapter 2 provides some support for this prediction. When I first met with Patient SM, I asked him if he had any problems with sensation. The 67-year-old right-hemisphere patient spontaneously reached for his affected left hand and stroked, prodded and massaged his skin. Following this instinctive self-assessment, SM concluded that his sensation was "very good". In fact, SM's capacity to detect touch administered by the Examiner was significantly impaired when compared to his capacity to detect the same intensity stimulation when self-administered (without vision). We assessed SM's sensory performance with a Semmes-Weinstein monofilament of 0.6958 grams, indicating diminished protective sensation. When his affected left hand was positioned in the left side of space, SM detected 72% of stimulations administered by the Examiner, compared to 96% of stimulations when these were self-administered ($p = .0055$). Hence SM's prior appraisal of "very good" sensation was reasonable for self-administered, but not for Examiner-administered stimulation.

work investigating the connections between these sensory phenomena will provide important clinical and theoretical information.

Part Two: The Illusion of Self-Touch

Part Two of the current thesis was primarily intended to investigate the constraints on the illusion of self-touch in neurologically healthy participants. However, partway through the investigation, it became apparent that some of the assumptions about this illusion required review. The results of the visual experiment presented in Chapter 4 (and further investigated in Chapter 5) raised questions about what the participant experiences during the (non-visual) illusion of self-touch, and in particular, the types of proprioceptive mislocalisation that are involved (Chapter 6). Part Two of the General Discussion will have two sections: first, a discussion of how the results of the experiments reported in this thesis change the way that we conceptualise the illusion of self-touch; and second, a discussion of the constraints on the illusion of self-touch.

A New Interpretation of the Illusion of Self-Touch

The self-touch rubber hand paradigm was developed by Ehrsson et al. (2005) as a *non-visual version* of the widely investigated visual rubber hand paradigm (Botvinick & Cohen, 1998). In the visual rubber hand paradigm, the participant looks at a prosthetic hand being touched by the Examiner while the participant's own hand – hidden from view – is also touched by the Examiner. When touches administered to the prosthetic hand and to the participant's hidden hand are synchronous, the participant has an experience in which she seems to "feel the touch not of the hidden brush but that of the viewed brush, as if the rubber hand ha[s] sensed the touch" (Botvinick & Cohen, p. 756). Thus, the illusion involves displacement of the felt location of touch from the participant's receptive hand to the prosthetic hand. This is referred to as visual capture of touch. It may also seem to the participant that the viewed hand is the participant's own hand.

In the (non-visual) self-touch rubber hand paradigm, the Examiner guides the participant to touch a prosthetic hand, and at the same time, the Examiner administers touch to the participant's other hand. When the touches that the participant administers to the prosthetic hand are synchronous with the touches that the Examiner administers to the participant's receptive hand, the participant experiences the touch on her receptive hand as if it is self-produced; that is, it seems to the participant that she is touching her own hand. Prior to the current thesis, the illusion of self-touch was explained with reference to the more widely investigated visual rubber hand illusion. The participant was thought to experience a "feeling of ownership of [the] touched rubber limb" (Ehrsson et al., 2005, p. 10569). On this view, the illusion involved displacement of the felt location of touch from the participant's receptive hand to the prosthetic hand (capture of touch), and the participant felt that her hand was in the location where she was administering touch (capture of proprioception). Consequently, one of the methods that Ehrsson et al. used to assess the illusion of self-touch was a measure of proprioceptive drift of the perceived position of the participant's *receptive hand*; that is, the researchers assessed change in the proprioceptively perceived position of the receptive hand toward the location of the prosthetic hand. This follows standard practice with the visual rubber hand paradigm, where the strength of the illusion is assessed by measuring proprioceptive drift of the perceived position of the participant's receptive hand toward the location of the viewed prosthetic hand.

Chapter 4 presented the first set of experiments with neurologically healthy participants. Whereas the illusion of self-touch is traditionally elicited with vision of the hands precluded (Ehrsson et al., 2005), the second experiment in Chapter 4 set out to elicit the illusion of self-touch under conditions permitting visual feedback. There were two viewing conditions. In one condition, the participant viewed the prosthetic hand as per the traditional visual rubber hand paradigm (the participant's receptive hand and the Examiner's administering hand were hidden from view). In the second and more interesting condition, the participant viewed her receptive hand receiving touch from the Examiner (the participant's administering hand and the prosthetic hand were hidden from view). The participant experienced the illusion of self-touch in both of these viewing conditions.

The second condition deserves special attention. This condition was unique amongst rubber hand experiments because the participant was not looking at a prosthetic hand receiving touch from the Examiner, but rather, she was looking at her own receptive hand receiving touch from the Examiner. A follow-up experiment presented in Chapter 5 confirmed that participants not only experienced the illusion of self-touch, but also experienced the illusion that the hidden right hand was administering touch in the location of the viewed Examiner's administering hand (visual capture of action), and the illusion that the viewed Examiner's administering hand was the participant's own hand (ownership). Moreover, subsequent to the synchronous stimulation trial, participants demonstrated proprioceptive drift of the perceived position of the (hidden) administering hand toward the location of the viewed Examiner's administering hand.

The implications of the findings in this second visual condition are important. Participants can experience a change in the proprioceptively perceived position of the administering hand (rather than the receptive hand) when they experience the illusion of self-touch. And, participants can experience the illusion of self-touch without experiencing ownership of the *prosthetic* hand. These findings from a visual self-touch rubber hand paradigm raise a number of questions about the non-visual paradigm. Why do we make assumptions about how the participant experiences the illusion of self-touch when the paradigm is conducted *without vision*? Why do we assume that the participant experiences a change in the proprioceptively perceived position of the receptive hand rather than the administering hand? And, why do we assume that the participant experiences ownership of the prosthetic hand?

These questions about how the participant experiences the non-visual illusion of self-touch motivated the experiment presented in Chapter 6. In this experiment, we assessed the proprioceptively perceived position of the participant's receptive hand and the participant's administering hand, before and after the experience of the *non-visual* illusion of self-touch. The direction of proprioceptive drift provides information about the perceived location of the prior event. This is most easily demonstrated using the example of the visual rubber hand illusion in which the viewed prosthetic hand is clearly identified as the location of the illusory event: it seems to the participant that she is being touched in the location where she can see the prosthetic hand being touched, and it may also seem as if the prosthetic hand is the participant's own hand. Subsequent to experiencing the visual rubber hand illusion, participants demonstrate proprioceptive drift of the receptive hand toward the location of the viewed prosthetic hand; that is, the receptive hand is experienced as being in a location that is displaced *toward* the location of the illusory event.

The results of the experiment presented in Chapter 6 indicated that there was significantly more proprioceptive drift of the participant's administering hand (toward the receptive hand) than of the participant's receptive hand (toward the prosthetic hand). We examined the proprioceptive drift demonstrated by each participant, and confirmed that this general pattern – more proprioceptive drift of the administering hand – was true of most participants in the study

(62.5%). We therefore concluded that some, or even most, participants experience the apparent single event of self-touch as occurring toward the location of the receptive hand (rather than the location of the prosthetic hand).

Given that the perceived location of a sensory event is biased toward the location specified by the sensory information with the least variance (Ernst & Bülthoff, 2004), the results suggest that there may be less variance associated with locating the receptive hand compared with the administering hand. The participant's receptive hand is stationary on the table, and she therefore *knows* that it has not moved during the trial. In contrast, the guided movement of the administering hand may increase the variance associated with its location and, although the Examiner never moves the administering hand leftward (toward the receptive hand), the very fact that it is being guided by another person may increase the variance associated with its location (see Paillard & Brouchon, 1968).

The implications of the findings presented in Chapter 6 extend beyond (1) the presentation of a new procedure, in which proprioceptive drift is assessed for both the receptive *and the administering hand*, and (2) the discovery that this illusion involves mislocalisation of the proprioceptively perceived position of the administering hand. The findings require that we reconsider the concept of *ownership* as it applies to the illusion of self-touch. In their pioneering use of the self-touch rubber hand paradigm, Ehrsson et al. (2005) suggested that "blindfolded persons felt that a rubber hand they touched was their own hand" thus indicating that "the rubber-hand illusion is not simply generated by the dominance of vision over somesthesis, but that temporally correlated and matching tactile and proprioceptive signals from two body parts is sufficient to change the feeling of ownership of a touched rubber limb" (p. 10569). This conclusion was premised on the view that the participant experienced touch as displaced to the location of the prosthetic hand, as in the visual rubber hand illusion. But the experiment presented in Chapter 6 demonstrates that this is not the participant's experience, or at least, that this is not the experience of the majority of participants.

In any case, one must seriously consider whether the non-visual illusion of self-touch is indeed an illusion of ownership. When the self-touch rubber hand paradigm is conducted *with vision* – either of the participant's hand administering touch to the prosthetic hand (Chapter 4: Experiment 2) or the Examiner's hand administering touch to the participant's receptive hand (Chapter 4: Experiment 2, and Chapter 5) – the participant has an experience in which it seems as if the viewed hands are her own *two* hands. This is apparent in the participant's spontaneous comments as well as ratings for statements on the questionnaire that directly ask about this experience: "It seemed as if I were observing my right hand stroking my left hand" (Chapter 4: Experiment 2) and "It felt as if the Examiner's hand were my hand" (Chapter 5). However, when the paradigm is conducted with vision of the hands precluded, the illusion of ownership is more difficult to comprehend. It seems to the participant that she is touching her own hand, but does this necessarily mean that it seems to the participant that the prosthetic hand is her own hand?

There is a nice comparison to be made between the traditional visual rubber hand illusion and the non-visual illusion of self-touch. In their pioneering use of the visual rubber hand paradigm, Botvinick and Cohen (1998) reported that eight of ten participants "spontaneously employed terms of ownership in their free-report descriptions, for example: 'I found myself looking at the dummy hand thinking it was actually my own'" (p. 756). Similarly, Armel and Ramachandran (2003) note that "subjects reported that the illusion was so convincing that they found themselves wondering why their hand was so white or how they had bruised their hand (there was a small ink smudge on the fake hand)" (p. 1502). And when a finger of the viewed prosthetic hand was bent backward, many participants flinched and "even pulled their real hand away from the experimenter" (p. 1503, see also Giummarra, Georgiou-Karistianis, Nicholls, Gibson, & Bradshaw, 2010). Thus, the spontaneous comments and behaviours of participants tested with the visual rubber hand paradigm demonstrate a compelling illusion of ownership of the viewed prosthetic hand.

This is to be contrasted with the *non-visual* self-touch rubber hand paradigm. Of 137 neurologically healthy participants assessed with the paradigm as part of this thesis, no single participant employed terms of ownership to describe her experience of either the prosthetic hand or the Examiner's administering hand.[22] Rather, the participants emphasised the sense of their *own two hands* coming into contact. Consequently, we have suggested that when the participant experiences the non-visual illusion of self-touch, the prosthetic hand and the Examiner's administering hand cease to be a part of the participant's phenomenology: all that the participant is left with is the experience of her own two hands.

The Constraints on the Illusion of Self-Touch

The first part of this section provided a reconceptualisation of the illusion of self-touch. The second part of this section presents a discussion of the constraints on the illusion of self-touch. This discussion parallels the discussion of constraints on the visual rubber hand illusion presented in the Introduction to this thesis.

Studies investigating the constraints on illusions such as the visual rubber hand illusion and the illusion of self-touch provide valuable information. To experience either of these two illusions, the participant integrates information from two spatial locations into a *single-event* interpretation. In the visual rubber hand illusion, the participant integrates into a single-event interpretation: (1) visual information about the seen position of the prosthetic hand as it is being

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[22] Note that this is also true of 104 further participants who took part in experiments that were conducted during the period of my doctoral research, but are not reported in this thesis.

touched and (2) proprioceptive information about the felt position of the receptive hand as it is being touch. The participant's experience is as if she is both seeing and feeling her hand being touched and as if this touching event is occurring at the location of the viewed prosthetic hand. In the non-visual illusion of self-touch, the participant integrates into a single-event interpretation: (1) proprioceptive-motor information about the felt position of the administering hand as it is administering touch and (2) proprioceptive-tactile information about the felt position of the receptive hand as it is being touched. The participant's experience is as if she is administering touch to her own hand. By manipulating different aspects of the experimental set-up (e.g., synchrony, distance, alignment), we obtain valuable information about sensory integration under conditions of cue conflict.

The discrepant information that is available to the participant is different in the visual rubber hand paradigm and the non-visual self-touch rubber hand paradigm. As but one example, consider the situation in which the timing of stimulation administered to the prosthetic hand is different to the timing of stimulation administered to the participant's receptive hand. In the visual rubber hand illusion, the participant detects asynchrony using visual information (the timing of stimulation administered to the viewed hand) combined with tactile feedback (the timing of stimulation administered to the participant's hidden receptive hand). She infers that there is a mismatch based on what she can see and her assumptions about how this should feel. In contrast, in the illusion of self-touch, the participant detects asynchronous stimulation using proprioceptive feedback from the administering hand and tactile feedback from the receptive hand. She *feels* the mismatch between the timing of the stimulation that she administers and the timing of the stimulation that she receives. Based on these differences in the way that discrepant information is perceived, we were open to the possibility that tolerance to discrepant information may be different in each of the two illusions.

The pioneering study by Ehrsson et al. (2005) investigated two constraints on the illusion of self-touch, timing and the correspondence of the prosthetic hand to the structural description of the body. In Ehrsson et al.'s study, the prosthetic hand and the participant's receptive hand were separated by 15 cm and positioned side-by-side with the fingers pointing away from the participant's body. Both hands received stimulation from an index finger; the participant tapped the prosthetic hand with her index finger while the Examiner tapped the participant's receptive hand with his index finger. The illusion of self-touch was only elicited when the timing of stimulation that the participant administered to the prosthetic hand matched the timing of stimulation that the Examiner administered to the participant's receptive hand. Correspondence with the structural description of the body was also important; the illusion of self-touch was elicited when the participant administered stimulation to a prosthetic hand, but not when the participant administered stimulation to the upturned bristles of a dish brush.

The experiments in the current thesis investigated four further constraints on the illusion of self-touch: (1) *object administering stimulation*, whether the stimulus that the participant administered to the prosthetic hand matched the stimulus that the Examiner administered to the participant's receptive hand (Chapter 4: Experiments 1a, 1b, and 2), (2) *distance* (15 cm, 30 cm, 45 cm, 60 cm) between the prosthetic hand and the participant's receptive hand (Chapter 7: Experiment 1), (3) *alignment* of the prosthetic hand relative to the participant's receptive hand (Chapter 7: Experiment 2), and (4) *anatomical plausibility*, the likelihood that the participant could be self-administering touch (Chapter 8).

Object Administering Stimulation

The results of the experiments presented in Chapter 4 suggest that the non-visual illusion of self-touch is elicited even when the stimulus that the participant administers to the prosthetic hand is different from the stimulus that the Examiner administers to the participant's receptive hand. Participants experienced the illusion of self-touch when they used the index finger to touch the prosthetic hand while receiving touch on the receptive hand from a paintbrush. On the self-touch illusion questionnaire, there was no difference in ratings between the congruent (finger-finger) and incongruent (finger-paintbrush) stimulation trials, indicating that the subjective illusion of self-touch was equally compelling whether stimulation was congruent or incongruent (Experiments 1a and 1b). Similarly, there was no difference in proprioceptive drift (of the participant's receptive hand) when the participant administered touch with a finger and was synchronously touched with a finger compared with when the participant administered touch with a finger and was synchronously touched with a paintbrush (Experiment 1b).

