



Research report

A sensational illusion: Vision-touch synaesthesia and the rubber hand paradigm

Anne M. Aimola Davies^{a,b,c,d,*} and Rebekah C. White^{a,*}

^a Department of Experimental Psychology, University of Oxford, United Kingdom

^b Faculty of Philosophy, University of Oxford, United Kingdom

^c NIHR Biomedical Research Centre, University of Oxford, United Kingdom

^d Department of Psychology, The Australian National University, Australia

ARTICLE INFO

Article history:

Received 2 August 2010

Reviewed 12 October 2010

Revised 19 May 2011

Accepted 24 January 2012

Action editor Robert McIntosh

Published online 30 January 2012

Keywords:

Body representation

Mirror touch

Rubber hand illusion

Synaesthesia

ABSTRACT

For individuals with vision-touch synaesthesia, the sight of touch on another person elicits synaesthetic tactile sensation on the observer's own body. Here we used the traditional rubber hand paradigm (Botvinick and Cohen, 1998) and a no-touch rubber hand paradigm to investigate and to authenticate synaesthetic tactile sensation. In the traditional rubber hand paradigm, the participant views a prosthetic hand being touched by the Examiner while the participant's hand – hidden from view – is also touched by the Examiner. Synchronous stimulation of the prosthetic hand and the participant's hidden hand elicits the rubber hand illusion. It may seem to the participant that she is feeling touch at the location of the viewed prosthetic hand – visual capture of touch, and that the prosthetic hand is the participant's own hand – illusion of ownership. Thus, for participants who experience the traditional rubber hand illusion, tactile sensation on the participant's hidden hand is referred to the prosthetic hand. In our no-touch rubber hand paradigm, the participant views a prosthetic hand being touched by the Examiner but the participant's hand – hidden from view – is not touched by the Examiner. Questionnaire ratings indicated that only individuals with vision-touch synaesthesia experienced the no-touch rubber hand illusion. Thus, synaesthetic tactile sensation on the (untouched) hidden hand was referred to the prosthetic hand. These individuals also demonstrated proprioceptive drift (a change, from baseline, in proprioceptively perceived position) of the hidden hand towards the location of the prosthetic hand, and a pattern of increased proprioceptive drift with increased trial duration (60 sec, 180 sec, 300 sec). The no-touch rubber hand paradigm was an excellent method to authenticate vision-touch synaesthesia because participants were naïve about the rubber hand illusion, and they could not have known how they were expected to perform on either the traditional or the no-touch rubber hand paradigm.

© 2012 Elsevier Ltd. All rights reserved.

* Corresponding authors. Department of Experimental Psychology, University of Oxford, South Parks Road, Oxford OX1 3UD, United Kingdom.

E-mail addresses: Anne.Aimola@psy.ox.ac.uk (A.M. Aimola Davies), Rebekah.White@psy.ox.ac.uk (R.C. White).

0010-9452/\$ – see front matter © 2012 Elsevier Ltd. All rights reserved.

doi:10.1016/j.cortex.2012.01.007

1. Introduction

Synaesthetic tactile sensation can be so compelling that an individual may mistake synaesthetic sensation for physical touch. In auditory-touch synaesthesia, sound elicits tactile sensation (Beauchamp and Ro, 2008; Ro et al., 2007); in smell-touch synaesthesia, odour elicits tactile sensation (Cytowic, 2002); in taste-touch synaesthesia, flavour elicits tactile sensation (Cytowic); and, in vision-touch synaesthesia, the sight of touch on another person elicits tactile sensation on the observer's own body (Blakemore et al., 2005). This paper is concerned with vision-touch synaesthesia, which is also referred to as mirror-touch synaesthesia (Ward et al., 2008, p. 259).

Patient studies (e.g., Bradshaw and Mattingley, 2001; Ramachandran and Rogers-Ramachandran, 1996) provide some of the earliest examples of how visual information can trigger tactile sensation. Bradshaw and Mattingley presented information about a man with severe health problems (including extensive metastatic carcinomatosis), who was so sensitive to touch that even slight contact with his skin was experienced as “sharp fingernails” (p. 136). In describing how this man responded to observed touch, his wife said “If I slightly knocked my finger, spontaneously showing him, he would immediately grasp his own finger and say ‘don’t do that’ (meaning not to show him suddenly); he actually felt it. If I merely commented (that I had knocked my finger), there was no such reaction” (p. 136 and p. 821). More recent studies document vision-touch synaesthesia in healthy individuals (see Banissy and Ward, 2007; Banissy et al., 2009a, 2009b, 2011; Blakemore et al., 2005; Holle et al., 2011, and for an overview, see Ward et al., 2008). Banissy et al. (2009a) have estimated the prevalence rate for vision-touch synaesthesia to be as high as 1.6 in 100, which makes it one of the most common forms of synaesthesia; the prevalence rate for colour-grapheme synaesthesia is approximately 1.4 in 100 (Simner et al., 2006).

Blakemore et al. (2005) provided the first investigation of vision-touch synaesthesia in a neurologically healthy individual. Participant C (41-year-old female) claimed that she had always “perceived observed touch on other people as touch to her own body” (p. 1573), and she was surprised to learn that this experience was atypical. In a functional magnetic resonance imaging (fMRI) study, Participant C and control participants without vision-touch synaesthesia demonstrated activation in the primary and secondary somatosensory cortices, and the motor and premotor regions, when they were touched. More interestingly, the primary and secondary somatosensory cortices “were activated by the mere observation of touch to a human” (Blakemore et al., p. 1579). Related fMRI studies support these findings for control participants without vision-touch synaesthesia: McCabe et al. (2008) found activation in the primary somatosensory cortex when control participants observed touch (with a finger) to a human arm, and Keysers et al. (2004) found activation in the secondary somatosensory cortex when control participants observed touch (with an object) to a human leg. In the Blakemore et al. study, Participant C (when compared to control participants without vision-touch synaesthesia) exhibited significantly more activation bilaterally in the primary and secondary

somatosensory cortices and in the left premotor cortex when she observed touch (with a finger) to a human face or neck relative to touch to a similarly-shaped object with face- and neck-like properties (e.g., a lamp). Participant C also exhibited bilateral activation in the anterior insula, but there was no evidence of insula cortex activation in control participants. Blakemore et al. suggested that in most people “it is possible that the somatosensory mirror system, which matches observed and felt touch, is involved in understanding the effect of tactile stimulation on others” (p. 1581). The authors concluded that what distinguished Participant C from control participants who did not feel observed touch was over-activation in the mirror system along with activation in the anterior insula, which contains tactile receptive fields and has been shown to play a role in self-attribution.

Banissy and Ward (2007) hypothesised that the somatosensory mirror system may have an important role in empathy. Consistent with this, they found that individuals with vision-touch synaesthesia scored significantly higher on the emotional reactivity subscale of the Empathy Quotient, when compared to control participants without synaesthesia and control participants with other forms of synaesthesia. Banissy et al. (2011) have since demonstrated a link between vision-touch synaesthesia and another aspect of emotion. Participants with and without vision-touch synaesthesia were presented with an adjective describing an emotional state, and the task was to identify which of three faces best depicted this emotional state. Individuals with vision-touch synaesthesia demonstrated superior performance on this expression-recognition task whereas their performance was identical to control participants on non-emotive tasks, such as tasks investigating memory for faces. Taken side-by-side, these studies suggest that vision-touch synaesthesia may be linked to “general enhancements in emotion processing” (Banissy et al., p. 1823).

Researchers who investigate synaesthesia emphasise how important it is to *authenticate* the individual's experience (see Gheri et al., 2008; Simner et al., 2006). For example, in the study by Blakemore et al. (2005), fMRI was used to authenticate Participant C's report that she experienced observed touch on another person as if it were touch on her own body. Banissy and Ward (2007) have since introduced a reaction-time task to authenticate vision-touch synaesthesia. The participant's task was to report the location of touch administered to his or her own body while observing touch administered to another person. The location of touch administered to the participant's body was either congruent or incongruent with the location of viewed touch. This task was difficult for the individuals with vision-touch synaesthesia because of the requirement to distinguish actual physical touch from synaesthetic tactile sensation. Individuals with vision-touch synaesthesia were faster to report the location of physical touch when it was congruent (as compared to incongruent) with the location of viewed touch. Control participants without vision-touch synaesthesia did not demonstrate this effect. Moreover, individuals with vision-touch synaesthesia were prone to errors in the incongruent condition; for example, they reported touch at two locations – the location of physical touch and the location of viewed touch. Control

participants without vision-touch synaesthesia were not prone to these errors. Here we present a third method to authenticate vision-touch synaesthesia: a no-touch rubber hand paradigm.

In the traditional rubber hand paradigm (Botvinick and Cohen, 1998), the participant views a prosthetic hand being touched by the Examiner while the participant's hand – hidden from view – is also touched by the Examiner. When touch administered to the viewed prosthetic hand is synchronous with touch administered to the participant's hidden hand, it may seem to the participant that he or she is feeling touch at the location of the viewed prosthetic hand. The participant experiences “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 own hand. These experiences, termed visual capture of touch and the illusion of ownership of the prosthetic hand, are collectively referred to as the rubber hand illusion. The rubber hand illusion is often assessed with questionnaire ratings and with a measure of proprioceptively perceived hand position. When asked to point to the location of their own hidden hand, participants demonstrate a shift in proprioceptively perceived position of the hidden hand, and this shift is displaced towards the prosthetic hand (e.g., Botvinick and Cohen, 1998; Costantini and Haggard, 2007; Haans et al., 2008; Longo et al., 2008b; Tsakiris and Haggard, 2005). This shift in perceived hand position is referred to as proprioceptive drift (see Paillard and Brouchon, 1968; Wann and Ibrahim, 1992) and it is commonly regarded as a behavioural proxy for the rubber hand illusion (Tsakiris et al., 2007, 2010, but see Holmes et al., 2006 and Rohde et al., 2011). The magnitude of the shift is typically about 15–30% of the full distance between the participant's hidden (receptive) hand and the prosthetic hand (Makin et al.).

In our no-touch rubber hand paradigm, the participant views a prosthetic hand being touched by the Examiner but the participant's hand – hidden from view – is not touched by the Examiner. The rubber hand illusion (visual capture of touch and the illusion of ownership of the prosthetic hand) depends on synchronous touch of the viewed prosthetic hand and the participant's hidden hand (but see Durgin et al., 2007 and Giummarra et al., 2010 for other no-touch paradigms). Thus we make the obvious yet bold proposal that individuals with vision-touch synaesthesia will experience the no-touch rubber hand illusion because, when they view a prosthetic hand being touched by the Examiner, they will experience synchronous synaesthetic tactile sensation on their hidden hand.

The no-touch rubber hand paradigm is an excellent method to use to authenticate vision-touch synaesthesia. An individual who is naïve about the rubber hand illusion will not know how he or she is expected to perform. Indeed, an individual with vision-touch synaesthesia who is naïve about the illusion will not know how individuals without vision-touch synaesthesia will perform on either the traditional or the no-touch rubber hand paradigm. This inability to predict performance is important. Gheri et al. (2008) note that “it is much harder for an observer to feign a condition if they do not know whether they are supposed to be better or worse than the normal observer” (p. 841).

2. General methods

2.1. Participants

2.1.1. Control participants

Twelve control participants (11 females and 1 male; 18–28 years: $M = 21.5$ years, $SD = 2.97$ years) took part in Experiment 1, and twelve new control participants (9 females and 3 males; 18–29 years: $M = 20.7$ years, $SD = 3.31$ years) took part in Experiment 2. All 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. All participants were naïve to the objectives of the experiment.

2.1.2. Vision-touch synaesthesia participants

Two individuals with specular¹ vision-touch synaesthesia (RS and NC) were recruited from the University of Oxford community. RS (23-year-old female) had signed up for a study investigating tactile sensation in non-visual testing conditions. It is standard in our laboratory to begin experiments by confirming that the participant is comfortable with receiving touch on the hand. The Examiner demonstrates the different types of stimulation that are involved in the study by administering touch to a prosthetic hand. Of 180 participants screened in this way over three years, RS was the only participant spontaneously to report that observing touch on the prosthetic hand had elicited tactile sensation on her own hand. RS stated that her visuotactile experiences dated back to an early age, and she recalled for us a vivid memory from age eight. While seated in the classroom, RS watched the teacher at the front of the room rub her two hands together. RS said “I was mesmerised and felt that I could feel her touch”. Banissy et al. (2009a) report that vision-touch synaesthesia tends to co-occur with other forms of synaesthesia. Consistent with this, RS has grapheme-colour synaesthesia (visually-presented letters and numbers lead to a synaesthetic experience of colour), and she perceives the letters of the alphabet and the months of the year as having a three-dimensional arrangement in space. RS was naïve about the rubber hand paradigm.

NC (19-year-old female) was recruited as a control participant for the current study. However, subsequent to testing with the no-touch rubber hand paradigm, NC explained that she might not be an appropriate participant. NC said that she feels a strong sensation on her own body when she sees

¹ Banissy and Ward (2007) have distinguished between two subtypes of vision-touch synaesthesia: anatomical and specular. When positioned face-to-face with an individual who receives touch on the left side of her face, an individual with anatomical vision-touch synaesthesia experiences sensation on the left side of her own face. In contrast, an individual with specular vision-touch synaesthesia experiences sensation on the right side of her face, as if looking at herself receiving touch in a mirror. In a prevalence study by Banissy et al. (2009a), the specular subtype was found to be significantly more common than the anatomical subtype.

another person being touched, and that observing touch on the prosthetic hand had elicited tactile sensation on her own hand. NC recalled reading 'A Brave New World' at age 12 and being particularly struck by a scene describing a futuristic cinema referred to as 'Feelies', rather than movies. At the Feelies, filmgoers sit in a special chair that allows them to feel the movie. On reading about this visuotactile cinematic experience, NC had thought "I have that sensation anyway". NC also reported that some visually-presented words lead to a synaesthetic experience of colour, and that smells are associated with a "very strong colour feeling". NC was naïve about the rubber hand paradigm.

2.2. Experimental procedure

The participant was seated at a table, opposite the Examiner. A realistic prosthetic left hand (see Fig. 1) was positioned on the table at the participant's body midline. The participant's left hand was positioned 15 cm to the left of the prosthetic hand, and both hands were palm downward on the table with the fingers pointing straight ahead and away from the participant's body. Care was taken to align the hands side-by-side. A visual divider was placed between the prosthetic hand and the participant's left hand, so that the participant's left hand was hidden from view. The participant's right hand rested on the participant's lap, and was also hidden from view. A piece of black fabric was draped over the stump of the prosthetic hand. The Examiner used a paintbrush to administer stimulation (consisting of brushstrokes and taps) to the index finger of the prosthetic hand and the index finger of the participant's hidden left hand. Strokes were unidirectional, from the knuckle (where the index finger meets the hand) towards the fingertip.

Experiment 1 consisted of three 60-sec conditions of the rubber hand paradigm: (1) no-touch condition, with stimulation of the viewed prosthetic hand but 'no-touch' of the participant's hidden hand; (2) synchronous condition, with synchronous stimulation of the viewed prosthetic hand and the participant's hidden hand; (3) asynchronous condition, with asynchronous stimulation of the viewed prosthetic hand and the participant's hidden hand. The novel manipulation was the no-touch condition, and our prediction was that individuals with vision-touch synaesthesia would experience the rubber hand illusion in this condition but that control



Fig. 1 – Photograph of the prosthetic hand (Regal brand).

participants would not. Previous research with the traditional rubber hand paradigm has shown that the rubber hand illusion is elicited with synchronous stimulation but not with asynchronous stimulation. Thus our prediction was that individuals with vision-touch synaesthesia and control participants would experience the rubber hand illusion in the synchronous condition. The asynchronous condition was the baseline condition for individuals with vision-touch synaesthesia, and our prediction was that individuals with vision-touch synaesthesia would not experience the rubber hand illusion in this condition. Thus, individuals with vision-touch synaesthesia were tested in three conditions of the rubber hand paradigm but control participants were tested only in the two conditions (no-touch and synchronous) of most interest for comparisons.