A questionnaire was used to verify that participants were aware of the stimulus discrepancy (Experiment 1b). On the incongruent stimulation trial, all 22 participants correctly reported that they had received stimulation from a paintbrush. Thus it is not the case that the discrepant information was *unavailable* to the participant. It is however possible that, with vision precluded, it was easy for the participant to disregard the incongruent stimulation. For example, the participant may have constructed a visual mental image of the set-up in which she was administering and receiving touch from her own index finger, and this mental image may have been sufficiently compelling to override the discrepant tactile information. But this explanation does not provide a satisfactory account of experience of the illusion in the incongruent condition; in a second experiment the paradigm was conducted with vision permitted, and participants experienced the illusion of self-touch despite the fact that they now had visual evidence of the tactile mismatch. Most notably, when the participant looked at her receptive left hand, she could see that it was being stimulated with a paintbrush and, although the participant could not see her administering right hand, the participant was aware that she was not holding an instrument, but rather, was using her index finger to administer touch.

The finding that tactile incongruence did not affect the illusion of self-touch needs to be considered in light of Körding et al.'s (2007) work on causal inference in multisensory perception. These researchers note that:

> If two events are close to each other in space, time, and structure, subjects tend to perceive a single underlying cause, while if they are far away from one another subjects tend to infer two independent causes. If cues are close to one another, they interact and influence the perception of each other, whereas they are processed independently when the discrepancy is large (p. e943).

It is possible that the illusion of self-touch was not affected by the tactile manipulation because the texture of stimulation administered by the paintbrush was *close* to the texture of stimulation administered by a finger. Although all 22 participants identified that they were being touched with a paintbrush on the incongruent trial, stimulation administered with the paintbrush may have felt similar to stimulation administered with an index finger. Perhaps the illusion would be impacted by the use of more disparate stimuli. For example, the participant might administer stimulation with her finger and receive stimulation from coarse sandpaper. Here, the structure of the two administering stimuli may be sufficiently different so as to impact the illusion of self-touch.[23] Notably however, in a study by Schütz-Bosbach, Tausche, and Weiss (2009) the visual

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[23] In pilot experiments, we guided the participant to administer stimulation to the prosthetic hand using a paintbrush and the participant's own hand was touched with a stick (and vice versa). Participants experienced the illusion of self-touch in these incongruent conditions despite the different textures of the two administering stimuli. However, we were concerned that participants may have simply attended to administering touch with, and receiving touch from, an instrument; thus failing to register the stimulus incongruence. It was for this reason that we chose to have the participant administer touch with her own finger in the experiments proper.

rubber hand illusion was not affected by the use of incongruent stimuli – cotton versus sponge – even though participants rated these stimuli as feeling significantly different from one another on the dimensions of roughness and softness.

As noted above, Körding et al. (2009) suggest that cues that are close to one another in structure can interact and influence the perception of one another. Consistent with this, the participants not only experienced a single event of self-touch in the incongruent stimulation condition but also, on a questionnaire assessing perceived sensation (Experiment 1b), more than half of all participants (63.64%) responded affirmatively to the statement "My right index finger felt like a brush". This finding may be conceptualised as a tactile (albeit unimodal) analogue of the McGurk effect (McGurk & MacDonald, 1976). The McGurk effect is a perceptual phenomenon, used to demonstrate the interaction of what we 'hear' and what we 'see' in the perception of speech. Participants view a video in which repeated utterances are dubbed onto lip movements. If the participant hears an auditory 'ba' while she sees see a visual 'ga', the participant will perceive the sound 'da'; that is, discrepant auditory and visual information are fused to form a single percept. This effect is robust, in that knowledge of the McGurk effect does not change the individual's perception. There are striking similarities between the McGurk effect and the tactile incongruence effect presented in Chapter 4. Under conditions of illusory self-touch, the stimulus that the participant administers (i.e., touch with a finger) and the stimulus that the participant receives (i.e., touch from a paintbrush) may be fused to form a single percept. The participant may perceive that her administering finger is brush-like. Importantly, the participant knows that she is administering touch to a prosthetic hand using her finger, and receiving touch on her own hand from a paintbrush. Thus, as with the McGurk effect, the participant's experience of a brush-like finger (and indeed, her experience of self-touch) is robust in the face of the participant's knowledge and beliefs.

Distance

Whereas the illusion of self-touch is not diminished by the use of incongruent stimuli, it is diminished when the distance between the prosthetic hand and the participant's receptive hand is increased. The results of the distance experiment presented in Chapter 7 (Experiment 1) indicated that, as the distance between the prosthetic hand and the participant's receptive hand increased: (1) participants provided lower agreement ratings for the illusion statement on the questionnaire, (2) participants indicated that the illusion of self-touch took longer to be elicited, and (3) participants demonstrated less proprioceptive drift of perceived hand position.

How are we to explain the finding that the subjective illusion of self-touch is diminished by the distance manipulation? A possible explanation of the effects of the distance manipulation in our study involves proprioception. When the participant's two hands are separated by only 15cm, a small rotation of the elbow joint would be sufficient to bring the hands into contact. Thus, the illusion of self-touch would seem to require proprioceptive recalibration of the perceived position of just the forearms and hands. But, as the distance between the hands is increased, a large rotation of the shoulder joint (as well as the elbow joint) would be necessary to bring the hands into contact. Thus, the illusion would seem to require proprioceptive recalibration of the perceived position of the upper arms, forearms and hands. It may also be important that, with the arms outstretched, a substantial amount of proprioceptive information about the actual position of the hands and arms needs to be overridden if a compelling illusion is to emerge. Finally, in the greater distance conditions with the receptive left hand positioned far to the left of midline, the shoulder was abducted and the elbow was more extended. Fuentes and Bastian (2010) reported that, as the elbow approaches the limit of its range (of extension or flexion), estimates of the elbow angle based on proprioception are biased towards the limit; and this effect is greater when the shoulder is abducted. So in the greater distance conditions, proprioceptive evidence against the self-touch hypothesis may even be amplified. In summary, with increasing distance between the hands, there is stronger proprioceptive evidence against the self-touch hypothesis and this may account for the reduced ratings of the illusion of self-touch.

A possible limitation of the current work is that the spatial perturbations were fairly dramatic: 15 cm between each distance condition. The participant may experience a stronger illusion of self-touch if perturbations were gradually introduced. If the Examiner slowly separated the participant's two hands, perhaps by positioning the receptive hand on a sliding trolley, the participant may adapt to the different hand positions without conscious awareness and experience an equally intense illusion in the 15 cm and 60 cm distance conditions. We propose that the more gradual introduction of spatial discrepancy (and other types of discrepancy) will provide an interesting avenue for future research.

Alignment

In the same way that the subjective illusion of self-touch was diminished by distance manipulation, so too was it diminished by a different spatial manipulation, namely the misalignment of the prosthetic hand relative to the participant's receptive hand. In Experiment 2 of Chapter 7, a misaligned hand-placement condition was investigated. In the misaligned hand-placement condition, the participant's receptive hand was positioned with the fingers pointing straight ahead, and the prosthetic hand was rotated anti-clockwise by 90º so that the fingers pointed toward the left. Given that the participant's eyes were closed, the participant experienced the 90º misalignment as a mismatch in the direction of strokes on her receptive hand (from the body outward), compared with the direction of strokes that she administered to the prosthetic hand (right to left across the body).

Participants experienced the subjective illusion of self-touch in the misaligned hand-placement condition, but the illusion was diminished by the alignment manipulation. For example, participants provided significantly lower ratings for the illusion statement on the self-touch illusion questionnaire, and fewer participants reported a time of onset of the illusion, as compared to the condition in which the prosthetic hand and the participant's receptive hand were aligned. But, whereas subjective illusion ratings were diminished by alignment manipulation, proprioceptive drift of perceived hand position was abolished. In the misaligned hand-placement condition, participants did not demonstrate any change in the proprioceptively perceived position of the hands. Thus, the results of the alignment experiment demonstrate an important dissociation between questionnaire ratings and proprioceptive drift. Rohde et al. (2011) have very recently demonstrated a similar dissociation between subjective ratings of illusion strength and proprioceptive drift in the visual rubber hand illusion (see also Holmes et al., 2006), prompting these researchers (Rohde et al.) to question the validity of using proprioceptive drift as a proxy to measure the subjective intensity of the visual rubber hand illusion. But, whereas the study by Rohde et al. demonstrated proprioceptive drift in the absence of a subjective visual rubber hand illusion, we demonstrate a subjective illusion of self-touch in the absence of proprioceptive drift.

In the misaligned hand-placement condition presented in Chapter 7, one participant spontaneously remarked that, with time, she felt as if she was administering and receiving strokes on the diagonal. For this participant, the subjective impression was that the two directions of stimulation – away from the body and across the body – were merged. It seemed to the participant that her receptive hand was aligned at the 45º orientation. Here there are interesting parallels with the experiment presented in Chapter 4, in which participants perceived that the administering finger was brush-like when they administered touch with a finger and received touch from a paintbrush. But, whereas the experiment in Chapter 4 demonstrates merging of the *objects* used to administer stimulation to the prosthetic hand and the receptive hand (finger and paintbrush), the experiment in Chapter 7 hints at an illusion in which the participant experiences merging of the *directions* of the stimulation administered to the prosthetic hand and the receptive hand (across the body and away from the body). It will be valuable for future work to assess the participant's subjective impression of the misaligned hand-placement condition systematically, so as to acquire further information about the nature of sensory integration in this illusion.

It is noteworthy that a 90° misalignment of the hands does not abolish the illusion of self-touch as elicited with the non-visual self-touch rubber hand paradigm, whereas it does abolish the illusion of ownership as elicited with the visual rubber hand paradigm. This difference is perhaps not surprising since, in the non-visual self-touch rubber hand paradigm, all mismatches need to be detected using proprioception, which does not share the spatial acuity of vision.

Another possible explanation for the robustness of the non-visual illusion to the alignment manipulation appeals to the *role of prediction* in self-touch. When an individual touches her own hand, she knows when she will experience the sensory consequences of her administering hand action, and she can therefore predict or estimate the sensory feedback that would be expected as a result of her action. As the experiments in Chapters 2 and 3 demonstrate, individuals with impaired sensation experience self-touch as being more intense than identical touch administered by another person. However, for neurologically-healthy individuals without a sensory impairment the converse pattern is true: self-touch is experienced as *less* intense than identical touch administered by another person (see Bays et al., 2006; Blakemore et al., 1998, 2000; Claxton, 1975; Hesse et al., 2010; Weiskrantz et al., 1971), and this effect is termed self-touch attenuation.

It may be possible to achieve a better understanding of the illusion of self-touch and its robustness against the alignment manipulation if we consider the illusion alongside the phenomenon of self-touch attenuation. Self-touch attenuation occurs when the individual is fully in control of the movement and also when the individual is being guided to administer stimulation (Weiskrantz et al., 1971) as was the case in the current experiments. In some studies, self-touch attenuation has been investigated using a set-up that is very closely matched to the self-touch rubber hand paradigm. In a study by Blakemore et al. (1999), the participant's administering and receptive hands were not in direct contact. The participant held a cylindrical object in her administering hand and, as she moved the cylindrical object, information was transmitted to a robotic device, which administered stimulation to the participant's receptive hand. The participant rated touch on her receptive hand on the dimensions of tickliness, intensity, and pleasantness, and self-produced touch was perceived as less tickly, less intense, and less pleasant than externally-produced touch. (In the externally-produced condition, the robotic device was programmed to administer touch to the participant's receptive hand but the participant did not move the cylindrical object in her administering hand.)

In a highly relevant manipulation, Blakemore et al. (1999) varied the direction of stimulation: trajectory rotations of 30°, 60°, and 90° were introduced between the movement made by the participant's administering hand and the movement made by the robotic device. The condition using the 90° trajectory rotation is most similar to the misaligned condition of our Experiment 2. In this condition, ratings for tickliness were significantly higher than in the aligned condition and not significantly different from the externally-produced condition. But for intensity and pleasantness there was only a non-significant trend to higher ratings as misalignment increased.

We propose that it would be illuminating to investigate whether the sensation of touch on the participant's receptive hand is attenuated in various conditions of the self-touch rubber hand paradigm and specifically, in the misaligned condition with synchronous stimulation. Perhaps the touch on the receptive hand is experienced as being less intense and less pleasant than in the misaligned condition with asynchronous stimulation. If sensory attenuation reliably co-occurs with the illusion of self-touch, then we should investigate the causal relationship between the two phenomena and the role, in each, of predictability of the otherwise fairly unpredictable sequence of stimulation on the participant's receptive hand. One apparent possibility is that the predictability of the felt touches leads directly to sensory attenuation and that this, in turn, functions as evidence in support of the self-touch hypothesis, outweighing the evidence against the hypothesis provided by misalignment.

As a starting point for the proposed investigation, the self-touch illusion questionnaire could be expanded to include questions that relate to the perceived tickliness, intensity, and pleasantness of stimulation on the receptive hand during assessment with the self-touch rubber hand paradigm. Based on Blakemore et al.'s results (1999), I predict that participants will rate touch on the receptive hand as being ticklier, less intense, and less pleasant in the synchronous-stimulation condition as compared with the asynchronous-stimulation condition. Moreover, I predict a positive correlation between ratings of tickliness and ratings of the subjective illusion of self-touch, and a negative correlation between ratings of intensity/pleasantness and ratings of the subjective illusion of self-touch. Questions about perceived tickliness, intensity, and pleasantness will make a valuable addition to the questionnaire, because a naïve participant will not be able to predict how she would be expected to respond. Therefore, the statements will help to overcome issues of response bias that are inherent in this field of research.

Anatomical Plausibility

The results of the experiment presented in Chapter 8 indicate that the illusion of self-touch is sensitive to anatomical plausibility. In the final experiment presented in this thesis, we investigated a novel illusion of self-touch: the experience of touching one's left elbow with one's own index finger – right or left. In everyday life, individuals can touch the left elbow with the right index finger (plausible condition), but they cannot touch the left elbow with the left index finger (implausible condition). We set out to investigate whether the illusion of self-touch was sensitive to the structural configuration of the body. Participants provided significantly lower illusion ratings, and indicated a longer time before onset of the illusion in the implausible (left-index-finger) condition. But, although the illusion was diminished by anatomical implausibility, it was still the case that most participants reported an experience of self-touch. In the implausible (left-index-finger) condition, fifteen participants (93.75%) provided an agreement rating with the illusion statement on the questionnaire, and twelve participants (75%) alerted the Examiner to the fact that they were experiencing self-touch during the experimental trial. Thus, nearly all of the participants experienced an illusion that defied the structural configuration of the body. This finding highlights the malleability of body representation: when sensory inputs are consistent with there being a single event of self-touch, this sensory information overrides years of experience with one's body.

Vibration paradigms have also been used to elicit illusions that defy the structural configuration of the body. These paradigms were introduced to the literature in 1972 (Eklund, 1972; Goodwin, McCloskey, & Matthews, 1972a; Goodwin, McCloskey, & Matthews, 1972b). Lackner (1988) provides an excellent description of how these paradigms elicit illusory movement, and I draw on his description here. When a muscle (body or tendon) is mechanically vibrated, the muscle reflexively contracts. For example, mechanical vibration of the biceps brachii muscle elicits the reflexive contraction of the forearm. If the forearm is restrained, so that it cannot physically contract, the individual will experience the illusion that the forearm is extending. It will seem to the individual that the forearm is moving in the opposite direction to that predicted by the vibration of the muscle.

Craske (1977) demonstrated that vibration of muscle tendons can lead to a dramatic distortion of position sense, involving a physically impossible limb configuration. In this study, the participant was seated with her left hand, palm downwards, on a testing pad. The participant was asked to "move the hand until maximum wrist extension was attained" (p. 73); that is, so that the fingers were pointing upward. The Examiner used this pre-assessment to ascertain the range of movement that the participant could comfortably attain. Next, the Examiner vibrated the flexor carpi radialis (a muscle located in the forearm). The vibration elicited reflexive contraction of the wrist. As soon as the Examiner observed movement of the participant's hand, he "stretch[ed] the reflexly contracting muscle" (p. 73) by slowly moving the hand into the position previously defined as the comfortable maximum. With this procedure, participants perceived that the hand was in an impossible posture, bent backward toward the dorsal surface of the forearm.

Whereas Craske (1977) used muscle vibration to elicit illusions involving change in the perceived position of body parts, Lackner (1988) used muscle vibration to elicit illusions involving change in the perceived shape of body parts. This was achieved by manipulating the position of the participant's body parts in relation to one another before vibration was administered. For example, the participant held her nose between her right index finger and thumb. Next, the Examiner mechanically vibrated the participant's right biceps brachii. This mechanical vibration would ordinarily lead to the reflexive contraction of the forearm, but because the forearm was restrained (because the participant was holding her own nose) the participant instead experienced the illusion that the forearm was extending. Five of 14 participants tested with this paradigm experienced the illusion that the nose was elongated ("Oh my gosh, my nose is a foot long! I feel like Pinocchio", p. 284), three participants experienced the illusion that the fingers were elongated, and two participants experienced the illusion that the nose *and* fingers were elongated. Thus, mechanical vibration combined with 'self-touch' elicited an illusion involving an impossible configuration of the body. In a discussion of the anomalous experiences created through mechanical vibration of the muscle, Lackner stressed that the participant's experience represents a good solution to the prevailing pattern of stimulation given the actual configuration of the body. In the example presented above, the participant experienced spindle activity that was consistent with the muscle being stretched and the forearm extended. Somatosensory feedback indicated that the participant was holding her own nose. The forearm can only move while the nose is grasped if the nose is also moving, and yet, sensory and motor information indicated that the participant's head was still. Consequently, "the nose had to be 'represented' as changing length or position, or the hand and fingers as elongating, because these are the only interpretations consistent with the hand and nose maintaining physical contact while the hand is moving and the head stationary" (Lackner, p. 291).

As this discussion demonstrates, meaningful interpretations of prevailing patterns of stimulation are sometimes at odds with the structural configuration of the body. Our elbow illusion provides such an example: a meaningful interpretation of sensory stimulation that defies the structural configuration of the body. Recently, we have experimented with a new self-touch procedure that tests anatomical plausibility, and provides a more dramatic example of the malleability of body representation.

The experimental procedure is simple. The participant's eyes are closed. The Examiner guides the participant to administer strokes and taps to the right side of the participant's face with the right index finger. At the same time, the Examiner strokes and taps the corresponding location on the left side of the participant's face. The Examiner controls and carefully matches the direction of strokes administered to the two sides of the participant's face (Figure 30a). When tested with this new paradigm, it is common for participant to report that it seems as if they are administering strokes to the face with a disembodied 'third' hand (Figure 30b).

Figure 30. (a) Experimental procedure presented in the first three panels; (b) 'Visual' depiction of the participant's experience of touching the left side of the face with a disembodied third hand.

This new illusion consists of (1) the illusion of self-touch and (2) the illusion of a disembodied third hand. The illusion of self-touch has been established in the literature as well as the empirical chapters of this thesis: the illusion of touching one's nose when one is touching another person's nose (Ramachandran & Hirstein, 1997); the illusion of touching one's hand when one is touching a prosthetic hand (Ehrsson et al., 2005; see also Chapters 4, 5, 6, and 7); the illusion of touching one's elbow when one is touching another person's forearm (Chapter 8). In each example, the participant administers touch to *another* person (or object) while the Examiner administers corresponding touch to the participant's body. The temporal correspondence between the action of the participant's administering hand and tactile sensation at a location on the participant's body (nose, hand, elbow) is consistent with the participant's experience that the administering and receptive body parts are involved in a single event. Hence the participant experiences the illusion of self-touch.

The cheeky illusion instead involves temporal correspondence between the action of the participant and sensation at *two* locations on the participant's body (right and left side of the face). There is a very low probability that the action of the participant's administering hand and the sensation on the right and left side of the participant's face could correspond so precisely by chance. Thus the participant's experience is that she is simultaneously administering touch to both sides of the face. Of course the participant really *is* touching the right side of the face with the right index finger; the *illusion* of self-touch concerns the sense of causal responsibility for the touch on the left side of the participant's face.

Participants report touching the two sides of the face with two different hands – the right side of the face with the right hand and the left side with a disembodied third hand. Descriptions of the disembodied hand include: 'a third hand', 'not my left or right hand', 'another hand', 'a dead hand'. In each case the participant reports that the third hand does not seem to be attached to the participant's own body. Given the participant's experience that she is administering touch to both sides of the face, it is not difficult to comprehend the participant's experience of a disembodied third hand. We propose that this illusion of a disembodied third hand occurs because of a lack of proprioceptive feedback. The participant experiences self-touch on both sides of the face and the proprioceptive feedback indicates that the right hand is touching the right side of the face but that the left hand is not involved. Thus, a third hand is involved, and this hand is experienced as disembodied.

Parallels can be drawn between the experience of participants tested with our cheeky paradigm and the experience of stroke patients with a supernumerary phantom limb. These patients experience the illusion (Khateb et al., 2009) or delusion (Halligan, Marshall, & Wade, 1993) that they have a third limb, again highlighting the malleability of body representation. In an attempt to explain and understand this phenomenon, researchers have developed elegant paradigms to enable neurologically healthy individuals to experience the *visual* illusion of an additional arm (e.g., Ehrsson, 2009; Guterstam, Petkova, & Ehrsson, 2011; Newport et al., 2010; Schaefer, Heinze, & Rotte, 2009). But for most stroke patients, the supernumerary phantom limb has "only somesthetic characteristics and cannot be seen" (Khateb et al., p. 698).[24] We hope that our new self-touch paradigm will lead to a better understanding of the *non-visual* and purely kinaesthetic illusion of a third limb, as it is experienced by patients with supernumerary phantom limb.

Concluding Remarks and Prospectus for Further Research

This thesis has presented a series of experiments using the self-touch rubber hand paradigm to investigate (1) self-touch enhancement following stroke and (2) the illusion of self-touch itself. The experiments presented in Part One highlight the value of the self-touch rubber hand paradigm as a tool for deconstructing the different elements of the self-touch experience. The experiments confirm that stroke patients with impaired sensation are better at detecting self- compared with Examiner-administered touch. This is an important contribution to the literature, in that it rules out an alternative explanation for self-touch enhancement in terms of patients

[24] Just as our participants experience a supernumerary limb that administers touch, so too has this experience been reported in the literature on stroke patients with supernumerary phantom limb. Khateb et al. (2009) worked with a stroke patient who reported the experience of tactile sensation when a part of her body was touched by her supernumerary phantom hand. An fMRI experiment confirmed activation in the brain areas representing cheek sensation when the patient was asked to touch her cheek using her phantom hand.

using proprioceptive information to *infer* self-administered touch. We are hopeful that this work will have implications for patient care and that self-touch may be built into rehabilitation for patients who have impaired sensation following stroke.

The experiments presented in Part Two led to a reconceptualisation of the illusion of self-touch. Previously, participants were thought to experience a change in the proprioceptively perceived position of the receptive hand toward the location of the prosthetic hand when they experienced self-touch. However, the experiments in this thesis demonstrate that participants may instead experience a change in the proprioceptively perceived position of the administering hand toward the location of the Examiner's administering hand, or considered differently, toward their own receptive hand. This is an important contribution and one that raises questions about notions of ownership in this illusion; in particular, the idea that the participant experiences ownership of the prosthetic hand is called into question. We are hopeful that this work will inspire further studies investigating body ownership and body representation in non-visual illusion paradigms.

Part Two also presented a series of experiments manipulating different elements of the self-touch experience: (1) object administering stimulation, whether the stimulus that the participant administered to the prosthetic hand matched the stimulus that the Examiner administered to the participant's receptive hand, (2) distance, between the prosthetic hand and the participant's receptive hand, (3) alignment, of the prosthetic hand relative to the participant's receptive hand, and (4) anatomical plausibility, the likelihood that the participant could be self-administering touch. The experiments provide information about sensory integration under conditions of cue conflict and highlight the robust nature of the illusion of self-touch. Provided that stimulation is synchronous, participants can experience self-touch in the face of dramatic manipulations; that is, when administering stimulation with a finger and receiving stimulation from a paintbrush, when the participant's two hands are separated by 60 cm, when administering strokes in one direction and receiving strokes in a different direction, and when the anatomical structure of the body precludes contact between the administering and receptive body parts. Indeed, participants can even experience the illusion of self-touch when the paradigm is conducted with vision, so that the participant has clear visual evidence either (1) that it is not her own hand that she is touching, but rather, a prosthetic hand, or (2) that her own hand is receiving touch from another person.

Throughout the General Discussion, further experiments have been outlined. These have been natural extensions of the work presented in the thesis. To follow-up on the experiments presented in Part One, two sets of possible experiments were outlined. We propose to investigate the role of temporal expectation in self-touch enhancement, with a focus on the *types* of temporal cues (e.g., auditory cues versus motor cues) that are sufficient to produce self-touch enhancement. We also propose to investigate the interplay of self-touch enhancement, visual enhancement of touch and anosognosia for somatosensory impairments, with a focus on determining whether anosognosia for somatosensory impairments is more common in patients who demonstrate improved sensation when they self-monitor; for example, when they view the body as it receives touch or when they self-administer touch. To follow-up on the experiments presented in Part Two, two sets of possible experiments were outlined. We propose to investigate the constraints on the illusion of self-touch using a procedure in which discrepancies (e.g., distance) are gradually introduced. We also propose to investigate self-touch attenuation in the context of the illusion of self-touch, with a focus on determining whether participants experience self-touch attenuation when they experience the illusion of self-touch, and whether this sensory attenuation may have a causal role in the participant's experience of the illusion.

In addition to these *follow-up* studies, the work presented in this thesis inspires a broader programme of research that will use illusion paradigms to investigate different conditions that affect the individual's experience of his or her body. One such extension of the work in thesis arose by chance. It is standard in our laboratory to begin experiments by confirming that the participant is comfortable with receiving touch on the hand. At the beginning of each experiment reported in this thesis, I demonstrated the different types of stimulation that would be involved in the study by administering touch to a prosthetic hand. During this screening protocol, one participant (RS) spontaneously reported that the observation of touch on the prosthetic hand elicited tactile sensation on her own hand. RS went on to explain that this visuo-tactile experience dates back to an early age, and she recalled a vivid memory from age eight. While seated in the classroom, she watched the teacher at the front of the room as she rubbed her two hands together. RS said "I was mesmerised and felt that I could feel her touch".

Patient studies (e.g., Bradshaw & Mattingley, 2001; Ramachandran & Rogers-Ramachandran, 1996) provided some of the earliest reports of visual information triggering tactile sensation. More recently, this has been shown to occur in neurologically healthy individuals with vision-touch (or mirror-touch) synaesthesia, such as Participant RS. In vision-touch synaesthesia, the sight of touch on another person elicits a tactile sensation on the observer's own body (Blakemore, Bristow, Bird, Frith, & Ward, 2005). Alongside the thesis experiments investigating the illusion of self-touch, we carried out a separate investigation of vision-touch synaesthesia, in which we used the visual rubber hand paradigm as a tool for authenticating and understanding this phenomenon. Two individuals with vision-touch synaesthesia were assessed, alongside a control group of 36 participants without vision-touch synaesthesia. A *no-touch* version of the traditional visual rubber hand paradigm was used: the participant viewed touch on a prosthetic hand, but no touch was administered to the participant's hidden hand. The two individuals with vision-touch synaesthesia experienced a compelling visual rubber hand illusion, evidenced by spontaneous reports, questionnaire ratings, and proprioceptive drift toward the viewed prosthetic hand. In contrast, control participants without vision-touch synaesthesia did not experience the no-touch visual rubber hand illusion (Aimola Davies & White, Under Revision). Our no-touch visual rubber hand paradigm is easy to implement, and we are hopeful that it will prove to be a valuable tool for future investigations of vision-touch synaesthesia.

In addition to continuing our work with vision-touch synaesthesia, we also plan to use illusion paradigms to investigate different aspects of impaired body awareness following stroke. For example, we intend to use muscle vibration paradigms (described in the section on Anatomical Plausibility) to investigate illusory limb movements in patients following stroke. It has been proposed that patients with anosognosia, who claim that they are able to move the paralysed limb, may experience an illusory limb movement when they send a motor command to the paralysed limb. Patients may fail to distinguish between the illusory limb movement and an actual limb movement, with the result that it seems to the patient that she has successfully executed the intended movement (Feinberg, Roane, & Ali, 2000). We plan to use muscle vibration paradigms to investigate the patient's experience of illusory limb movements under different testing conditions; for example, when the patient does and does not intend to move the affected limb. This work will provide further insight as to the role of illusory limb movements in anosognosia. We also plan to use variations of our 'cheeky illusion' paradigm (described in the section on Anatomical Plausibility) to investigate the experience of a supernumerary phantom limb in patients following stroke (see also Curt, Yengue, Hilti, & Brugger, 2011). The objective of this research programme is to understand body awareness and body experience better.

Ultimately, we hope that this work will lead to possible methods for the rehabilitation of impaired body representation in patients following stroke.

REFERENCES

Aglioti, S., Smania, N., & Peru, M. (1999). Frames of reference for mapping tactile stimuli in brain-damaged patients. *Journal of Cognitive Neuroscience, 11*, 67-69.

Aimola Davies, A. M., & White, R. C (Under Revision). Touching my face with my supernumerary hand: A cheeky illusion. *Perception*.

Aimola Davies, A. M., & White, R. C. (Under Revision). A *sensation*al illusion: Vision-touch synaesthesia and the rubber hand paradigm. *Cortex*.

Aimola Davies, A. M., White, R. C., Thew, G., Aimola, N. M. V., & Davies, M. (2010). Visual capture of action, experience of ownership and the illusion of self touch: A new rubber hand paradigm. *Perception, 39*, 830-838.

Albrecht, M.A., Martin-Iverson, M.T., Price, G., Lee, J., Iyyalol, R., & Waters, F. (in press). Dexamphetamine effects on separate constructs in the rubber hand illusion test. *Psychopharmacology*.