Experiment 2 consisted of three trial durations (60 sec, 180 sec, 300 sec) of the no-touch condition of the rubber hand paradigm, with stimulation of the viewed prosthetic hand but no-touch of the participant's hidden hand. There was a 3-min break between trials in which the participant was encouraged to move his or her hands. Previous research using the synchronous condition of the rubber hand paradigm has shown that participants demonstrate greater proprioceptive drift following a prolonged experience of the rubber hand illusion (Botvinick and Cohen, 1998). The aim of Experiment 2 was to investigate this effect in the no-touch condition. Our prediction was that individuals with vision-touch synaesthesia would demonstrate greater proprioceptive drift when trial duration was increased but that, irrespective of trial duration, control participants would not demonstrate proprioceptive drift in the no-touch condition of the rubber hand paradigm.

Table 1 outlines all of the experimental conditions and predictions.

2.2.1. Assessment of vision-touch synaesthesia: perceived intensity ratings

Following each no-touch condition (Experiment 1: Condition 1; Experiment 2: Trials 1, 2, 3), the participant responded to this statement taken from Blakemore et al. (2005):

1. Please rate the intensity of the stimulation that you felt on your own hand.

The purpose of this statement was to determine whether the sight of touch on the prosthetic hand was experienced as tactile sensation on the participant's own hand. Rating of perceived intensity was reported on a seven-point visual analogue scale (0 = no perceived tactile sensation; 6 = very intense tactile sensation).

2.2.2. Assessment of the rubber hand illusion: questionnaire ratings

Following each condition (no-touch, synchronous, asynchronous) of Experiment 1, the participant responded to these three statements adapted from Botvinick and Cohen's (1998) rubber hand questionnaire:

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

Table 1 – Overview of experiments and predictions.

Experiment	Condition	Duration	Predictions			
			Vision-touch synaesthesia participants		Control participants	
			Questionnaire	Proprioceptive drift	Questionnaire	Proprioceptive drift
1	No-touch	60 sec	+	+	–	–
	Synchronous	60 sec	+	+	+	+
	Asynchronous	60 sec	–	–	Not tested	Not tested
2	No-touch	60 sec	Not tested	+	Not tested	–
	No-touch	180 sec	Not tested	++	Not tested	–
	No-touch	300 sec	Not tested	+++	Not tested	–

+ Predicted to demonstrate the experience.
– Predicted not to demonstrate the experience.

2. I felt as if the rubber hand were my hand.
3. It seemed as if I may have more than one left hand or arm.

Statement 1 assessed visual capture of touch, Statement 2 assessed the illusion of ownership of the prosthetic hand, and Statement 3 was included as a control statement because it described an experience that the paradigm was not expected to elicit. The order of the three statements was randomised across participants and conditions. Rating of agreement with each statement was reported on a seven-point visual analogue scale (0 = not at all; 6 = very strongly agree).

2.2.3. Assessment of proprioceptive drift

For each condition (no-touch, synchronous, asynchronous) of Experiment 1, and for all trial durations (60 sec, 180 sec, 300 sec) of the no-touch condition of Experiment 2, a pre-(baseline) and post-stimulation measurement of proprioceptively perceived hand position was obtained using the method developed by Ehrsson et al. (2005). The participant's eyes were closed and the visual divider was removed from the table for this assessment. The participant extended his or her right arm, which the Examiner positioned at 45° to the right of the midsagittal plane of the participant's body. The participant was asked to slide the right index finger along the table in a single movement until it was in line with the 'felt' position of the left index finger. That is, to point to (just in front of) the tip of the left index finger. (Practice with this procedure was provided before the experiment began because it was important for the participant not to touch the left index finger, since this would provide feedback about the actual location.)

Proprioceptive drift was calculated as change (from baseline) in the proprioceptively perceived position of the participant's hidden left hand, and it was recorded as either positive or negative drift. Positive proprioceptive drift (when the participant slid the right index finger along the table but stopped before reaching the position of the left index finger) means that the participant perceived the hidden left hand as shifted towards the location of the previously-viewed prosthetic hand. Negative proprioceptive drift (when the participant slid the right index finger along the table and

slid past the position of the left index finger) means that the participant perceived the hidden left hand as shifted away from the location of the previously-viewed prosthetic hand. Previous studies report that the experience of the rubber hand illusion is associated with positive proprioceptive drift.

3. Analysis

Questionnaire ratings and proprioceptive drift were analysed using case–control statistics. Crawford and Howell's (1998) modified t-test was used to test whether the difference between the single case (RS or NC) and control participants was statistically different. Despite clear predictions about the differences between individuals with vision-touch synaesthesia and control participants, conservative two-tailed t-tests were used. The effect size (z_{cc}) and the confidence interval around the effect size were calculated using the methods proposed by Crawford et al. (2010).

4. Experiment 1 results

4.1. No-touch condition

4.1.1. Perceived intensity ratings

Perceived intensity ratings (0 = no perceived tactile sensation; 6 = very intense tactile sensation) indicated that the two individuals with vision-touch synaesthesia experienced tactile sensation on their own untouched left index finger when they viewed touch administered to the prosthetic left hand (RS = 3; NC = 4). Importantly, this means that RS and NC experienced tactile sensation in the no-touch condition of the rubber hand paradigm, with stimulation of the viewed prosthetic hand but no-touch of the participant's hidden hand. In contrast, ratings provided by control participants indicated that they did not experience tactile sensation on the hidden hand in the no-touch condition of the rubber hand paradigm ($M = .167$, range = 0–1).

4.1.2. Rubber hand illusion: questionnaire ratings

(Fig. 2a, middle panel)

Questionnaire ratings (0 = not at all; 6 = very strongly agree) indicated that the two individuals with vision-touch synaesthesia experienced visual capture of touch (Statement 1: RS = 3; NC = 4) and ownership of the viewed prosthetic hand (Statement 2: RS = 4; NC = 3) in the no-touch condition. Control participants did not experience visual capture of touch ($M = .042$, range = 0–.5) or ownership of the viewed prosthetic hand ($M = .167$, range = 0–1). Modified t-tests confirmed that the ratings provided by RS and NC for Statement 1 and Statement 2 were significantly higher than the ratings provided by control participants. RS provided an agreement rating of ‘0’ for the control statement “It seemed as if I may have more than one left hand or arm”, and NC provided a low agreement rating (Statement 3: RS = 0; NC = 2; Control Participants $M = .083$, range = 0–1). A modified t-test confirmed that the rating provided by NC for Statement 3 was significantly higher than the ratings

provided by control participants. Results for t-tests conducted on questionnaire ratings for the no-touch condition are reported in Table 2a.

4.1.3. Proprioceptive drift (Fig. 2a, right panel)

The two individuals with vision-touch synaesthesia demonstrated positive proprioceptive drift; they perceived the hidden left hand as shifted towards the location of the previously-viewed prosthetic hand in the no-touch condition (RS = 4.75 cm; NC = 2 cm). Control participants demonstrated negative proprioceptive drift; they perceived the hidden left hand as shifted away from the location of the previously-viewed prosthetic hand ($M = -1.083$ cm, range = -3.5 cm–2 cm). Most control participants ($n = 8$) demonstrated this pattern of negative proprioceptive drift, two control participants demonstrated no drift (0 cm drift), and two demonstrated positive drift (1 cm drift; 2 cm drift). Modified t-tests confirmed that RS demonstrated significantly greater proprioceptive drift than did control participants, and

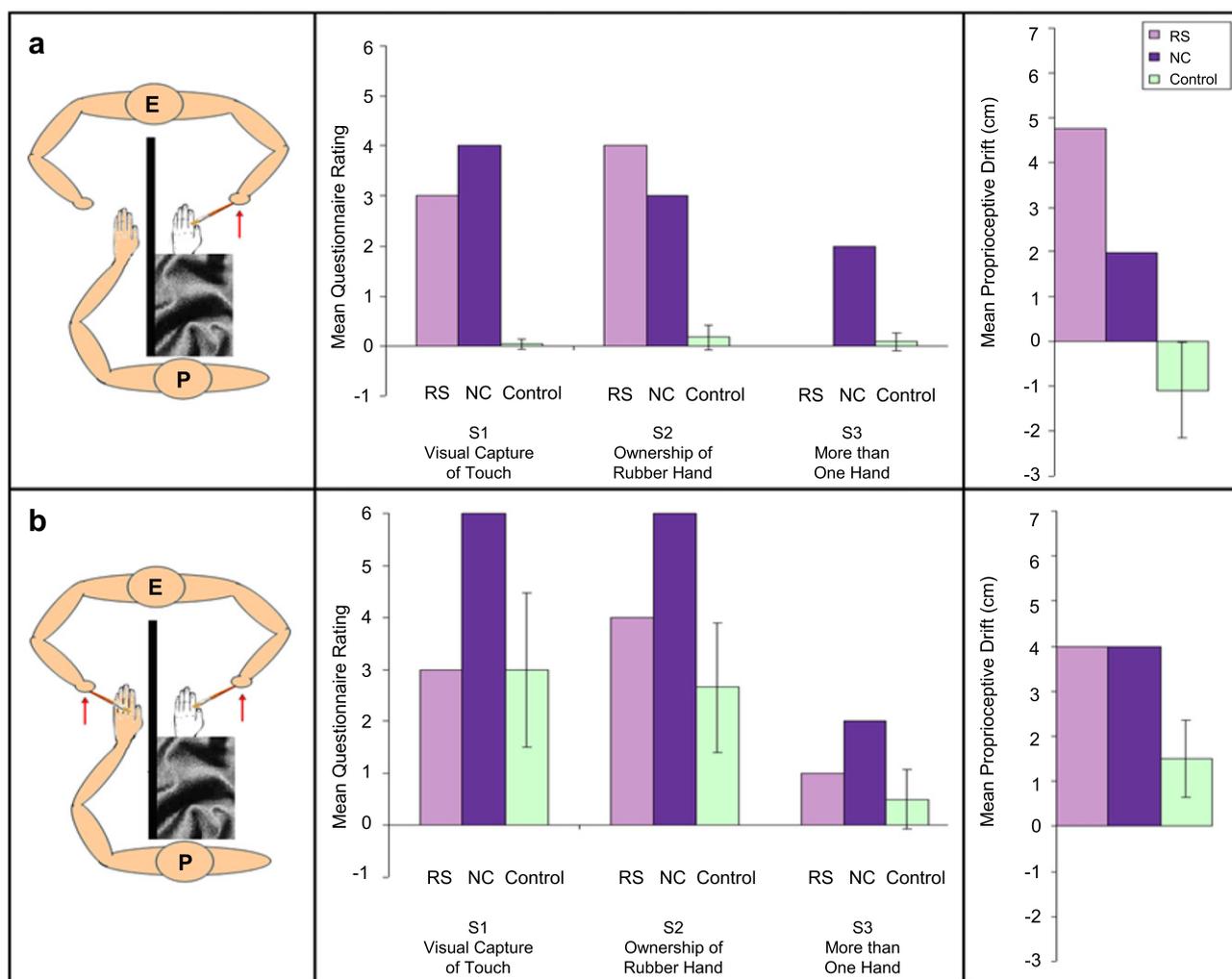


Fig. 2 – Rubber hand paradigm: (a) No-touch condition and (b) Synchronous condition. Left panel, experimental set-up. Middle panel, mean questionnaire rating (for the rubber hand illusion): • Statement 1 – visual capture of touch, • Statement 2 – ownership of (viewed prosthetic) rubber hand, • Statement 3 – more than one hand. Right panel, mean proprioceptive drift (cm). Error bars indicate 95% confidence intervals.

Table 2 – Experiment 1: comparing a single case (RS or NC) to control participants – (a) no-touch condition, (b) synchronous condition, (c) no-touch condition compared to synchronous condition.

	Case	Control participants		Significance test		Estimated percentage of control population obtaining a lower score than the case		Estimated effect size (z_{cc})			
		Score	n	Mean	SD	t	p (two-tailed)	Point	95% CI	Point	95% CI
<i>(a) No-touch condition</i>											
RS	Visual capture	3	12	.042	.144	19.736	<.00001	100	(100–100)	20.542	(12.077–29.015)
	Ownership	4	12	.167	.389	9.467	<.00001	99.999	(100–100)	9.853	(5.759–13.945)
	More than one hand	0	12	.083	.289	–.276	.78772	39.386	(19.514–61.679)	–.287	(–.859–.297)
	Proprioceptive drift	4.75	12	–1.083	1.662	3.372	.00623	99.688	(97.431–100)	3.510	(1.948–5.052)
NC	Visual capture	4	12	.042	.144	26.408	<.00001	100	(100–100)	27.486	(16.173–38.813)
	Ownership	3	12	.167	.389	6.997	.00002	99.999	(99.999–100)	7.283	(4.230–10.329)
	More than one hand	2	12	.083	.289	6.373	.00005	99.997	(99.994–100)	6.633	(3.842–9.416)
	Proprioceptive drift	2	12	–1.083	1.662	1.782	.10230	94.885	(81.307–99.738)	1.855	(.889–2.792)
<i>(b) Synchronous condition</i>											
RS	Visual capture	3	12	3	2.33	0	1.0000	50	(28.577–71.423)	0	(–.566–.566)
	Ownership	4	12	2.667	1.969	.650	.52876	73.562	(51.345–90.249)	.677	(.034–1.296)
	More than one hand	1	12	.5	.904	.531	.60571	69.715	(47.301–87.546)	.553	(–.068–1.153)
	Proprioceptive drift	4	12	1.5	1.33	1.806	.09833	95.083	(81.750–99.763)	1.880	(.906–2.825)
NC	Visual capture	6	12	3	2.33	1.237	.24183	87.909	(69.013–97.974)	1.288	(.496–2.048)
	Ownership	6	12	2.667	1.969	1.626	.13216	93.392	(78.213–99.501)	1.693	(.779–2.576)
	More than one hand	2	12	.5	.904	1.594	.13920	93.040	(77.534–99.433)	1.659	(.757–2.532)
	Proprioceptive drift	4	12	1.5	1.33	1.806	.09833	95.083	(81.750–99.763)	1.880	(.906–2.825)
<i>(c) No-touch condition for RS and NC compared to synchronous condition for control participants</i>											
RS	Visual capture	3	12	3	2.33	0	1.00000	50	(28.577–71.423)	0	(–.566–.566)
	Ownership	4	12	2.667	1.969	.650	.52876	73.562	(51.345–90.249)	.677	(.034–1.296)
	More than one hand	0	12	.5	.904	–.531	.60571	30.285	(12.454–52.699)	–.553	(–1.153–.068)
	Proprioceptive drift	4.75	12	1.5	1.33	2.348	.03864	98.068	(89.904–99.983)	2.444	(1.276–3.586)
NC	Visual Capture	4	12	3	2.33	.412	.68801	65.600	(43.153–84.454)	.429	(–.172–1.013)
	Ownership	3	12	2.667	1.969	.162	.87387	56.307	(34.285–76.897)	.169	(–.405–.735)
	More than one hand	2	12	.5	.904	1.594	.13920	93.040	(77.534–99.433)	1.659	(.757–2.532)
	Proprioceptive drift	2	12	1.5	1.33	.361	.72480	63.760	(41.348–83.105)	.376	(–.219–.955)

NC demonstrated a trend towards greater proprioceptive drift than did control participants. Results for t-tests conducted on proprioceptive drift for the no-touch condition are reported in Table 2a.

4.2. Synchronous condition

4.2.1. Rubber hand illusion: questionnaire ratings (Fig. 2b, middle panel)

Questionnaire ratings (0 = not at all; 6 = very strongly agree) indicated that the two individuals with vision-touch synaesthesia experienced visual capture of touch (Statement 1: RS = 3; NC = 6) and ownership of the viewed prosthetic hand (Statement 2: RS = 4; NC = 6) in the synchronous condition. Control participants also experienced visual capture of touch ($M = 3$, range = 0–6) and ownership of the viewed prosthetic hand ($M = 2.667$, range = 0–6). RS and NC provided low agreement ratings for the control statement “It seemed as if I may have more than one left hand or arm” and some control participants also agreed with this statement (Statement 3: RS = 1; NC = 2; Control Participants $M = .5$, range = 0–3).² Modified t-tests confirmed that the ratings provided by RS and NC were not significantly different from the ratings provided by control participants. Results for t-tests conducted on questionnaire ratings for the synchronous condition are reported in Table 2b.