Anema, H.A., Kessels, R.P.C., de Haan, E.H.F., Kappelle, L.J., Leijten, F.S., van Zandvoort, M.J.E., et al. (2008). Differences in finger localisation performance of patients with finger agnosia. *NeuroReport, 19*, 1429-1433.

Anema, H.A., van Zandvoort, M.J.E., de Haan, E.H.F., Kappelle, L.J., de Kort, P.L.M., Jansen, B.P.W., et al. (2009). A double dissociation between somatosensory processing for perception and action. *Neuropsychologia, 47*, 1615-1620.

Armel, K.C., & Ramachandran, V.S. (2003). Projecting sensations to external objects: Evidence from skin conductance response. *Proceedings of the Royal Society of London B, 270*, 1499-1506.

Asai, T., Mao, Z., Sugimori, E., & Tanno, Y. (in press). Rubber hand illusion, empathy, and schizotypal experiences in terms of self-other representations. *Consciousness and Cognition*.

Austen, E.L., Soto-Faraco, S., Enns, J.T., Kingstone, A. (2004). Mislocalizations of touch to a fake hand. *Cognitive, Affective, and Behavioral Neuroscience, 4*, 170-181.

Bays, P.M., Flanagan, J.R., & Wolpert, D.M. (2006). Attenuation of self-generated tactile sensations is predictive not postdictive. *PLoS: Biology, 4*, e28.

Bays, P.M., & Wolpert, D.M. (2007). Predictive attenuation in the perception of touch. In: P. Haggard, Y. Rossetti and M. Kawato, Editors, *Attention and Performance XXII, Sensorimotor Foundations of Higher Cognition*. Oxford University Press, Oxford, pp. 339-358.

Bays, P.M., Wolpert, D.M., & Flanagan, J.R. (2005). Perception of the consequences of self-action is temporally tuned and event driven. *Current Biology, 15*, 1125-1128.

Bender, M.B. (1952). *Disorders in perception*. Springfield: Charles C. Thomas.

Berberovic, N., Pisella, L., Morris, A.P., & Mattingley, J.B. (2004). Prismatic adaptation reduces biased temporal order judgements in spatial neglect. *Cognitive Neuroscience and Neuropsychology, 15*, 1199-1204.

Bertamini, M., Berselli, N., Bode, C., Lawson, R., & Ting Wong, L. (in press). The rubber hand illusion in a mirror. *Consciousness and Cognition.*

Bisiach, E., Vallar, V., Perani, D., Papagno, C., & Berti, A. (1986). Unawareness of disease following lesions of the right hemisphere: Anosognosia for hemiplegia and anosognosia for hemianopia. *Neuropsychologia 24*, 471-482.

Björkman, A., Weibull, A., Rosén, B., Svensson, J., & Lundborg, G. (2009). Rapid cortical reorganisation and improved sensitivity of the hand following cutaneous anaesthesia of the forearm. *European Journal of Neuroscience, 29*, 837-844.

Blakemore, S.-J, Bristow, D., Bird, G., Frith, C., & Ward, J. (2005). Somatosensory activations during the observation of touch and a case of vision-touch synaesthesia. *Brain, 128*, 1571-1583.

Blakemore, S.-J., Frith, C.D., & Wolpert, D.M. (1999). Spatio-temporal prediction modulates the perception of self-produced stimuli. *Journal of Cognitive Neuroscience, 11*, 551-559.

Blakemore, S.-J., Wolpert, D.M., & Frith, C.D. (1998). Central cancellation of self-produced tickle sensation. *Nature Neuroscience, 1*, 635-640.

Blakemore, S.-J., Wolpert, D.M., & Frith, C.D. (2000). Why can't you tickle yourself? *NeuroReport, 11*, 11-15.

Blefari, M.L., Cipriani, C., & Carrozza, M.C. (2011). A novel method for assessing sense of body ownership using electroencephalography. *IEEE Transactions on Bio-Medical Engineering, 58*, 12-15.

Bobath, B. (1990). *Adult hemiplegia: Evaluation and treatment.* 3rd Edition. London: Heinemann Publishing.

Botvinick, M. (2004). Neuroscience. Probing the neural basis of ownership. *Science, 305*, 782-783.

Botvinick, M., & Cohen, J. (1998). Rubber hands 'feel' touch that eyes see. *Nature, 391*, 756.

Bradshaw, J.L., & Mattingley, J.B. (2001). Allodynia: A sensory analogue of motor mirror neurons in a hyperaesthetic patient reporting instantaneous discomfort to another's perceived sudden injury? *Journal of Neurology, Neurosurgery, and Psychiatry, 70*, 135-136.

Braun, C., Ladda, J., Burkhardt, M., Wiech, K., Preissl, H., & Roberts, L.E. (2005). Objective measurement of tactile mislocalization. *IEEE Transactions on Biomedical Engineering, 52*, 728-735.

Braune, S., & Schady, W. (1993). Changes in sensation after nerve injury or amputation: The role of central factors. *Journal of Neurology, Neurosurgery, and Psychiatry, 56*, 393-399.

Bruno, N., & Bertamini, M. (2010). Haptic perception after a change in hand size. *Neuropsychologia, 48*, 1853-1856.

Calford, M. (1991). Curious cortical change. *Nature, 352*, 759-760.

Carey, L.M., & Matyas, T.A. (2010). Training of somatosensory discrimination after stroke: Facilitation of stimulus generalisation. *American Journal of Physical Medicine and Rehabilitation, 84*, 428-442.

Capelari, E.D.P., Uribe, C., & Brasil-Neto, J.P. (2009). Feeling pain in the rubber hand: Integration of visual, proprioceptive, and painful stimuli. *Perception, 38*, 92-99.

Claxton, G. (1975). Why can't we tickle ourselves? *Perceptual and Motor Skills, 41*, 335-338.

Collin, C., & Wade, D. (1990). Assessing motor impairment after stroke: A pilot reliability study. *Journal of Neurology, Neurosurgery, and Psychiatry, 53*, 576-579.

Connell, L.A., Lincoln, N.B., & Radford, K.A. (2008). Somatosensory impairment after stroke: Frequency of different deficits and their recovery. *Clinical Rehabilitation, 22*, 758-767.

Correa, A., Lupiáñez, J., & Tudela, P. (2005). The attentional mechanism of temporal orienting: Determinants and attributes. *Experimental Brain Research, 169*, 58-68.

Coslett, H.B., & Lie, E. (2004). Bare hands and attention: Evidence for a tactile representation of the human body. *Neuropsychologia, 42*, 1865-1876.

Costantini, M., & Haggard, P. (2007). The rubber hand illusion: Sensitivity and reference frame for body ownership. *Consciousness and Cognition, 16*, 229-240.

Coull, J.T., Frith, C.D., Büchel, C., & Nobre, A.C. (2000). Orienting attention in time: Behavioural and neuroanatomical distinction between exogenous and endogenous shifts. *Neuropsychologia, 38*, 808-819.

Coull, J.T., & Nobre, A.C. (1998). Where and when to pay attention: The neural systems for directing attention to spatial locations and to time intervals as revealed by both PET and fMRI. *The Journal of Neuroscience, 18*, 7426-7435.

Craske, B. (1977). Perception of impossible limb positions induced by tendon vibration. *Science, 196*, 71-73.

Curt, A., Yengue, C.N., Hilti, L.M., & Brugger, P. (2011). Supernumerary phantom limbs in spinal cord injury. *Spinal Cord, 49*, 588-595.

Demeurisse, G., Demol, O., & Robaye, E. (1980). Motor evaluation in vascular hemiplegia. *European Neurology, 19*, 382-389.

De Domenico, G., & McCloskey, D.I. (1987). Accuracy of voluntary movements at the thumb and elbow joints. *Experimental Brain Research, 65*, 471-478.

de Vignemont, F., Ehrsson, H.H., & Haggard, P. (2005). Bodily illusions modulate tactile perception. *Current Biology, 15*, 1286-1290.

Dijkerman, H.C., & de Haan, E.H.F. (2007). Somatosensory processes subserving perception and action. *Behavioral and Brain Sciences, 30*, 189-239.

Dijkerman, H.C., Webeling, M., ter Wal, J.M., Groet, E., & van Zandvoort, M.J.E. (2004). A long-lasting improvement of somatosensory function after prism adaptation, a case study. *Neuropsychologia, 42*, 1697-1702.

Dolk, T., Hommel, B., Colzato, L.S., Schütz-Bosbach, S., Prinz, W., & Liepelt, R. (2011). How "social" is the social Simon effect? *Frontiers in Psychology, 2*, 1-9.

Douglass, C., & McDermott, C.J. (2009). Assessment and diagnosis of sensory disturbance. *InnovAIT, 2*, 531-537.

Dummer, T., Picot-Annand, A., Neal, T., & Moore, C. (2009). Movement and the rubber hand illusion. *Perception, 38*, 271-280.

Durgin, F.H., Evans, L., Dunphy, N., Klostermann, S., & Simmons, K. (2007). Rubber hands feel the touch of light. *Psychological Science, 18*, 152-157.

Ehrsson, H.H. (2009). How many arms make a pair? Perceptual illusion of having an additional limb. *Perception, 38*, 310-312.

Ehrsson, H.H., Holmes, N.P., & Passingham, R.E. (2005). Touching a rubber hand: Feeling of body ownership is associated with activity in multisensory brain areas. *Journal of Neuroscience, 25*, 10564-10573.

Ehrsson, H.H., Spence, C., & Passingham, R.E. (2004). That's my hand! Activity in premotor cortex reflects feeling of ownership of a limb. *Science, 305*, 875-877.

Ehrsson, H.H., Wiech, K., Weiskopf, N., Dolan, R.J., & Passingham, R.E. (2007). Threatening a rubber hand that you feel is yours elicits a cortical anxiety response. *Proceedings of the National Academy of Sciences of the United States of America, 104*, 9828-9833.

Ehrsson, H.H., Rosén, B., Stockselius, A., Ragnö, C., Köhler, P., & Lundborg, G. (2008). Upper limb amputees can be induced to experience a rubber hand as their own. *Brain, 131*, 3443-3452.

Eklund, G. (1972). Position sense and state of contraction: The effects of vibration. *Journal of Neurology, Neurosurgery, and Psychiatry, 35*, 606-611.

Elbert, T., Flor, H., Birbaumer, N., Knecht, S., Hampson, S., Larbig, W., et al. (1994). Extensive reorganization of the somatosensory cortex in adult humans after nervous system injury. *NeuroReport, 5*, 2593-2597.

Ernst, M.O., & Bülthoff, H.H. (2004). Merging the senses into a robust percept. *Trends in Cognitive Sciences, 8*, 162-169.

Farnè, A., Pavani, F., Meneghello, F., & Làdavas, E. (2000). Left tactile extinction following visual stimulation of a rubber hand. *Brain, 123*, 2350-2360.

Feinberg, T.E., Roane, D.M., & Ali, J. (2000). Illusory limb movements in anosognosia for hemiplegia. *Journal of Neurology, Neurosurgery, and Psychiatry, 68*, 511-513.

Fiorio, M., & Haggard, P. (*2005*). Visual enhancement of touch in primary somatosensory cortex. *European Journal of Neuroscience, 22*, 773-777.

Fiorio, M., Weise, D., Önal-Hartmann, C., Zeller, D., Tinazzi, M., & Classen, J. (2011). Impairment of the rubber hand illusion following focal hand dystonia. *Brain, 134*, 1428-1437.

Fogassi, L., & Gallese, V. (2004). Action as a binding key to multisensory integration. In: G. Calvert, C. Spence and B.E. Stein, Editors, *The handbook of multisensory processes*, Cambridge MA: MIT Press, pp. 425-442.

Fogassi, V., Gallese, L., Fadiga, G., Luppino, M., Matelli, M., & Rizzolatti, G. (1996). Coding of peripersonal space in inferior premotor cortex (area F4). *Journal of Neurophysiology, 76*, 141-157.

Folegatti, A., de Vignemont, F., Pavani, F., Rossetti, Y., & Farnè, A. (2009). Losing one's hand: Visual-proprioceptive conflict affects touch perception. *PLoS One, 4*, e6920.

Folstein, M., Folstein, S., & McHugh, P.R. (1975). Mini-mental state. A practical method for grading the cognitive state of patients for the clinician. *Journal of Psychiatric Research, 12*, 189-198.

Frassinetti, F., Angeli, V., Meneghello, F., Avanzi, S., & Làdavas, E. (2002). Long-lasting amelioration of visuospatial neglect by prism adaptation. *Brain, 125*, 608-623.

Fuentes, C.T., & Bastian, A.J. (2011). Where is your arm? Variations in proprioception across space and tasks. *Journal of Neurophysiology, 103*, 164-171.

Gallagher, S. (2000). Philosophical concepts of the self: Implications for cognitive sciences. *Trends in Cognitive Sciences, 4*, 14-21.

Gallagher, S. (2005). *How the body shapes the mind*. Oxford: Oxford University Press.

Gandevia, S.C., & Phegan, C.M.L. (1999). Perceptual distortions of the human body image produced by local anaesthesia, pain and cutaneous stimulation. *Journal of Physiology, 514*, 609-616.

Giummarra, M.J., Fitzgibbon, B.M., Georgiou-Karisianis, N., Nicholls, M.E.R., Gibson, S.J., & Bradshaw, J.L. (2010). Ouch! My phantom leg jumps/hurts when you stab my "virtual" hand. *Perception, 39*, 1396-1407.

Giummarra, M.J., Georgiou-Karisianis, N., Nicholls, M.E.R., Gibson, S.J., & Bradshaw, J.L. (2010). The phantom in the mirror: A modified rubber-hand illusion in amputees and normals. *Perception, 39*, 103-118.

Goodenough, F. (1926). A new approach to the measurement of intelligence of young children. *Journal of Genetic Psychology, 33*, 185-211.

Goodrich, S.J., & Ward, R. (1997). Anti-extinction following unilateral parietal damage. *Cognitive Neuropsychology, 14*, 595-612.

Goodwin, G.M., McCloskey, D.I., & Matthews, P.B.C. (1972a). Proprioceptive illusions induced by muscle vibration: Contribution by muscle spindles to perception? *Science, 175*, 1382-1384.

Goodwin, G.M., McCloskey, D.I., & Matthews, P.B.C. (1972b). The contribution of muscle afferents to kinaesthesia shown by vibration induced illusions of movement and by the effects of paralysing joint afferents. *Brain, 95*, 705-748.

Guterstam, A., Petkova, V.I., & Ehrsson, H.H. (2011). The illusion of owning a third arm. *PLoS One, 6*, e17208.

Haans, A., IJsselsteijn, W.A., & de Kort, Y.A.W. (2008). The effect of similarities in skin texture and hand shape on perceived ownership of a fake limb. *Body Image, 5*, 389-394.

Haggard, P. & Jundi, S. (2009). Rubber hand illusions and size-weight illusions: self-representation modulates representation of external objects. *Perception, 3*8, 1796-1803.

Haggard, P., Kitadono, K., Press, C., & Taylor-Clarke, M. (2005). The brain's fingers and hands. *Experimental Brain Research, 172*, 94-102.

Haggard, P., Taylor-Clarke, M., & Kennett, S. (2003). Tactile perception, cortical representation and the bodily self. *Current Biology, 13*, R170-R173.

Halligan, P. W., Hunt, M., Marshall, J.C., & Wade, D.T. (1995). Sensory detection without localization. *Neurocase, 1*, 259-266.

Halligan, P. W., Hunt, M., Marshall, J.C., & Wade, D.T. (1996). When seeing is feeling; acquired synaesthesia or phantom touch? *Neurocase, 2*, 21-29.

Halligan, P.W., Marshall, J.C., Hunt, M., & Wade, D.T. (1997). Somatosensory assessment: Can seeing produce feeling? *Journal of Neurology, 244,* 199-203.

Halligan, P.W., Marshall, J.C., & Wade, D.T. (1993). Three arms: A case study of supernumerary phantom limb after right hemisphere stroke. *Journal of Neurology, Neurosurgery, and Psychiatry, 56*, 159-166.

Hartcher-O'Brien, J., Levitan, C., & Spence, C. (2010). Extending visual dominance over touch for input off the body. *Brain Research, 1362*, 48-55.

Head, H., & Holmes, G. (1911). Sensory disturbances from cerebral lesions. *Brain, 34*, 102-254.

Hesse, M.D., Nishitani, N., Fink, G.R., Jousmäki, V., & Hari, R. (2010). Attenuation of somatosensory responses to self-produced tactile stimulation. *Cerebral Cortex, 20*, 425-432.

Hohwy, J., & Paton, B. (2010). Explaining away the body: Experiences of supernaturally caused touch and touch on non-hand objects within the rubber hand illusion. *PLoS One, 5*, e9416.

Holmes, N. P., Crozier, G., & Spence, C. (2004). When mirrors lie: 'Visual capture' of arm position impairs reaching performance. *Cognitive, Affective, and Behavioral Neuroscience, 4*, 193-200.

Holmes, N.P., Snijders, H.J., & Spence, C. (2006). Reaching with alien limbs: Visual exposure to prosthetic hands in a mirror biases proprioception without accompanying illusions of ownership. *Perception and Psychophysics, 68*, 685-701.

Holmes, N.P., & Spence, C. (2005). Multisensory integration: Space, time, and superadditivity. *Current Biology, 15*, R762-R764.

Honma, M., Koyama, S., Osada, Y. (2009). Double tactile sensations evoked by a single visual stimulus on a rubber hand. *Neuroscience Research, 65*, 307-311.

Husain, M., & Rorden, C. (2003). Non-spatially lateralized mechanisms in hemispatial neglect. *Nature, 4*, 26-36.

IJsselsteijn, W.A., de Kort, Y.A.W., & Haans, A. (2006). Is this *my* hand I see before me? The Rubber Hand Illusion in Reality, Virtual Reality, and Mixed Reality. *Presence: Teleoperators and Virtual Environments, 15*, 455-464.

Irika, A., Tanaka, M., & Iwamura, Y. (1996). Coding of modified body schema during tool use by macaque postcentral neurones. *NeuroReport, 7*, 2325-2330.

Jacquin-Courtois, S., Rode, G., Pisella, L., Boisson, D., & Rossetti, Y. (2008). Wheel-chair driving improvement following visuo-manual prism adaptation. *Cortex, 44*, 90-96.

James, W. (1990). *The principles of psychology*. Cambridge MA: Harvard University Press.

Jones, L.A. (2000). Kinaesthetic Sensing. In M. Srinivasan & M. Cutkosky (Eds.) *Human and Machine Haptics*. Cambridge: MIT Press.

Kammers, M.P., de Vignemont, F., Verhagen, L., & Dijkerman, H.C. (2009). The rubber hand illusion in action. *Neuropsychologia, 47*, 204-211.

Kammers, M.P., Kootker, J.A., Hogendoorn, H., & Dijkerman, H.C. (2010). How many motoric body representations can we grasp? *Experimental Brain Research, 202*, 203-212.

Kammers, M.P., Longo, M.R., Tsakiris, M., Dijkerman, H.C., & Haggard, P. (2009). Specificity and coherence of body representations. *Perception, 38*, 1804-1820.

Kammers, M.P.M., Rose, K., & Haggard, P. (2011). Feeling numb: Temperature, but not thermal pain, modulates feeling of body ownership. *Neuropsychologia, 49*, 1316-1321.

Kammers, M.P., Verhagen, L., Dijkerman, H.C., Hogendoorn, H., de Vignemont, F., Schutter, D.J. (2009). Is this hand for real? Attenuation of the rubber hand illusion by transcranial magnetic stimulation over the inferior parietal lobule. *Journal of Cognitive Neuroscience, 21*, 1311-1320.

Kanayama, N., Sato, A., & Ohira, H. (2007). Crossmodal effect with rubber hand illusion and gamma-band activity. *Psychophysiology, 44*, 392-402.

Kanayama, N., Sato, A., & Ohira, H. (2009). The role of gamma band oscillations and synchrony on rubber hand illusion and crossmodal integration. *Brain and Cognition, 69*, 19-29.

Kennett, S., Taylor-Clarke, M., & Haggard, P. (2001). Noninformative vision improves the spatial resolution of touch in humans. *Current Biology, 11*, 1188-1191.

Kew, J.J.M., Ridding, M.C., Rothwell, J.C., Passingham, R.E., Leigh, P.N., Sooriakumaran, S., et al. (1994). Reorganization of cortical blood flow and transcranial magnetic stimulation maps in human subjects after upper limb amputation. *Journal of Neurophysiology, 72*, 2517-2524.

Khateb, A., Simon, S.R., Dieguez, S., Lazeyras, F., Momjian-Mayor, I., Blanke, O., Landis, T., Pegna, A.J., Annoni, J.-M. (2009). Seeing the phantom: A functional magnetic resonance imaging study of a supernumerary phantom limb. *Annals of Neurology, 65*, 698-705.

Kinsbourne, M. (1995). Awareness of one's own body: An attentional theory of its nature, development, and brain basis. In: J.L. Bermúdez, A. Marcel and N. Eilan, Editors, *The body and the self*, England: MIT Press, pp. 205-224.

Kitadono, K., & Humphreys, G.W. (2007). Short-term effects of the 'rubber hand' illusion on aspects of visual neglect. *Neurocase, 13*, 260-271.

Körding, K.P., Beierholm, U., Ji Ma, W., Quartz, S., Tenenbaum, J.B., & Shams, L. (2007). Causal inference in multisensory perception. *PLoS One, 2*, e943.

Kusoffsky, A., Wadell, I., & Nilsson, B.Y. (1982). The relationship between sensory impairment and motor recovery in patients with hemiplegia. *Scandinavian Journal of Rehabilitation Medicine, 14*, 27-32.

Lackner, J.R. (1988). Some proprioceptive influences on the perceptual representation of body shape and orientation. *Brain, 111*, 281-297.

Lahav, R. (1993). What neuropsychology tells us about consciousness. *Philosophy of Science, 60*, 67-85.

Lewis, E., & Lloyd, D. (2010). Embodied experience: A first-person investigation of the rubber hand illusion. *Phenomenology and the Cognitive Sciences, 9*, 317-339.

Lincoln, N.B., Jackson, J.M., & Adams, S.A. (1998). Reliability and revision of the Nottingham Sensory Assessment for stroke patients. *Physiotherapy, 84*, 358-365.

Lloyd, D.M. (2007). Spatial limits on referred touch to an alien limb may reflect boundaries of visuo-tactile peripersonal space surrounding the hand. *Brain and Cognition, 64*, 104-109.

Lloyd, D., Morrison, I., & Roberts, N. (2006). Role for human posterior parietal cortex in visual processing of aversive objects in peripersonal space. *Journal of Neurophysiology, 95*, 205-214.

Longo, M.R., Azañón, E., & Haggard, P. (2010). More than skin deep: Body representation beyond primary somatosensory cortex. *Neuropsychologia, 48*, 655-668.

Longo, M.R., & Haggard, P. (2009). Sense of agency primes manual motor responses. *Perception, 38*, 69-78.

Longo, M.R., Cardozo, S., & Haggard, P. (2008). Visual enhancement of touch and the bodily self. *Consciousness and Cognition, 17*, 1181-1191.

Longo, M.R., Schüür, F., Kammers, M.P.M., Tsakiris, M., & Haggard, P. (2008). What is embodiment? A psychometric approach. *Cognition, 107*, 978-998.

Longo, M.R., Schüür, F., Kammers, M.P.M., Tsakiris, M., & Haggard, P. (2009). Self awareness and the body image. *Acta Psychologica, 132*, 166-172.

Lopez, C., Lenggenhager, B., & Blanke, O. (2010). How vestibular stimulation interacts with illusory hand ownership. *Consciousness and Cognition, 19*, 33-47.

Luauté, J., Schwartz, S., Rossetti, Y., Spiridon, M., Rode, G., Boisson, D., et al. (2009). Dynamic changes in brain activity during prism adaptation. *The Journal of Neuroscience, 29*, 169-178.

Macaluso, E., Driver, J., & Frith, C.D. (2003). Multimodal spatial representations engaged in human parietal cortex during both saccadic and manual spatial orienting. *Current Biology, 13*, 990-999.

Makin, T.R., Holmes, N.P., & Ehrsson, H.H. (2008). On the other hand: Dummy hands and peripersonal space. *Behavioural Brain Research, 191*, 1-10.

Marasco, P.D., Kim, K., Edward Colgate, J., Peshkin, M.A., & Kuiken, T.A. (2011). Robotic touch shifts perception of embodiment to a prosthesis in targeted reinnervation amputees. *Brain, 134*, 747-758.

Maravita, A., McNeil, J., Malhotra, P., Greenwood, R., Husain, M., & Driver, J. (2003). Prism adaptation can improve contralesional tactile perception in neglect. *Neurology, 60*, 1829-1831.

Marcel, A. J., Tegnér, R., & Nimmo-Smith, I. (2004). Anosognosia for plegia: Specificity, extension, partiality and disunity of bodily unawareness. *Cortex, 40*, 19-40.

McGurk, H., & MacDonald, J. (1976). Hearing lips and seeing voices. *Nature, 264*, 746-748.

McIntosh, R.D., Brodie, E.E., Beschin, N., & Robertson, I.H. (2000) Improving the clinical diagnosis of personal neglect: Reformulating the comb and razor test. *Cortex, 36*, 289-292.

Merzenich, M.M., Nelson, R.J., Stryker, M.P., Cynader, M.S., Schoppmann, A., & Zook, J.M. (1984). Somatosensory cortical map changes following digit amputation in adult monkeys. *The Journal of Comparative Neurology, 224*, 591-605.

Michael, G.A. (2007). A significance test of interaction in 2 x K designs with proportions. *Tutorials in Quantitative Methods for Psychology, 3*, 1-7.

Michel, C., Rossetti, Y., Rode, G., & Tilikete, C. (2003). After-effects of visuo-manual adaptation to prisms on body posture in normal subjects. *Experimental Brain Research, 148*, 219-226.

Miles, E. (2008). What can the rubber hand illusion tell us about body representation in people with unexplained symptoms. In *Symposium conducted at the Body Representation Workshop*, University of Nottingham, UK.

Mogilner, A., Grossman, J.A.I., Ribary, U., Joliot, M., Volkmann, J., Rapaport, D., et al. (1993). Somatosensory cortical plasticity in adult humans revealed by magnetoencephalography. *Proceedings of the National Academy of Sciences of the United States of America, 90*, 3593-3597.

Morgan, H.L., Turner, D.C., Corlett, P.R., Absalom, A.R., Adapa, R., Arana, F.S. et al. (2011). Exploring the impact of ketamine on the experience of illusory body ownership. *Biological Psychiatry, 69*, 35-41.

Moro, V., Zampini, M., & Aglioti, S.M. (2004). Changes in spatial position of hands modify tactile extinction but not disownership of contralesional hand in two right brain-damaged patients. *Neurocase, 10*, 437-443.

Moscovitch, M., & Behrmann, M. (1994). Coding of spatial information in the somatosensory system: Evidence from patients with neglect following parietal lobe damage. *Journal of Cognitive Neuroscience, 6*, 151-155.

Moseley, G.L., Olthof, N., Venema, A., Don, S., Wijers, M., Gallace, A., & Spence, C. (2008). Psychologically induced cooling of a specific body part caused by the illusory ownership of an artificial counterpart. *Proceedings of the National Academy of Sciences, 105*, 13169-13173.

Mussap, A. J., & Salton, N. (2006). A 'rubber-hand' illusion reveals a relationship between perceptual body image and unhealthy body change. *Journal of Health Psychology, 11*, 627-639.

Newport, R., Pearce, R., & Preston, C. (2010). Fake hands in action: Embodiment and control of supernumerary limbs. *Experimental Brain Research, 204*, 385-395.

Niebauer, C.L., Aselage, J., & Schutte, C. (2002). Hemispheric interaction and consciousness: degree of handedness predicts the intensity of a sensory illusion. *Laterality, 7*, 85-96.

Nielsen, T. I. (1963). Volition: A new experimental approach. *Scandinavian Journal of Psychology, 4*, 225-230.

Nobre, A.C. (2001). Orienting attention to instants in time. *Neuropsychologia, 39*, 1317-1328.

Ocklenburg, S., Ruther, N., Peterburs, J., Pinnow, M., & Gunturkun, O. (2010). Laterality in the rubber hand illusion. *Laterality, 16*, 174-187.

Ogden, J.A. (1985) Anterior-posterior interhemispheric differences in the loci of lesions producing visual hemineglect. *Brain and Cognition, 4*, 59-75.

Oldfield, R.C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia, 9*, 97-113.

Paillard, J., & Brouchon, M. (1968). Active and passive movements in the calibration of position sense. In: Freedman SJ, editor. *The neuropsychology of spatially oriented behavior*. Illinois: Dorsey Press, pp. 37-56.

Paillard, J., Michel, F., & Stelmach, G. (1983). Localization without content: A tactile analogue of 'Blind Sight'. *Archives of Neurology, 40*, 548-551.

Pardo, J.V., Fox, P.T., & Raichle, M.E. (1991). Localization of a human system for sustained attention by positron emission tomography. *Nature, 349*, 61-64.

Pavani, F., Spence, C., & Driver, J. (2000). Visual capture of touch: Out-of-body experiences with rubber gloves. *Psychological Science, 11*, 353-359.

Pavani, F., & Zampini, M. (2007). The role of hand size in the fake-hand illusion paradigm. *Perception, 36*, 1547-1554.

Peled, A., Ritsner, M., Hirschmann, S., Geva, A.B., & Modai, I. (2000). Touch feel illusion in schizophrenic patients. *Biological Psychiatry, 48*, 1105-1108.

Peled, A., Pressman, A., Geva, A.B., & Modai, I. (2003). Somatosensory evoked potentials during a rubber hand illusion in schizophrenia. *Schizophrenia Research, 64*, 157-163.

Perez-Marcos, D., Slater, M., & Sanchez-Vives, M.V. (2009). Inducing a virtual hand ownership illusion through a brain-computer interface. *NeuroReport, 20*, 589-594.

Petkova, V.I., & Ehrsson, H.H. (2008). If I were you: Perceptual illusion of body swapping. *PLoS One, 3*, e3832.