Taken together, the results for the no-touch condition and the synchronous condition of the rubber hand paradigm indicate that RS and NC experienced the rubber hand illusion in both conditions whereas control participants experienced the illusion only in the synchronous condition. Given our expectation that RS and NC would experience the no-touch condition as if it were a synchronous condition (i.e., they would view touch on the prosthetic hand and experience synchronous synaesthetic tactile sensation on the untouched hidden hand), we compared questionnaire ratings provided by RS and NC for the no-touch condition to the ratings provided by control participants for the synchronous condition. Questionnaire ratings provided by RS and NC for the no-touch condition were not significantly different from ratings provided by control participants for the synchronous condition:

- Statement 1 (visual capture of touch): RS = 3; NC = 4; Control Participants $M = 3$, range = 0–6.
- Statement 2 (ownership of the viewed prosthetic hand): RS = 4; NC = 3; Control Participants $M = 2.667$, range = 0–6.

² In the synchronous condition, RS, NC and four (of twelve) control participants provided positive agreement ratings for the control statement (rating = 1, $n = 3$ control participants; rating = 3, $n = 1$ control participant). Although we expected an agreement rating of ‘0’ for all participants, we appreciate that the illusion might lead to the interpretation “It seemed as if I may have more than one left hand or arm”. At the beginning of the synchronous stimulation trial, the participant feels touch at the location of her own hand; as the trial progresses, it seems to the participant that he or she is feeling touch at the location of the viewed prosthetic hand. Thus the participant does ‘experience’ touch at the location of two left hands during the course of the trial.

- Statement 3 (control statement): RS = 0; NC = 2; Control Participants $M = .5$, range = 0–3.

Results for t-tests comparing questionnaire ratings for the individuals with vision-touch synaesthesia in the no-touch condition with questionnaire ratings for control participants in the synchronous condition are reported in Table 2c.

4.2.2. Proprioceptive drift (Fig. 2b, right panel)

Positive proprioceptive drift was demonstrated by both individuals with vision-touch synaesthesia (RS = 4 cm; NC = 4 cm) and by control participants ($M = 1.5$ cm, range = $-.5$ cm–3.5 cm) in the synchronous condition. Thus participants perceived the hidden left hand as shifted towards the location of the previously-viewed prosthetic hand in the synchronous condition. Modified t-tests confirmed that the proprioceptive drift demonstrated by RS and NC was not significantly different from the proprioceptive drift demonstrated by control participants, although RS and NC demonstrated a trend towards greater proprioceptive drift. Results for t-tests conducted on proprioceptive drift for the synchronous condition are reported in Table 2b.

Taken together, the results for the no-touch condition and the synchronous condition of the rubber hand paradigm indicate that RS and NC demonstrated positive proprioceptive drift in both conditions whereas control participants demonstrated positive proprioceptive drift only in the synchronous condition. Given our expectation that RS and NC would experience the no-touch condition as if it were a synchronous condition, we compared proprioceptive drift results for RS and NC for the no-touch condition to the results provided by control participants for the synchronous condition. RS demonstrated significantly greater proprioceptive drift for the no-touch condition (RS = 4.75 cm) than did control participants for the synchronous condition ($M = 1.5$ cm, range = $-.5$ cm–3.5 cm). The proprioceptive drift demonstrated by NC for the no-touch condition (NC = 2 cm) was not significantly different from the proprioceptive drift demonstrated by control participants for the synchronous condition. Results for t-tests comparing proprioceptive drift for individuals with vision-touch synaesthesia in the no-touch condition with proprioceptive drift for control participants in the synchronous condition are reported in Table 2c.

4.3. Asynchronous condition

4.3.1. Rubber hand illusion: questionnaire ratings

Questionnaire ratings (0 = not at all; 6 = very strongly agree) indicated that the two individuals with vision-touch synaesthesia did not experience the rubber hand illusion in the asynchronous condition. RS and NC provided an agreement rating of ‘0’ for all three statements on the questionnaire.

4.3.2. Proprioceptive drift

The two individuals with vision-touch synaesthesia demonstrated negative proprioceptive drift; they perceived the hidden left hand as shifted away from the location of the previously-viewed prosthetic hand in the asynchronous condition (RS = -2 cm; NC = -2.5 cm).

Table 3 – Experiment 2: comparing the proprioceptive drift of a single case (RS or NC) to control participants – no-touch condition for three trial durations (60 sec, 180 sec, 300 sec).

	Case	Control participants			Significance test		Estimated percentage of control population obtaining a lower score than the case		Estimated effect size (z_{cc})		
		Score	n	Mean	SD	t	p (two-tailed)	Point	95% CI	Point	95% CI
<i>No-touch condition</i>											
RS	60 sec	3	12	-1.521	1.949	2.229	.04764	97.618	(88.413–99.968)	2.320	(1.196–3.417)
	180 sec	4	12	-.917	2.224	2.124	.05716	97.142	(86.971–99.946)	2.211	(1.125–3.270)
	300 sec	5	12	-.896	2.675	2.118	.05781	97.110	(86.877–99.944)	2.204	(1.121–3.261)
NC	60 sec	3.5	12	-1.521	1.949	2.475	.03084	98.458	(91.329–99.992)	2.576	(1.361–3.767)
	180 sec	5	12	-.917	2.224	2.556	.02670	98.665	(92.150–99.995)	2.661	(1.415–3.882)
	300 sec	9.5	12	-.896	2.675	3.734	.00330	99.835	(98.540–100.00)	3.886	(2.181–5.575)

5. Experiment 2 results

5.1. No-touch condition with three trial durations

5.1.1. Perceived intensity ratings

Perceived intensity ratings (0 = no perceived tactile sensation; 6 = very intense tactile sensation) indicated that, for all trial durations (60 sec, 180 sec, 300 sec) of the no-touch condition, the two individuals with vision-touch synaesthesia experienced tactile sensation on their own untouched left index finger when they

viewed touch administered to the prosthetic left hand. In contrast, ratings provided by control participants indicated that they did not experience tactile sensation on the hidden hand in the no-touch condition of the rubber hand paradigm:

- 60-sec trial: RS = 3; NC = 4; Control Participants M = .625, range = 0–1.
- 180-sec trial: RS = 4; NC = 6; Control Participants M = .415, range = 0–1.
- 300-sec trial: RS = 5; NC = 6; Control Participants M = .667, range = 0–2.