Petkova, V.I., & Ehrsson, H.H. (2009). When right feels left: Referral of touch and ownership between the hands. *PLoS One, 4*, e6933.

Press, C., Taylor-Clarke, M., Kennett, S., & Haggard, P. (2004). Visual enhancement of touch in spatial body representation. *Experimental Brain Research, 154*, 238-245.

Press, C., Heyes, C., Haggard, P., & Eimer, M. (2008). Visuotactile learning and body representation: an ERP study with rubber hands and rubber objects. *Journal of Cognitive Neuroscience, 20*, 312-323.

Ramachandran, V.S. (1993). Behavioral and magnetoencephalographic correlates of plasticity in the adult human brain. *Proceedings of the National Academy of Sciences of the United States of America, 90*, 10413-10420.

Ramachandran, V.S., & Hirstein, W. (1997). Three laws of qualia. *Journal of Consciousness Studies, 4*, 429-457.

Ramachandran, V.S., & Hirstein, W. (1998). The perception of phantom limbs: The D. O. Hebb lecture. *Brain, 121*, 1603-1630.

Ramachandran, V.S., & Rogers-Ramachandran, D. (1996). Synaesthesia in phantom limbs induced with mirrors. *Proceedings of the Royal Society of London B, 263*, 377-386.

Ramachandran, V.S., Stewart, M., & Rogers-Ramachandran, D.C. (1992). Perceptual correlates of massive cortical reorganization. *NeuroReport, 3*, 583-586.

Rapp, B., Hendel, S.K., & Medina, J. (2002). Remodeling of somatosensory hand representations following cerebral lesions in humans. *NeuroReport, 13*, 207-211.

Redding, G.M., & Wallace, B. (2006). Prism adaptation and unilateral neglect: Review and analysis. *Neuropsychologia, 44*, 1-20.

Reed, C.L., Garza, J.P., & Roberts Jr, R.J. (2007). The influence of the body and action on spatial attention. *Lecture Notes in Computer Science, 4840*, 42-58.

Rizzolatti, G., Riggio, L., Dascola, I., & Umilta, C. (1987). Reorienting attention across the horizontal and vertical meridians: Evidence in favor of a premotor theory of attention. *Neuropsychologia, 25*, 31-40.

Rode, G., Rossetti, Y., & Boisson, D. (2001). Prism adaptation improves representational neglect. *Neuropsychologia, 39*, 1250-1254.

Rohde, M., Di Luca, M., & Ernst, M.O. (2011). The rubber hand illusion: Feeling of ownership and proprioceptive drift do not go hand in hand. *PLoS ONE, 6*, e21659.

Roland, P. E. (1987). Somatosensory detection in patients with circumscribed lesions of the brain. *Experimental Brain Research, 66*, 303-317.

Rolke, B., & Hofmann, P. (2007). Temporal uncertainty degrades perceptual processing. *Psychonomic Bulletin and Review, 14*, 522-526.

Romo, R., & Salinas, E. (1999). Sensing and deciding in the somatosensory system. *Current Opinion in Neurobiology, 9*, 487-493.

Rorden, C., Heutink, J., Greenfield, E., & Robertson, I.H. (1999). When a rubber hand 'feels' what the real hand cannot, *NeuroReport, 10*, 135-138.

Rosén, B., Ehrsson, H.H., Antfolk, C., Cipriani, C., Sebelius, F., & Lundborg, G. (2009). Referral of sensation to an advanced humanoid robotic hand prosthesis. *Scandanavian Journal of Plastic and Reconstructive Surgery and Hand Surgery, 43*, 260-266.

Rossetti, Y., Rode, G., & Boisson, D. (1995). Implicit processing of somaesthetic information: A dissociation between where and how? *NeuroReport, 15*, 506-510.

Rossetti, Y., Rode, G., Pisella, L., Farné, A., Li, L., Boisson, D., et al. (1998). Prism adaptation to a rightward optical deviation rehabilitates left hemispatial neglect. *Nature, 395*, 166-169.

Roux, F. E., Boulanouar, K., Ibarrola, D., Tremoulet, M., Chollet, F., & Berry, I. (2000). Functional MRI and intraoperative brain mapping to evaluate brain plasticity in patients with brain tumours and hemiparesis. *Journal of Neurology, Neurosurgery, and Psychiatry, 69*, 453-463.

Rueckert, L., & Grafman, J. (1996). Sustained attention deficits in patients with right frontal lesions. *Neuropsychologia, 34*, 953-963.

Sanchez-Vives, M.V., Spanlang, B., Frisoli, A., Bergamasco, M., & Slater, M. (2010). Virtual hand illusion induced by visuomotor correlations. *PLoS One, 5*, e10381.

Schaechter, J.D., Moore, C.I., Connell, B.D., Rosen, B.R., & Dijkhuizen, R.M. (2006). Structural and functional plasticity in the somatosensory cortex of chronic stroke patients. *Brain, 129*, 2722-2733.

Schaefer, M., Noennig, N., Heinze, H.J., & Rotte, M. (2006). Fooling your feelings: artificially induced referred sensations are linked to a modulation of the primary somatosensory cortex. *Neuroimage, 29*, 67-73.

Schaefer, M., Flor, H., Heinze, H.-J., & Rotte, M. (2007). Morphing the body: Illusory feeling of an elongated arm affects somatosensory homunculus. *NeuroImage, 36*, 700-705.

Schaefer, M., Heinze, H.-J., & Rotte, M. (2009). My third arm: Shifts in topography of the somatosensory homunculus predict feeling of an artificial supernumerary arm. *Human Brain Mapping, 30*, 1413-1420.

Schenkenberg, T., Bradford, D.C., & Ajax, E.T. (1980). Line bisection and unilateral visual neglect in patients with neurologic impairment. *Neurology, 30*, 509-517.

Schütz-Bosbach, S., Avenanti, A., Aglioti, S. M., & Haggard, P. (2009). Don't do it! Cortical inhibition and self-attribution during action observation. *Journal of Cognitive Neuroscience, 21*, 1215-1227.

Schütz-Bosbach, S., Mancini, B., Aglioti, S.M., & Haggard, P. (2006). Self and other in the human motor system. *Current Biology, 16*, 1830-1834.

Schütz-Bosbach, S., Musil, J.J., & Haggard, P. (2009). Touchant-touché: The role of self-touch in the representation of body structure. *Consciousness and Cognition, 18*, 2-11.

Schütz-Bosbach, S., Tausche, P., & Weiss, C. (2009). Roughness perception during the rubber hand illusion. *Brain and Cognition, 70*, 136-144.

Schwartz, R.L., Barrett, A.M., Kim, M., & Heilman, K.M. (1999). Ipsilesional intentional neglect and the effect of cueing. *Neurology, 53*, 2017-2022.

Schweizer, R., Maier, M., Braun, C., & Birbaumer, N. (2000). Distribution of mislocalizations of tactile stimuli on the fingers of the human hand. *Somatosensory and Motor Research, 17*, 309-316.

Serino, A., Farnè, A., Rinaldesi, M.L., Haggard, P., & Làdavas, E. (2007). Can vision of the body ameliorate impaired somatosensory function? *Neuropsychologia, 45*, 1101-1107.

Shimada, S., Fukuda, K., & Hiraki, K. (2009). Rubber hand illusion under delayed visual feedback. *PLoS One, 4*, e6185.

Slater, M., Spanlang, B., Sanchez-Vives, M.V., & Blanke, O. (2010). First person experience of body transfer in virtual reality. *PLoS One, 5*, e10564.

Smania, N., & Aglioti, S. (1995). Sensory and spatial components of somaesthetic deficits following right brain damage. *Neurology, 45*, 1725-1730.

Smania, N., Montagnana, B., Faccioli, S., Fiaschi, A., & Aglioti, S.M. (2003). Rehabilitation of somatic sensation and related deficit of motor control in patients with pure sensory stroke. *Archives of Physical Medicine and Rehabilitation, 84*, 1692-1702.

Spence, C., & Squire, S. (2003). Multisensory integration: Maintaining the perception of synchrony. *Current Biology, 13*, R519-R521.

Spinazzola, L., Pia, L., Folegatti, A., Marchetti, C., & Berti, A. (2008). Modular structure of awareness for sensorimotor disorders: Evidence from anosognosia for hemiplegia and anosognosia for hemianaesthesia. *Neuropsychologia, 46*, 915-926.

Sturm, W., & Willmes, K. (2001). On the functional neuroanatomy of intrinsic and phasic alertness. *NeuroImage, 14*, S76-S84.

Takasugi, J., Matsuzawa, T., Murayama, T., Nakazawa, K., Numata, K., & Shimizu, E. (2011). Referred sensations induced by a mirror box in healthy subjects. *Psychological Research, 75*, 54-60.

Taylor-Clarke, M., Kennett, S., & Haggard, P. (2002).Vision modulates somatosensory cortical processing. *Current Biology, 12*, 233-236.

Taylor-Clarke, M., Kennett, S. & Haggard, P. (2004). Persistence of visual-tactile enhancement in humans. *Neuroscience Letters, 354*, 22-25.

Tessari, A., Tsakiris, M., Borghi, A.M., & Serino, A. (2010). The sense of body: A multidisciplinary approach to body representation. *Neuropsychologia, 48*, 643-644.

Tham, K., & Tegnér, R. (1996). The baking tray task. A test of spatial neglect. *Neuropsychological Rehabilitation, 6*, 19-25.

Tilikete, C., Rode, G., Rossetti, Y., Pichon, J., Li, L., & Boisson, D. (2001). Prism adaptation to rightward optical deviation improves postural imbalance in left-hemiparetic patients. *Current Biology, 11*, 524-528.

Tinazzi, M., Ferrari, G., Zampini, M., & Aglioti, S.M. (2000). Neuropsychological evidence that somatic stimuli are spatially coded according to multiple frames of reference in a stroke patient with tactile extinction. *Neuroscience Letters, 23*, 133-136.

Tsakiris, M. (2010). My body in the brain: A neurocognitive model of body-ownership. *Neuropsychologia, 48*, 703-712.

Tsakiris, M., Carpenter, L., James, D., & Fotopoulou, A. (2010). Hands only illusion: Multisensory integration elicits sense of ownership for body parts but not for non-corporeal objects. *Experimental Brain Research, 204*, 343-352.

Tsakiris, M., Costantini, M., & Haggard, P. (2008). The role of the right temporo-parietal junction in maintaining a coherent sense of one's body. *Neuropsychologia, 46*, 3104-3018.

Tsakiris, M., & Haggard, P. (2005). The rubber hand illusion revisited: Visuotactile integration and self-attribution. *Journal of Experimental Psychology: Human Perception and Performance, 31*, 80-91.

Tsakiris, M., Hesse, M.D., Boy, C., Haggard, P., & Fink, G.R. (2007). Neural signatures of body ownership: A sensory network for bodily self-consciousness. *Cerebral Cortex, 17*, 2235-2244.

Tsakiris, M., Prabhu, G., & Haggard, P. (2006). Having a body *versus* moving your body: How agency structures body-ownership. *Consciousness and Cognition, 15*, 423-432.

Tsakiris, M., Tajadura-Jiménez, A., & Costantini, M. (2011). Just a heartbeat away from one's body: Interoceptive sensitivity predicts malleability of body-representations. *Proceedings of the Royal Society of London B, 278*, 2470-2476.

Umilta, C. (2000). Visuospatial Attention. In F. Boller, J. Grafman, G. Rizzolatti, L.S. Cermak (eds.). *Handbook of Neurology. 7: Introduction.* Elsevier Health Sciences, pp. 393-426.

Valentini, M., Kischka, U., & Halligan, P.W. (2008). Residual haptic sensation following stroke using ipsilateral stimulation. *Journal of Neurology, Neurosurgery, and Psychiatry, 79*, 266-270.

Vallar, G. (1997). Spatial frames of reference and somatosensory processing: A neuropsychological perspective. *Philosophical Transactions of the Royal Society of London B, 352*, 1401-1409.

van Beers, R.J., Sittig, A.C., & Denier van der Gon, J.J. (1998). The precision of proprioceptive position sense. *Experimental Brain Research, 122*, 367-377.

van Beers, R.J., Sittig, A.C., & Denier van der Gon, J.J. (1999). Integration of proprioceptive and visual position-information: An experimentally supported model. *Journal of Neurophysiology, 81*, 1355-1364.

Van Mierlo, C.M., Brenner, E., & Smeets, J.B. (2007). Temporal aspects of cue combination. *Journal of Vision, 7*, 1-11.

Von Hofsten, C., & Rösblad, B. (1988). The integration of sensory information in the development of precise manual pointing. *Neuropsychologia, 26*, 805-821.

Waberski, T.D., Gobbelé, R., Kawohl, W., Cordes, C., & Buchner, H. (2003). Immediate cortical reorganization after local anaesthetic block of the thumb: Source localization of somatosensory evoked potentials in human subjects. *Neuroscience Letters, 347*, 151-154.

Wall, J.T., Huerta, M.F., & Kaas, J.H. (1992). Changes in the cortical map of the hand following postnatal median nerve injury in monkeys: Modification of somatotopic aggregates. *The Journal of Neuroscience, 12*, 3445-3455.

Walsh, L.D., Moseley, L., Taylor, J.L., & Gandevia, S.C. (2011). Proprioceptive signals contribute to the sense of body ownership. *Journal of Physiology, 589*, 3009-3021.

Walton, M., & Spence, C. (2004). Crossmodal congruency and visual capture in a visual elevation-discrimination task. *Experimental Brain Research, 154*, 113-120.

Wann, J.P., & Ibrahim, S.F. (1992). Does limb proprioception drift? *Experimental Brain Research, 91*, 162-166.

Weiskrantz, L. (1986). *Blindsight: A case study and implications*. Oxford: Clarendon Press.

Weiskrantz, L., Elliot, J., & Darlington, C. (1971). Preliminary observations on tickling oneself. *Nature, 230*, 598-599.

Weiskrantz, L., & Zhang, D. (1987). Residual tactile sensitivity with self-directed stimulation in hemianaesthesia. *Journal of Neurology, Neurosurgery, and Psychiatry, 50*, 632-634.

Wolpert, D.M., & Flanagan, J.R. (2001). Motor prediction. *Current Biology, 11*, R729-R732.

White, R. C., & Aimola Davies, A. M. (2011). Touching my left elbow: The anatomical structure of the body affects the illusion of self-touch. *Perception, 40*, 95-98.

White, R.C., Aimola Davies, A.M., & Davies, M. (2011). Two hands are better than one: A new assessment method and a new interpretation of the non-visual rubber hand illusion. *Consciousness and Cognition, 20*, 956-964.

White, R.C., Aimola Davies, A.M., Halleen, T.J., & Davies, M. (2010). Tactile expectations and the perception of self-touch: An investigation using the rubber hand paradigm. *Consciousness and Cognition, 19*, 505-519.

White, R. C., Aimola Davies, A. M., & Kischka, U. (2010). Errors of somatosensory localisation in a patient with right hemisphere stroke. *Neurocase, 16*, 238-258.

White, R. C., Aimola Davies, A. M., Kischka, U., & Davies, M. (2010). Touch and Feel? Using the rubber hand paradigm to investigate self-touch enhancement in right-hemisphere stroke patients. *Neuropsychologia*, *48*, 26-37.

Wilkins, A.J., Shallice, T., & McCarthy, R. (1987). Frontal lesions and sustained attention. *Neuropsychologia, 25*, 359-365.

Wilson, B., Cockburn, J., & Halligan, P. (1987). Development of a behavioural test of visuo-spatial neglect. *Archives of Physical Medicine and Rehabilitation, 68*, 98-102.

Wilson, E.B. (1927). Probable inference, the law of succession, and statistical inference. *Journal of the American Statistical Association, 22*, 209-212.

Wolpert, D.L. (1997). Computational approaches to motor control. *Trends in Cognitive Sciences, 1*, 209-216.

Zeller, D., Gross, C., Bartsch, A., Johansen-Berg, H., & Classen, J. (2011). Ventral premotor cortex may be required for dynamic changes in the feeling of limb ownership: A lesion study. *The Journal of Neuroscience, 31*, 4852-4857.

Zoccolotti, P., & Judica, A. (1991). Functional evaluation of hemineglect by means of a semistructured scale: Personal and extrapersonal differentiation. *Neuropsychological Rehabilitation, 1*, 33-44.

Zopf, R., Savage, G., & Williams, M.A. (2010). Crossmodal congruency measures of lateral distance effects on the rubber hand illusion. *Neuropsychologia, 48*, 713-725.

Zopf, R., Truong, S., Finkbeiner, M., Friedman, J., & Williams, M.A. (2011). Viewing and feeling touch modulates hand position for reaching. *Neuropsychologia, 49*, 1287-1293.

APPENDIX 1. METHODS FOR ASSESSING PROPRIOCEPTIVELY PERCEIVED HAND POSITION

Reference	**Method**	**Instruction to Participant**
Botvinick & Cohen (1998).	Intermanual pointing under the table	Finger drawn below the table until it was judged to be in alignment with the index finger of the left hand.
Tsakiris & Haggard (2005).	Reporting numbers off a ruler	"Where is your index finger?"
IJsselsteijn et al. (2006).	Intermanual pointing under the table	Finger drawn below the table until it was judged to be in alignment with the index finger of the left hand.
Schütz-Bosbach et al. (2006).	ns	ns
Tsakiris et al. (2006).	Reporting numbers off a ruler	"Where is your index/little finger?"
Costantini & Haggard (2007).	Reporting numbers off a ruler	"Where is the knuckle of your middle finger?"
Durgin et al. (2007).	Intermanual pointing on top of the table	Participant indicated the felt location of the left thumb.
Pavani & Zampini (2007).	Intermanual pointing under the table	Participant asked to indicate the perceived position of the fingertip of the left middle finger.
Tsakiris et al. (2007).	Reporting numbers off a ruler	"Where is your middle finger?"
Ehrsson et al. (2008).	Intermanual pointing on top of the table	Participant closed eyes and pointed to where s/he had felt the touches.
Haans et al. (2008).	Intermanual pointing on top of a testing unit	Participant asked to slide her/his hand over the table to indicate the felt position of her/his left hand.
Longo et al. (2008a).	Reporting numbers off a ruler	Participant asked to indicate where it felt like the tip of her/his index finger was located.
Slater et al. (2008).	Participant placed blue-tack in felt location	Participant asked to place blue-tack in a position corresponding to where s/he felt the centre of her/his right palm to be.
Capelari et al. (2009).	Intermanual pointing under the table	Finger drawn below the table until judged to be in alignment with the index finger of the right hand.
Folegatti et al. (2009).	Reporting numbers off a ruler	Participant asked to report the number corresponding to the position of the middle finger.
Haggard & Jundi (2009).	Intermanual pointing	Participant reached with the right hand to point to the location of the left hand.

Reference	Method	Instruction to Participant
Kammers, de Vignemont et al. (2009).	1. Ballistic reaching movement toward hand 2. Grasping the ends of sticks of different lengths 3. Indicating when Examiner's hands mirror the position of the participant's own hands 4. Indicating which stick resembles perceived distance between hands	1. Participant asked to reach directly with one hand to the tip of the index finger of the other hand in a single smooth movement. 2. Participant asked to grasp horizontally-presented stick at the two ends between both index fingers. 3. Participant asked to mentally draw a line from the location of the Examiner's index fingers to the felt location of her own index fingers, and to report when the Examiner mirrored the perceived position of her own fingers. 4. Participant asked to indicate verbally which stick (of eight) resembled the perceived distance between her two index fingers.
Kammers, Verhagen et al. (2009).	1. Indicating when Examiner's hands mirror the position of the participant's own hands 2. Ballistic reaching movement toward hand	1. Participant was free to verbally instruct the Examiner to move his index fingers until the participant thought they mirrored the felt location of her own unseen index fingers. 2. Participant asked to reach to the perceived location of the index finger.
Kammers, Longo et al. (2009).	1. Reporting numbers off a ruler 2. Pointing to an external object with the hidden hand	1. Participant verbally reported the number corresponding to the location of the tip of the right index finger. 2. Participant pointed (beneath a board) to the location corresponding to the base of a vertical stick presented on top of the board.
Perez-Marcos et al. (2009).	Participant placed blue-tack in felt location	Participant asked to point under the table to the felt position of the left hand (centre of palm).
Petkova & Ehrsson (2009).	Intermanual pointing on top of the table	Participant asked to move finger until it was immediately above where s/he felt the right hand to be.
Rosén et al. (2009).	Intermanual pointing on top of the table	Participant closed eyes and pointed to where s/he had felt the touches.
Schütz-Bosbach, Avenanti et al. (2009).	Reporting numbers off a ruler	Cf. Tsakiris and Haggard (2005) – presumably "Where is your index finger?"
Schütz-Bosbach, Tausche, & Weiss (2009).	Reporting numbers off a ruler	Participant asked to report the number corresponding to the perceived position of the index finger.
Shimada et al. (2009).	Intermanual pointing under the table	Participant asked to reach to the estimated position of the right index finger.

Reference	Method	Instruction to Participant
Lewis & Lloyd (2010).	Indicate when Examiner had slid marker over the index finger	Participant asked to indicate when the Examiner slid a marker over the perceived location of the index finger.
Lopez et al. (2010).	Reporting numbers off a ruler	Participant asked to indicate the perceived position of the left index finger by reporting the precise number corresponding to the position of the index finger.
Sanchez-Vives et al. (2010).	Participant placed blue-tack in felt location	Participant asked to place blue-tack under the board where the forearm rested.
Tsakiris et al. (2010).	Reporting numbers off a ruler	"Where is your index finger?"
Zopf et al. (2010).	Reporting numbers off a ruler	Participant asked to report the number corresponding to the position of the index finger.
Albrecht et al. (in press).	Pointing to space above middle finger	Participant asked to point, on an imaginary line above the hand, to the location of the middle finger.
Asai et al. (in press).	Reporting numbers off a ruler	Participant asked to report the location of the middle finger as accurately as possible.
Bertamini et al. (in press).	Pointing to the position of the left middle finger	With eyes closed, the participant pointed to the position of the left middle finger.
Curt et al. (2011).	Reporting numbers off a ruler	"Proprioceptive drift was assessed by having the patient indicate the felt position of his invisible [supernumerary] middle finger by means of rulers with arbitrary scaling."
Fiorio et al. (2011).	Reporting numbers off a ruler	Participant asked to report the number corresponding to the felt position of the index finger.
Kammers et al. (2011).	Reporting numbers off a ruler	The participant was asked to report the coordinate on the ruler corresponding to the perceived location of the right index finger.
Morgan et al. (2011).	Reporting numbers off a ruler	Participant asked to imagine a vertical line from the right index finger to the ruler, reporting the corresponding number.
Rohde et al. (2011).	1. Indicating whether an illuminated white dot was to the left or to the right of the participant's hidden hand 2. Lining up an illuminated white dot with the participant's hidden hand	1. Two alternative forced-choice: Participant asked to judge if the dot was to the left or to the right of the perceived position of the unseen index finger. 2. Participant asked, using the scroll of a computer mouse, to adjust the position of a projected dot to match the lateral perceived position of the occluded left index finger.
Tsakiris et al. (2011).	Reporting numbers off a ruler	Participants were asked, "Where do you feel your left index finger is?" and in response, they verbally reported numbers on a ruler.
Walsh et al. (2011).	Reporting numbers off a ruler	Participants asked to report "the number of the line that is level with the tip of your index finger."

APPENDIX 2. METHODOLOGICAL DETATILS FOR 81 STUDIES INVESTIGATING THE VISUAL RUBBER HAND ILLUSION

	Reference	Paradigm	Viewed Hand	Distance Between Hands	Instrument	Stimulation	Trial Length	Assessment
1	Botvinick & Cohen (1998).	Visuo-tactile	Prosthetic left hand	ns	Paintbrush	Stroking	E1. 10 min E2. 30 min	1. Open-ended description 2. Questionnaire 3. Proprioceptive drift
2	Rorden et al. (1999).	Visuo-tactile	Examiner's right hand or prosthetic left hand	ns	Patient viewed LED lights on the Examiner's hand or a rubber hand	Patient received stimulation (taps) via a solenoid	2 blocks of 50 trials	1. Tactile detection task
3	Farnè et al. (2000).	Visuo-tactile	Prosthetic right hand	approx. 40 cm	Synthetic monofilament	Brief touches	4 blocks of 20 trials	1. Tactile detection
4	Pavani et al. (2000).	Visuo-tactile	Prosthetic left and right hands	ns	Participants viewed LED lights on rubber hands	Participants received vibro-tactile stimulation	4 blocks of 112 trials	1. Questionnaire 2. Crossmodal congruency task
5	Peled et al. (2000).	Visuo-tactile	Prosthetic left hand	ns	Paintbrush	Stroking	10 min	1. Open-ended description 2. Questionnaire
6	Niebauer et al. (2002).	Visuo-tactile	Prosthetic left and right hands	ns	ns	Stroking and tapping	E1: 1 min E2: 2 min	1. Questionnaire 2. Time of illusion onset
7	Armel & Ramachandran (2003).	Visuo-tactile	Prosthetic right hand	91 cm in one condition; not specified for remaining conditions	Examiner's finger	Examiner stroked, tapped and lifted fingers	2.5 min	1. Open-ended description 2. 1 question 3. Skin conductance responses

	Reference	Paradigm	Viewed Hand	Distance Between Hands	Instrument	Stimulation	Trial Length	Assessment
8	Peled et al. (2003).	Visuo-tactile	Prosthetic left hand	ns	Paintbrush	Stroking	15 min	1. Time of illusion onset 2. Open-ended description 3. Questionnaire 4. Somatosensory evoked potentials
9	Austen et al. (2004).	Visuo-tactile	Prosthetic left and right hands	ns	Participant viewed LED lights on rubber hands	Participant received vibro-tactile stimulation	5 (E2), 6 (E1, E4) or 8 (E3) blocks of 96 trials	1. Crossmodal congruency task
10	Ehrsson et al. (2004).	Visuo-tactile	Prosthetic right hand	Approx. 40 cm	Paintbrush	Stroking	Pre: 1 min Scan: 42 s	1. fMRI 2. Illusion ratings
11	Walton & Spence (2004).	Visuo-tactile	Prosthetic left and right hands	18 cm	Participant viewed LED lights	Vibration	4 blocks of 112 trials	1. Questionnaire 2. Crossmodal congruency task
12	Tsakiris & Haggard (2005).	Visuo-tactile	Prosthetic left hand	17.5 cm	E1-E3: Paintbrush E4: Motorised paintbrushes:	Stroking	4 min	1. Proprioceptive drift
13	IJsselsteijn et al. (2006).	Visuo-tactile	Video projection of prosthetic left hand	30 cm	Paintbrush	Stroking	7.5 min	1. Open-ended description 2. Questionnaire 3. Proprioceptive drift
14	Lloyd et al. (2006).	Visuo-tactile	Prosthetic right hand	Placed directly on top of the participant's right hand	Examiner's finger – to elicit illusion. Plus, participant viewed cotton tip or syringe administered to the prosthetic hand in fMRI	Stroking	15 s	1. fMRI

	Reference	Paradigm	Viewed Hand	Distance Between Hands	Instrument	Stimulation	Trial Length	Assessment
15	Mussap & Salton (2006).	Visuo-tactile	Prosthetic left and right hands	ns	Paintbrush	Stroking	1 min	1. Questionnaire 2. Eating disorder, body satisfaction, self-esteem questionnaires
16	Schaefer et al. (2006).	Visuo-tactile	Video of life-sized left hand	ns	*Viewed*: Stick *Received*: pneumatically driven stimulation	Stroking	15 min	1. MEG 2. Questionnaire
17	Tsakiris et al. (2006).	Visuo-tactile	Video projection of participant's right hand	15 cm	Paintbrush	Stroking	90 s	1. Proprioceptive drift
		Visuo-motor	Video projection of participant's right hand	15 cm	-	Participant raised/ lowered finger		
18	Schütz-Bosbach et al. (2006).	Visuo-tactile with viewed action after induction	Examiner's right hand	34 cm	Motorised paintbrush	Stroking (variable speed)	3 min induction before viewed hand moved	1. Questionnaire 2. Proprioceptive drift 3. Motor evoked potentials
19	Costantini & Haggard (2007).	Visuo-tactile	Prosthetic right hand	30 cm	Motorised paintbrush	Stroking (variable direction and speed)	2 min	1. Proprioceptive drift

	Reference	Paradigm	Viewed Hand	Distance Between Hands	Instrument	Stimulation	Trial Length	Assessment
20	Durgin et al. (2007).	Visuo-tactile	E1: Prosthetic right hand viewed in mirror E2: Prosthetic left hand viewed directly; prosthetic right hand viewed in mirror	15 cm	1. Paintbrush 2. Laser light	1. Stroking 2. None	2 min	1. Questionnaire 2. Proprioceptive drift
21	Ehrsson et al. (2007).	Visuo-tactile	Prosthetic right hand	30-40 cm	Paintbrush	Stroking	88 s	1. Rating of illusion vividness 2. Rating of anxiety 3. fMRI
22	Lloyd (2007).	Visuo-tactile	Prosthetic right hand	17.5 cm; 27.5 cm; 37.5 cm; 47.5 cm; 57.5 cm; 67.5 cm	Examiner's finger	Stroking	1 min	1. 1 question 2. Time of illusion onset
23	Kanayama et al. (2007).	Visuo-tactile	Prosthetic left hand	ns	Participants viewed LED lights on rubber hands	Participant received vibrotactile stimulation	4 blocks of 80 trials	1. Questionnaire 2. Crossmodal congruency task 3. EEG
24	Kitadono & Humphreys (2007).	Visuo-tactile	Prosthetic right hand	ns	Paintbrush	Stroking	3 min	1. Questionnaire 2. Performance on neglect tests 3. Performance on arithmetic tasks 4. Perceptual report 5. Extinction