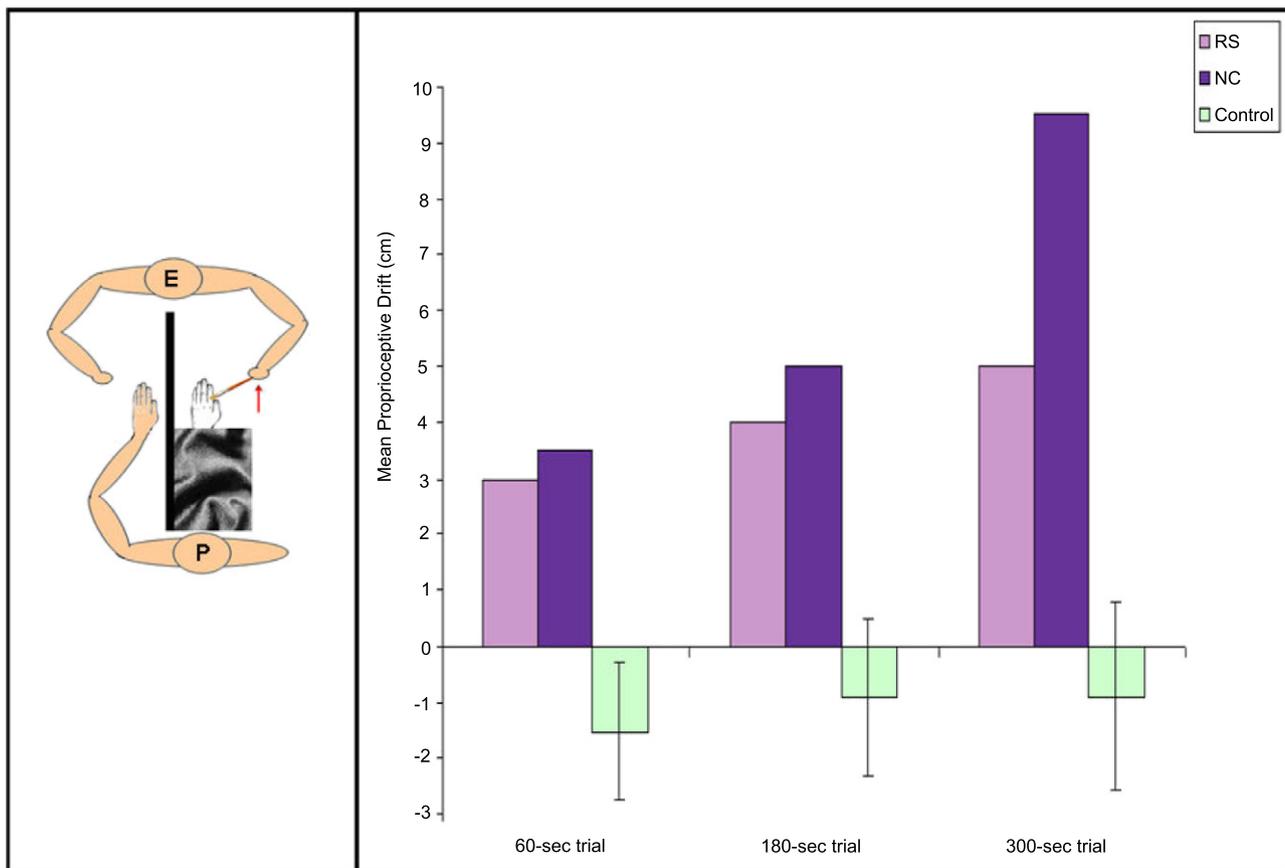


Fig. 3 – No-touch condition of the rubber hand paradigm: three trial durations (60 sec, 180 sec, 300 sec). Left panel, experimental set-up. Right panel, mean proprioceptive drift (cm). Error bars indicate 95% confidence intervals.

5.1.2. Proprioceptive drift (Fig. 3, right panel)

For all trial durations (60 sec, 180 sec, 300 sec) of the no-touch condition, the two individuals with vision-touch synaesthesia demonstrated positive proprioceptive drift. These individuals perceived the hidden left hand as shifted towards the location of the previously-viewed prosthetic hand whereas most control participants demonstrated negative proprioceptive drift or no drift:

- 60-sec trial: RS = 3 cm; NC = 3.5 cm; Control Participants $M = -1.521$ cm, range = -5.5 cm– 1 cm.
- 180-sec trial: RS = 4 cm; NC = 5 cm; Control Participants $M = -.917$ cm, range = -4.5 cm– 3 cm.
- 300-sec trial: RS = 5 cm; NC = 9.5 cm; Control Participants $M = -.896$ cm, range = -6 cm– 4.5 cm.³

Modified *t*-tests confirmed that for the 60-sec trial, RS demonstrated significantly greater proprioceptive drift than did control participants; the 180-sec ($p = .057$) and 300-sec ($p = .058$) trials bordered on significance. NC demonstrated significantly greater proprioceptive drift than did control participants for all three trial durations. Results for *t*-tests conducted on proprioceptive drift for the no-touch condition are reported in Table 3.

As can be seen in Fig. 3, RS and NC demonstrated a trend towards greater proprioceptive drift with increased trial duration whereas control participants did not. Paired *t*-tests confirmed that control participants showed no significant difference when proprioceptive drift was compared:

- 60-sec trial compared to 180-sec trial: $t(11) = -1.119$, $p = .287$.
- 60-sec trial compared to 300-sec trial: $t(11) = -1.005$, $p = .336$.
- 180-sec trial compared to 300-sec trial: $t(11) = -.026$, $p = .980$.

6. Discussion

We have presented a new method to authenticate vision-touch synaesthesia: a no-touch rubber hand paradigm. The main findings can be summarised as follows. In the no-touch condition of Experiment 1, with stimulation of the viewed prosthetic hand but no-touch of the participant's hidden hand, individuals with vision-touch synaesthesia experienced synaesthetic tactile sensation on the untouched hidden hand.⁴ These individuals also experienced the rubber hand illusion (visual capture of touch and the illusion of ownership of the prosthetic hand), and they demonstrated

³ Results for control participants who demonstrated positive proprioceptive drift: 60-sec trial, $n = 2$ (.5 cm; 1 cm); 180-sec trial, $n = 3$ (1 cm; 2 cm; 3 cm); 300-sec trial, $n = 4$ (.5 cm; .5 cm; 1.5 cm; 4.5 cm).

⁴ A recent study of individuals with vision-touch synaesthesia (Holle et al., 2011) has shown that synaesthetic tactile sensation is less intense when a 'dummy' hand is used. This could mean that our participants may have experienced an even stronger rubber hand illusion if we had used a human hand instead of a prosthetic hand. However, another difference in the two studies is that the realistic rubber hand (see Fig. 1) we used was viewed directly, rather than on a computer screen, as it was in the study by Holle et al.

positive proprioceptive drift; they perceived the hidden left hand as shifted towards the location of the previously-viewed prosthetic hand. In Experiment 2, three trial durations (60 sec, 180 sec, 300 sec) of the no-touch condition were investigated. RS showed 3 cm (60-sec trial), 4 cm (180-sec trial), and 5 cm (300-sec trial) proprioceptive drift; that is, proprioceptive drift of 20% (60-sec trial), 27% (180-sec trial), and 33% (300-sec trial) of the actual distance between the viewed prosthetic hand and her own hidden hand. NC showed 3.5 cm (60-sec trial), 5 cm (180-sec trial), and 9.5 cm (300-sec trial) proprioceptive drift; that is, proprioceptive drift of 23% (60-sec trial), 33% (180-sec trial), and 63% (300-sec trial) of the actual distance.⁵ This pattern – increased proprioceptive drift with increased trial duration – has previously been shown for control participants tested with the synchronous condition of the rubber hand paradigm (Botvinick and Cohen, 1998).

Control participants (individuals without vision-touch synaesthesia) did not experience the rubber hand illusion in the no-touch condition. In fact, many control participants queried Statement 1 "It seemed as if I were feeling the touch of the paintbrush in the location where I saw the rubber hand being touched". They told us that they had not been touched and therefore could not have felt anything. (Individuals with vision-touch synaesthesia completed the rubber hand questionnaire without hesitation.) Moreover, irrespective of trial duration (60 sec, 180 sec, 300 sec), most control participants demonstrated negative proprioceptive drift (away from rather than towards the previously-viewed prosthetic hand).

Proprioceptive drift away from the prosthetic hand is more commonly documented for a different kind of discrepant-stimulation condition, namely asynchronous stimulation of the viewed prosthetic hand and the participant's hidden hand (Botvinick and Cohen, 1998; Tsakiris and Haggard, 2005: Fig. 2, congruent-posture condition). Asynchronous stimulation is often used as a baseline condition in rubber hand experiments because participants do not experience the rubber hand illusion when stimulation of the two hands is not synchronous. The illusion is diminished with a temporal discrepancy of 300 msec, and it is abolished with a temporal discrepancy exceeding 500 msec (Shimada et al., 2009). For the two individuals with vision-touch synaesthesia, we used asynchronous stimulation to control for suggestibility, and to rule out any possibility that they could experience a rubber hand illusion irrespective of experimental manipulation. As predicted, RS and NC did not experience the rubber hand illusion in the asynchronous condition. They did not agree with any of the statements (illusion or control) on the questionnaire, and they demonstrated negative proprioceptive drift; they perceived the hidden left hand as shifted away from the location of the previously-viewed prosthetic hand.

⁵ When NC viewed touch on the prosthetic hand, she experienced a tingling sensation on her own hand. By the end of the 300-sec trial, NC explained that these sensations were 'building' in intensity. NC's left hand had become noticeably reddened (when compared to the right hand) and she reported that this longer trial was somewhat uncomfortable.

For individuals who experience the traditional rubber hand illusion, tactile sensation on the participant's hidden hand is referred to the prosthetic hand (Botvinick and Cohen, 1998). A complete understanding of the no-touch rubber hand illusion requires a two-step explanation. First, the individual's experience is that she is feeling touch on the (untouched) hidden hand when she views touch on the prosthetic hand: vision-touch synaesthesia accounts for this sensation. Second, the individual experiences touch at the location of the viewed prosthetic hand: synaesthetic tactile sensation on the (untouched) hidden hand is referred to the prosthetic hand. It may also seem as if the prosthetic hand is the individual's own hand. The no-touch rubber hand illusion occurs because touch on the viewed prosthetic hand is synchronous with the synaesthetic tactile sensation on the individual's own hand. A match between viewed touch and felt touch is a necessary condition for the rubber hand illusion. As noted by Pavani et al. (2000), when the touch that the participant sees matches the touch that the participant feels, "vision may dominate the perception of body part location" (p. 353) and thus "can affect the localization of bodily sensations" (p. 358). Importantly, the current study demonstrates that felt touch does not need to be physical touch. The rubber hand illusion can be elicited in individuals for whom felt touch is a synaesthetic tactile sensation.

Here it is interesting to contrast our results for control participants in the no-touch condition with those presented in a recent study by Giummarra et al. (2010), in which individuals without vision-touch synaesthesia did experience a no-touch rubber hand illusion. Their study made use of the elegant mirror-box apparatus devised by Ramachandran et al. (1995). A vertical mirror was positioned on the table, perpendicular to the participant's body, and at body midline. The participant's left hand was hidden, and it was to the left of the mirror on the non-reflective side. In one condition, a prosthetic right hand was positioned on the right side of the mirror. The placement of the mirror was such that the viewed prosthetic right hand appeared to occupy "the perceived body space of the [hidden] target hand" (Giummarra et al., 2010, p. 114). It was as if the participant was looking at her own left hand through a sheet of glass. When the Examiner administered touch to the prosthetic right hand, the participant saw this touch in the mirror and experienced illusory tactile sensation on the hidden left hand and ownership of the viewed prosthetic hand. Giummarra et al. suggest that viewing a hand that occupies perceived body space may activate neurons in the posterior parietal cortex, the temporo-parietal junction and motor regions of the brain, and that activation of these cortical regions that encode peripersonal body space may "increase tactile sensitivity and perception of illusory touch, and subsequently promote embodiment" (p. 114). In our study, the viewed hand did not occupy the perceived body space of the participant's hidden hand. The participant looked 15 cm to the right of her hidden left hand when she viewed the prosthetic hand. Thus, our finding that control participants did not experience illusory tactile sensation is consistent with the conclusion that an overlap, between the viewed location of a body part and the perceived location of one's own body, may be necessary to elicit illusory tactile sensation in individuals without vision-touch synaesthesia.

Contrasting our study with the study by Giummarra et al. (2010) allows us not only to speculate about the conditions that are necessary to elicit illusory tactile sensation in individuals without vision-touch synaesthesia, but also to speculate about mechanisms for illusory or synaesthetic tactile sensation in individuals with vision-touch synaesthesia. Perhaps the boundaries of perceived body space are more expansive in individuals with vision-touch synaesthesia? If so, 'other' bodies may be more likely to fall within perceived body space, and to activate the parietal network that is involved both in encoding peripersonal space and in processing multiple sources of sensory information. Experiments aimed at investigating perceived body space in individuals with and without vision-touch synaesthesia will shed further light on this proposal, and on the importance of perceived body space in distinguishing between self and other when observing touch.

7. Conclusions

This is the first study to use the rubber hand paradigm to authenticate vision-touch synaesthesia. The no-touch rubber hand paradigm provides a good method to authenticate vision-touch synaesthesia because individuals who are naïve about the rubber hand illusion will not anticipate how they are expected to perform. Indeed, individuals with vision-touch synaesthesia who are naïve about the illusion will not anticipate how individuals without vision-touch synaesthesia will perform on either the traditional or the no-touch rubber hand paradigm. In the current study, the two individuals with vision-touch synaesthesia were naïve about the experimental paradigm, and they experienced the no-touch rubber hand illusion. RS and NC provided high ratings of agreement with the illusion statements on the questionnaire, and they demonstrated positive proprioceptive drift (a change, from baseline, in proprioceptively perceived position) of the hidden hand towards the location of the previously-viewed prosthetic hand. Intuitively, we think that an individual feigning vision-touch synaesthesia would disagree with the questionnaire statements, and indicate that the proprioceptively perceived hand position was further from (rather than closer to) the prosthetic hand. The individual might presume that because she feels touch on her own hidden hand, she will not be fooled by the location of the viewed prosthetic hand.

Future studies could incorporate additional objective measures to substantiate the experience of the rubber hand illusion for individuals with vision-touch synaesthesia. Previous rubber hand studies have measured skin conductance responses (e.g., Armel and Ramachandran, 2003; Ehrsson et al., 2008; Ehrsson, 2009; Ocklenburg et al., 2010), somatosensory evoked potentials (Peled et al., 2003), and temperature of the hidden hand (Hohwy and Paton, 2010; Moseley et al., 2008). There have also been a number of studies that have used tactile tasks either to authenticate the experience of the rubber hand illusion or to investigate its impact on tactile processing (Bruno and Bertamini, 2010; Farnè et al., 2000; Folegatti et al., 2009; Haggard and Jundi, 2009; Kammers et al., 2010; Longo et al., 2008a; Moseley et al., 2008). Other studies have used imaging techniques to

investigate the neural underpinnings of the rubber hand illusion (e.g., fMRI: Ehrsson et al., 2004, 2007; Lloyd et al., 2006; MEG: Schaefer et al., 2006; PET: Tsakiris et al., 2007). Consequently, there is a wealth of information about the rubber hand illusion: we hope that the current study will inspire research using these different methods (with known outcome measures) to investigate vision-touch synaesthesia.