	Reference	Paradigm	Viewed Hand	Distance Between Hands	Instrument	Stimulation	Trial Length	Assessment
25	Pavani & Zampini (2007).	Visuo-tactile	Video projection of participant's left hand	25 cm	Paintbrush	Stroking	Not specified	1. Questionnaire 2. Proprioceptive drift
26	Tsakiris et al. (2007).	Visuo-tactile	Prosthetic left and right hands	15 cm	Motorised paintbrush	Stroking (variable speed)	125 s	1. PET 2. Questionnaire 3. Proprioceptive drift
27	Ehrsson et al. (2008).	Visuo-tactile	Prosthetic left or right hand	26 cm between index finger of prosthetic hand and the stump of the participant's amputated limb	Paintbrush	Stroking	E1: 2 min E2: 1 min E3: random periods of 40, 60 or 80 s	1. Questionnaire 2. Proprioceptive drift 3. Skin conductance responses
28	Haans et al. (2008).	Visuo-tactile	Prosthetic left hand	30 cm	Paintbrush	Stroking and tapping	5 min	1. Open-ended description 2. Questionnaire 3. Proprioceptive drift
29	Longo, Schüür et al. (2008).	Visuo-tactile	Prosthetic left or right hand	ns	Paintbrush	Stroking	1 min	1. Questionnaire 2. Proprioceptive drift
30	Longo, Cardozo, & Haggard (2008).	Visuo-tactile	Prosthetic left hand viewed in a mirror	Prosthetic hand appeared to the participant as if it was in the location of her own right hand	Paintbrush	Stroking	90 s	1. Questionnaire 2. Tactile acuity
31	Moseley et al. (2008).	Visuo-tactile	Prosthetic right hand	20-25 cm	Paintbrush	Stroking	7-8 min	1. Questionnaire 2. Temperature
					Tactile vibrator	Vibration	3 blocks of 200 trials	1. Discrimination task (JND)
32	Press et al. (2008).	Visuo-tactile	Prosthetic left or right hand	17.5 cm	Participants viewed LED lights on rubber hands	Participants received vibrotactile stimulation	12 blocks of 60 trials	1. EEG

	Reference	Paradigm	Viewed Hand	Distance Between Hands	Instrument	Stimulation	Trial Length	Assessment
33	Slater et al. (2008).	Visuo-tactile	Virtual reality left arm	Approx. 20 cm	Soft ball	Stroking and tapping (irregular and unpredictable)	5 min	1. Questionnaire 2. Proprioceptive drift 3. EMG
34	Capelari et al. (2009).	Visuo-tactile	Prosthetic right hand	ns	1. Paintbrush 2. Sharp pin	Stroking	4 min	1. Questionnaire 2. Proprioceptive drift
35	Dummer et al. (2009).	Visuo-tactile	Prosthetic right hand	ns	Paintbrush	Stroking	10 min	1. Questionnaire
		Visuo-motor				Participant moved her hand causing the prosthetic hand to move		
36	Ehrsson (2009).	Visuo-tactile	Two prosthetic right hands	10 cm	Paintbrush	Stroking	1-2 min	1. Skin conductance responses
37	Folegatti et al. (2009).	Visuo-tactile	Prosthetic right hand	15 cm	Paintbrush	Touches	2 min	1. Questionnaire 2. Proprioceptive drift 3. Tactile detection task
38	Haggard & Jundi (2009).	Visuo-tactile	Prosthetic left hand	Approx. 23 cm	Wooden peg	Stroking	30 s	1. Proprioceptive drift 2. Weight estimation: of objects placed in hand
39	Honma et al. (2009).	Visuo	Prosthetic right hand viewed in mirror	Prosthetic hand appeared to the participant as if it was in the location of her own left hand	Laser light	No stimulation on participant's hand	2 min	1. Skin conductance responses 2. Perceived sensation
40	Kammers, de Vignemont et al. (2009).	Visuo-tactile	Prosthetic right hand	15 cm	Not specified	Stroking	1 min	1. Questionnaire 2. Proprioceptive drift (perceptual and motor response)

	Reference	Paradigm	Viewed Hand	Distance Between Hands	Instrument	Stimulation	Trial Length	Assessment
41	Kammers, Verhagen et al. (2009).	Visuo-tactile	Prosthetic right hand	ns	Paintbrush	Stroking (variable speed and length)	90 s	1. Questionnaire 2. Proprioceptive drift (perceptual and motor response)
42	Kammers, Longo et al. (2009).	Visuo-motor	Video projection of participant's right hand	ns	-	Participant raised/ lowered finger	1 min	1. Proprioceptive drift (perceptual and motor response)
		Visuo-tactile	Prosthetic right hand	30 cm	Paintbrush	Stroking (variable speed and inter-stroke interval)	1 min	1. Questionnaire 2. Proprioceptive drift 3. Perceived shape of hand
43	Kanayama et al. (2009).	Visuo-tactile	Left and right prosthetic hands	ns	Participants viewed LED lights on rubber hands	Participant received vibrotactile stimulation	2 blocks of 140 trials	1. CDS questionnaire: assesses depersonalization 2. Questionnaire 3. Crossmodal congruency task
44	Longo & Haggard (2009).	Visuo-tactile	Video projection of participant's left or right hand viewed via monitor and mirror	ns	Paintbrush	Stroking	1 min	1. Questionnaire 2. Responding to visual stimuli presented near the hand
		Visuo-motor				Participant lifted and lowered index finger at own pace, or finger was lifted and lowered by the Examiner		
45	Longo et al. (2009).	Visuo-tactile	Prosthetic left or right hand	ns	Paintbrush	Stroking	1 min	1. Questionnaire

	Reference	Paradigm	Viewed Hand	Distance Between Hands	Instrument	Stimulation	Trial Length	Assessment
46	Perez-Marcos et al. (2009).	Visuo-motor (motor imagery)	Virtual reality left arm	ns	-	Participant 'imaged' movements while viewing movements of robotic arm	9 s	1. Questionnaire 2. Proprioceptive drift 3. EMG
47	Petkova & Ehrsson (2009).	Visuo-tactile	E1-E3: Prosthetic right hand E4: Prosthetic left hand	21 cm	Paintbrush	Stroking (irregular)	5 min	1. Questionnaire 2. Proprioceptive drift 3. Skin conductance responses
48	Rosén et al. (2009).	Visuo-tactile	Humanoid robotic right hand	10-20 cm from the stump of the participant's amputated limb	Paintbrush	Stroking (irregular)	E1: 2 min E2: 3 min	1. Open-ended questions 2. Questionnaire 3. Proprioceptive drift
49	Schütz-Bosbach, Avenanti et al. (2009).	Visuo-tactile	Examiner's right arm	34 cm	Motorised paintbrush	Stroking	3 min induction before viewed hand moved	1. Questionnaire 2. Proprioceptive drift 3. Motor evoked potentials
50	Schütz-Bosbach, Tausche, & Weiss (2009).	Visuo-tactile	Prosthetic left hand	23 cm	1. Soft Cotton 2. Rough Sponge	Stroking	3 min	1. Questionnaire 2. Proprioceptive drift 3. Visual and tactile discrimination
51	Shimada et al. (2009).	Visuo-tactile	Prosthetic right hand viewed on monitor	15 cm	Paintbrush	Stroking (unpredictable)	3 min	1. Questionnaire 2. Proprioceptive drift
52	Bruno & Bertamini (2010).	Visuo-tactile	Prosthetic left hand	ns	Paintbrush	Stroking	4 min	1. Questionnaire 2. Object size estimation

	Reference	Paradigm	Viewed Hand	Distance Between Hands	Instrument	Stimulation	Trial Length	Assessment
53	Giummarra, Fitzgibbon et al. (2010).	Visuo-tactile	Prosthetic left or right hand, or participant's left or right hand viewed in mirror	Viewed hand appeared to the participant as if it was in the location of her own left hand	1. Touch 2. Pressure 3. Movement 4. Vibration 5. Temperature	Participants viewed a hand receiving stimulation (stroking, touching, manipulation)	ns	1. Questionnaire 2. Perceived sensation 3. Questionnaire Measure of Emotional Empathy
54	Giummarra, Georgiou-Karistianis et al. (2010).	Visuo or visuo-tactile	Prosthetic left or right hand, or participant's left or right hand viewed in mirror	Viewed hand appeared to the participant as if it was in the location of her own left hand	1. Touch 2. Pressure 3. Movement 4. Vibration 5. Temperature	Participants viewed a hand receiving stimulation (stroking, touching, manipulation)	ns	1. Questionnaire 2. Perceived sensation
55	Hartcher-O'Brien et al. (2010).	Visuo-tactile	Prosthetic right hand	130 cm	Participants viewed LED light on the rubber hand	Participant viewed LED light on her own left hand and received vibrotactile stimulation	6 blocks of 120 trials	1. Questionnaire 2. Crossmodal congruency task
56	Hohwy & Paton (2010).	Visuo-tactile	Head-mounted display used to view prosthetic right hand or Examiner's right hand (or box)	Viewed hand appeared to the participant as if it was in the location of her own left hand	Examiner's finger	Tapping	E1: 110 s E2: 4 min E3: 3 min	1. Questionnaire 2. Open-ended questions 3. Temperature
57	Kammers et al. (2010).	Visuo-tactile	Prosthetic right hand	ns	Paintbrush	Stroking	1 min	1. Perceived grip aperture 2. Grasping response

	Reference	Paradigm	Viewed Hand	Distance Between Hands	Instrument	Stimulation	Trial Length	Assessment
58	Lewis & Lloyd (2010).	Visuo-tactile	Prosthetic right hand	10 cm	Examiner's finger	Stroking	9 min: 3 min sync 3 min async 3 min sync	1. Descriptions during experience of illusion (introspective interview) 2. Questionnaire 3. Proprioceptive drift
59	Lopez et al. (2010).	Visuo-tactile	Prosthetic left hand	24.5 cm	Paintbrush	Stroking	1 min	1. Questionnaire 2. Proprioceptive drift
60	Newport et al. (2010).	Visuo-tactile-motor	Video projection of participant's left hand viewed via monitor and mirror	Real-time hand appeared to the participant as if it was in the location of her own left hand	-	Participants stroked the bristles of a toothbrush	20 s	1. Questionnaire 2. Pointing to targets
61	Ocklenburg et al. (2010).	Visuo-tactile	Prosthetic left and right hands	17.5 cm	Paintbrush	Stroking	3 min	1. Questionnaire 2. Skin conductance responses
62	Sanchez-Vives et al. (2010).	Visuo-motor (virtual reality arm)	Virtual reality right arm	Approx. 20 cm	-	The participant moved her hand while viewing a virtual hand performing the same actions	3 min	1. Questionnaire 2. Proprioceptive drift
63	Tsakiris et al. (2010).	Visuo-tactile	Prosthetic left hand or block of wood	17.5 cm	Paintbrush	Stroking	4 min	1. Questionnaire 2. Proprioceptive drift

	Reference	Paradigm	Viewed Hand	Distance Between Hands	Instrument	Stimulation	Trial Length	Assessment
64	Zopf et al. (2010).	Visuo-tactile	Prosthetic left and right hands, or checkerboard – viewed directly or via a mirror	E1: Via the mirror, the prosthetic hand appeared to the participant as if it was in the location of her own hand. When viewed directly the hands were 30 cm apart. E2: 15 cm or 45 cm apart.	Paintbrush	Stroking	2.5 min	1. Questionnaire 2. Proprioceptive drift 3. Time of onset 4. Crossmodal congruency task
65	Albrecht et al. (in press).	Visuo-tactile	Prosthetic right hand	ns	Paintbrush	Stroking	5 min	1. Questionnaire 2. Proprioceptive drift 3. Blood pressure and heart rate
66	Asai et al. (in press).	Visuo-tactile	Prosthetic left and right hands	20 cm	Paintbrush	Stroking	2 min	1. Questionnaire 2. Proprioceptive drift 3. Personality questionnaires
67	Bertamini et al. (in press).	Visuo-tactile	Prosthetic left hand viewed directly or via a mirror	22 cm	Paintbrush	Stroking	ns	1. Questionnaire 2. Proprioceptive drift
68	Blefari et al. (2011).	Visuo-tactile	Prosthetic left hand	10-20 cm	Paintbrush	Stroking	1 min (syn) 30 s (asyn)	1. Questionnaire 2. EEG
69	Curt et al. (2011).	Visuo-tactile	Prosthetic right hand	20 cm	Paintbrush	Stroking and tapping	2 min	1. Questionnaire 2. Proprioceptive drift
70	Dolk et al. (2011).	Visuo-tactile	Co-actor's left hand	ns	Stroking device	Stroking	ns	1. Social Simon task
71	Fiorio et al. (2011).	Visuo-tactile	Prosthetic left and right hands	20 cm	Paintbrush	Stroking	2 min	1. Questionnaire 2. Proprioceptive drift

	Reference	Paradigm	Viewed Hand	Distance Between Hands	Instrument	Stimulation	Trial Length	Assessment
72	Guterstam et al. (2011).	Visuo-tactile	Prosthetic right hand	12.5 cm E5: 13 cm or 15 cm	Paintbrush	Stroking	2 min E4: 1 min	1. Questionnaire 2. Skin conductance response
73	Kammers et al. (2011).	Visuo-tactile	Prosthetic right hand	22 cm	Paintbrush	Stroking	90 sec	1. Questionnaire 2. Proprioceptive drift 3. Temperature
74	Marasco et al. (2011).	Visuo-tactile	Prosthetic left and right hands	ns	ns	Touch	5 min	1. Open-ended descriptions 2. Questionnaire 3. Temporal order judgment task 4. Temperature
75	Morgan et al. (2011).	Visuo-tactile	Prosthetic right hand	15 cm	Motorised paintbrush	Stroking	5 min	1. Questionnaire 2. Proprioceptive drift 3. Personality measures
76	Rohde et al. (2011).	Visuo-tactile	Prosthetic left hand	17 cm	Motorised paintbrush	Stroking	E1: 7 mins E2: 2 mins	1. Questionnaire 2. Proprioceptive drift
77	Takasugi et al. (2011).	Visuo-tactile	Participant's own left or right hand, Examiner's left or right hand, prosthetic left or right hand (all viewed via a mirror)	Via the mirror, the viewed hand appeared to the participant as if it was in the location of her own hand.	Semmes-Weinstein monofilament (30 g)	20 applications of monofilament	ns	1. Perceived intensity of referred sensation 2. Question about ownership
78	Tsakiris et al. (2011).	Visuo-tactile	Prosthetic left hand	ns	Paintbrush	Stroking	2 min	1. Questionnaire 2. Proprioceptive drift 3. Interoceptive sensitivity 4. Temperature 5. BMI and BIQ

	Reference	Paradigm	Viewed Hand	Distance Between Hands	Instrument	Stimulation	Trial Length	Assessment
79	Walsh et al. (2011).	Visuo-tactile	Prosthetic right hand	Prosthetic hand positioned 12 cm above the participant's hidden hand.	Paintbrush	Stroking	3 min	1. Questionnaire 2. Proprioceptive drift
		Visuo-motor	Prosthetic right hand	Prosthetic hand positioned 12 cm above the participant's hidden hand.	-	Movement of the participant's finger and the viewed finger	3 min	
80	Zeller et al. (2011).	Visuo-tactile	Prosthetic left and right hands (both of the participant's hands tested)	Prosthetic hand positioned above the participant's hidden hand.	Paintbrush	Stroking	2 min	1. Questionnaire 2. MRI scan
81	Zopf et al. (2011).	Visuo-tactile	Prosthetic right hand	20 cm	Paintbrush	Stroking	2 min induction and then top-ups of 22.5 s	1. Questionnaire 2. Reaching task

* ns indicates that this information was not specified.