REFERENCES

- Armell KC and Ramachandran VS. Projecting sensations to external objects: Evidence from skin conductance response. *Proceedings of the Royal Society of London B*, 270(1523): 1499–1506, 2003.
- Banissy MJ, Cohen Kadosh RC, Maus GW, Walsh V, and Ward J. Prevalence, characteristics and a neurocognitive model of mirror-touch synaesthesia. *Experimental Brain Research*, 198(2–3): 261–272, 2009a.
- Banissy MJ, Garrido L, Kusnir F, Duchaine B, Walsh V, and Ward J. Superior facial expression, but not identity recognition, in mirror-touch synaesthesia. *The Journal of Neuroscience*, 31(5): 1820–1824, 2011.
- Banissy MJ, Walsh V, and Ward J. Enhanced sensory perception in synaesthesia. *Experimental Brain Research*, 196(4): 565–571, 2009b.
- Banissy MJ and Ward J. Mirror-touch synesthesia is linked with empathy. *Nature Neuroscience*, 10(7): 815–816, 2007.
- Beauchamp MS and Ro T. Neural substrates of sound-touch synaesthesia after a thalamic lesion. *The Journal of Neuroscience*, 28(50): 13696–13702, 2008.
- Blakemore S-J, Bristow D, Bird G, Frith C, and Ward J. Somatosensory activations during the observation of touch and a case of vision-touch synaesthesia. *Brain*, 128(7): 1571–1583, 2005.
- Botvinick M and Cohen J. Rubber hands ‘feel’ touch that eyes see. *Nature*, 391(6669): 756, 1998.
- Bradshaw JL and Mattingley JB. Allodynia: A sensory analogue of motor mirror neurons in a hyperaesthetic patient reporting instantaneous discomfort to another’s perceived sudden minor injury? *Journal of Neurology, Neurosurgery, and Psychiatry*, 70(1): 135–136 and 70(6): 821, 2001.
- Bruno N and Bertamini M. Haptic perception after a change in hand size. *Neuropsychologia*, 48(6): 1853–1856, 2010.
- Costantini M and Haggard P. The rubber hand illusion: Sensitivity and reference frame for body ownership. *Consciousness and Cognition*, 16(2): 229–240, 2007.
- Crawford JR, Garthwaite PH, and Porter S. Point and interval estimates of effect sizes for the case–controls design in neuropsychology: Rationale, methods, implementations, and proposed reporting standards. *Cognitive Neuropsychology*, 27(3): 245–260, 2010.
- Crawford JR and Howell DC. Comparing an individual’s test score against norms derived from small samples. *The Clinical Neuropsychologist*, 12(4): 482–486, 1998.
- Cytowic RE. Touching tastes, seeing smells – and shaking up brain science. *Cerebrum*, 4: 7–26, 2002.
- Durgin FH, Evans L, Dunphy N, Klostermann S, and Simmons K. Rubber hands feel the touch of light. *Psychological Science*, 18(2): 152–157, 2007.
- Ehrsson HH. How many arms make a pair? Perceptual illusion of having an additional limb. *Perception*, 38(2): 310–312, 2009.
- Ehrsson HH, Holmes NP, and Passingham RE. Touching a rubber hand: Feeling of body ownership is associated with activity in multisensory brain areas. *The Journal of Neuroscience*, 25(45): 10564–10573, 2005.
- Ehrsson HH, Rosén B, Stockselius A, Ragnö C, Köhler P, and Lundborg G. Upper limb amputees can be induced to experience a rubber hand as their own. *Brain*, 131(12): 3443–3452, 2008.
- Ehrsson HH, Spence C, and Passingham RE. That’s my hand! Activity in premotor cortex reflects feeling of ownership of a limb. *Science*, 305(5685): 875–877, 2004.
- Ehrsson HH, Wiech K, Weiskopf N, Dolan RJ, and Passingham RE. 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(23): 9828–9833, 2007.
- Farnè A, Pavani F, Meneghello F, and Làdavas E. Left tactile extinction following stimulation of a rubber hand. *Brain*, 123(11): 2350–2360, 2000.
- Folegatti A, de Vignemont F, Pavani F, Rossetti Y, and Farnè A. Losing one’s hand: Visual-proprioceptive conflict affects touch perception. *PLoS One*, 4(9): e6920, 2009.
- Gheri C, Chopping S, and Morgan MJ. Synaesthetic colours do not camouflage form in visual search. *Philosophical Transactions of the Royal Society, B*, 275(1636): 841–846, 2008.
- Giummarra MJ, Georgiou-Karistianis N, Nicholls MER, Gibson SJ, and Bradshaw JL. The phantom in the mirror: A modified rubber-hand illusion in amputees and normals. *Perception*, 39(1): 103–118, 2010.
- Haans A, IJsselstein WA, and de Kort YAW. The effect of similarities in skin texture and hand shape on perceived ownership of a fake limb. *Body Image*, 5(4): 389–394, 2008.
- Haggard P and Jundi S. Rubber hand illusions and size-weight illusions: Self-representation modulates representation of external objects. *Perception*, 38(12): 1796–1803, 2009.
- Hohwy J and Paton B. Explaining away the body: Experiences of supernaturally caused touch and touch on non-hand objects within the rubber hand illusion. *PLoS One*, 5(2): e9416, 2010.
- Holle H, Banissy M, Wright T, Bowling N, and Ward J. “That’s not a real body”: Identifying stimulus qualities that modulate synaesthetic experiences of touch. *Consciousness and Cognition*, 20(3): 720–726, 2011.
- Holmes NP, Snijders HJ, and Spence C. Reaching with alien limbs: Visual exposure to prosthetic hands in a mirror biases proprioception without accompanying illusions of ownership. *Perception and Psychophysics*, 68(4): 685–701, 2006.
- Kammers MP, Kootker JA, Hogendoorn H, and Dijkerman HC. How many motoric body representations can we grasp? *Experimental Brain Research*, 202(1): 203–212, 2010.
- Keyers C, Wicker B, Gazzola V, Anton J-L, Fogassi L, and Gallese V. A touching sight: SII/PV activation during the observation and experience of touch. *Neuron*, 42(2): 335–346, 2004.
- Lloyd D, Morrison I, and Roberts N. Role for human posterior parietal cortex in visual processing of aversive objects in peripersonal space. *Journal of Neurophysiology*, 95(1): 205–214, 2006.
- Longo MR, Cardozo S, and Haggard P. Visual enhancement of touch and the bodily self. *Consciousness and Cognition*, 17(4): 1181–1191, 2008a.
- Longo MR, Schüür F, Kammers MPM, Tsakiris M, and Haggard P. What is embodiment? A psychometric approach. *Cognition*, 107(3): 978–998, 2008b.
- Makin TR, Holmes NP, and Ehrsson HH. On the other hand: Dummy hands and peripersonal space. *Behavioural Brain Research*, 191(1): 1–10, 2008.
- McCabe C, Rolls ET, Bilderbeck A, and McGlone F. Cognitive influences on the affective representation of touch and the sight of touch in the human brain. *Social Cognitive and Affective Neuroscience*, 3(2): 97–108, 2008.
- Moseley GL, Olthof N, Venema A, Don S, Wijers M, Gallace A, et al. Psychologically induced cooling of a specific body part caused

- by the illusory ownership of an artificial counterpart. *Proceedings of the National Academy of Sciences of the United States of America*, 105(35): 13169–13173, 2008.
- Ocklenburg S, Ruther N, Peterburs J, Pinnow M, and Gunturkun O. Laterality in the rubber hand illusion. *Laterality*, 16(2): 174–187, 2010.
- Paillard J and Brouchon M. Active and passive movements in the calibration of position sense. In Freedman SJ (Ed), *The Neuropsychology of Spatially Oriented Behavior*. Illinois: Dorsey Press, 1968: 37–56.
- Pavani F, Spence C, and Driver J. Visual capture of touch: Out-of-body experiences with rubber gloves. *Psychological Science*, 11(5): 353–359, 2000.
- Peled A, Pressman A, Geva AB, and Modai I. Somatosensory evoked potentials during a rubber-hand illusion in schizophrenia. *Schizophrenia Research*, 64(2–3): 157–163, 2003.
- Ramachandran VS and Rogers-Ramachandran D. Synaesthesia in phantom limbs induced with mirrors. *Proceedings of the Royal Society of London B*, 263(1369): 377–386, 1996.
- Ramachandran VS, Rogers-Ramachandran D, and Cobb S. Touching the phantom limb. *Nature*, 377(6549): 489–490, 1995.
- Ro T, Farnè A, Johnson RM, Wedeen V, Chu Z, Wang ZJ, et al. Feeling sounds after a thalamic lesion. *Annals of Neurology*, 62(5): 433–441, 2007.
- Rohde M, Di Luca M, and Ernst MO. The rubber hand illusion: Feeling of ownership and proprioceptive drift do not go hand in hand. *PLoS One*, 6(6): e21659, 2011.
- Schaefer M, Noennig N, Heinze HJ, and Rotte M. Fooling your feelings: Artificially induced referred sensations are linked to a modulation of the primary somatosensory cortex. *NeuroImage*, 29(1): 67–73, 2006.
- Shimada S, Fukuda K, and Hiraki K. Rubber hand illusion under delayed visual feedback. *PLoS One*, 4(7): e6185, 2009.
- Simner J, Sagiv N, Mulvenna C, Tsakanikos E, Witherby SA, Fraser C, et al. Synaesthesia: the prevalence of atypical cross-modal experiences. *Perception*, 35(8): 1024–1033, 2006.
- Tsakiris M and Haggard P. The rubber hand illusion revisited: Visuotactile integration and self-attribution. *Journal of Experimental Psychology: Human Perception and Performance*, 31(1): 80–91, 2005.
- Tsakiris M, Hesse MD, Boy C, Haggard P, and Fink GR. Neural signatures of body ownership: A sensory network for bodily self-consciousness. *Cerebral Cortex*, 17(10): 2235–2244, 2007.
- Tsakiris M, Carpenter L, James D, and Fotopoulou A. Hands only illusion: Multisensory integration elicits sense of ownership for body parts but not for non-corporeal objects. *Experimental Brain Research*, 204(3): 343–352, 2010.
- Wann JP and Ibrahim SF. Does limb proprioception drift? *Experimental Brain Research*, 91(1): 162–166, 1992.
- Ward J, Banissy MJ, and Jonas CN. Haptic perception and synaesthesia. In Grunewald M (Ed), *Human Haptic Perception*. Germany: Springer Publishers, 2008: 259–265.