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The rubber hand illusion in action

M.P.M. Kammers[a,*], F. de Vignemont[b], L. Verhagen[a,c], H.C. Dijkerman[a]

[a] Utrecht University, Heidelberglaan 2, 3584 CS Utrecht, The Netherlands
[b] Institut Jean- Nicod, Pavillon Jardin, Ecole Normale Supérieure 29, rue d'Ulm, 75005 Paris, France
[c] F.C. Donders Centre for Cognitive Neuroimaging, Radboud University, Kapittelweg 29, 6525 EN Nijmegen, The Netherlands

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ABSTRACT

In the well-known rubber hand illusion (RHI), watching a rubber hand being stroked while one's own unseen hand is synchronously stroked, induces a relocation of the sensed position of one's own hand towards the rubber hand [Botvinick, M., & Cohen, J. (1998). Rubber hands 'feel' touch that eyes see. *Nature, 391*(6669), 756]. As one has lost the veridical location of one's hand, one should not be able to correctly guide one's hand movements. An accurate representation of the location of body parts is indeed a necessary pre-requisite for any correct motor command [Graziano, M. S. A., & Botvinick, M. M. (1999). How the brain represents the body: Insights from neurophysiology and psychology. In D. Gopher, & A. Koriat (Eds.), *Attention and performance XVII—Cognitive regulation of performance interaction of theory and application* (pp. 136–157)]. However, it has not yet been investigated whether action is indeed affected by the proprioceptive drift towards the rubber hand, nor has the resistance of visual capture in the RHI to new proprioceptive information been assessed. In the present two kinematic experiments, we show for the first time that action resists the RHI and that the RHI resists action. In other words, we show a dissociation between illusion-insensitive ballistic motor responses and illusion-sensitive perceptual bodily judgments. Moreover, the stimulated hand was judged closer to the rubber hand for the perceptual responses, even after active movements. This challenges the view that any proprioceptive update through active movement of the stimulated hand erases the illusion. These results expand the knowledge about representations of the body in the healthy brain, and are in line with the currently most used dissociation between two types of body representations so far mainly based on neuropsychological patients [Paillard, J. (1991). Knowing where and knowing how to get there. In J. Paillard (Ed.), *Brain and space* (pp. 461–481); Paillard, J. (1999). Body schema and body image: A double dissociation in deafferented patients. In G. N. Gantchev, S. Mori, & J.Massion (Eds.), *Motor control, today and tomorrow* (pp. 197–214)].

1. Introduction

The way we use sensory information determines the way we encode it. Separate visual cortical processing pathways for perception and action are an illustration of this general principle (Milner & Goodale, 1995). On the one hand, there are mental representations dedicated to the recognition and identification of the input. On the other hand, there are representations used to plan and control actions performed towards the input. This distinction is founded on an impressive amount of evidence from physiology, psychophysics, neuropsychology and neuroscience (Jacob & Jeannerod, 2003). It has been shown not only for vision, but also for the auditory modality (Belin & Zatorre, 2000), and more recently for proprioception and touch (Dijkerman & de Haan, 2007). Moreover, not only the representation of the external world varies depending upon its functional role, but also the representation of one's own body in the brain seems to depend on the task.

At present there is an ongoing debate about the existence of dissociable body representations (de Vignemont, 2007; Gallagher, 2005; Paillard, 1991 (chap. 24), 1999; Schwoebel & Coslett, 2005; Sirigu, Grafman, Bressler, & Sunderland, 1991). Influenced by the Perception-Action model, Paillard (1991, 1999), suggested a distinction between 'knowing where' and 'knowing how to get there', that is between the body image for perception (i.e. judgment of one's own bodily properties) and the body schema for action (i.e. information about the body necessary to move such as posture, limb size, and strength). The evidence provided to support this distinction relies mainly on neuropsychological dissociations

* Corresponding author at: Helmholtz Research Institute, Experimental Psychology, Utrecht University, Room 16.24, Van Unnikbuilding, Heidelberglaan 2, 3584 CS Utrecht, The Netherlands. Tel.: +31 30 2534023; fax: +31 30 2534511.

E-mail addresses: m.p.m.kammers@uu.nl (M.P.M. Kammers), fvignemont@isc.cnrs.fr (F. de Vignemont), l.verhagen@uu.nl (L. Verhagen), h.c.dijkerman@uu.nl (H.C. Dijkerman).

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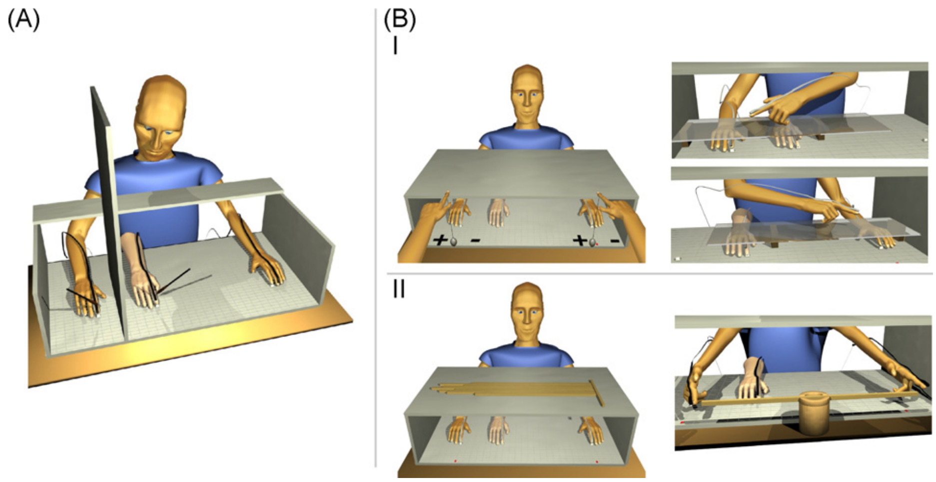


Fig. 1. Experimental set-up. (A) Set-up during stimulation period. (B) Perceptual and motor responses for Experiment 1 (I), and Experiment 2 (II).

between deafferentation and apraxia (disruption of body schema) (Buxbaum & Coslett, 2001), versus numbsense, neglect, and autotopagnosia (disruption of body image) (Gallagher, 2005; Head and Holmes, 1911–1912; Sirigu et al., 1991). However, there is almost a complete lack of evidence of a dissociation between different types of body representations in healthy individuals. One way of investigating these different body representations is through task-dependent effects of bodily illusions (Kammers, van der Ham, & Dijkerman, 2006). The rationale behind this is that the way the brain resolves the sensory conflict induced by the bodily illusion is a measurement of the plasticity and flexibility of the underlying body representation. Moreover, if the brain resolves this conflict differently depending on the type of task, this is taken as evidence that distinct body representations underlie these dissociable bodily experiences.

A well-known bodily illusion is the rubber hand illusion (RHI) (Botvinick & Cohen, 1998). In the RHI, participants see a rubber hand that lies in an anatomically congruent orientation to their own occluded hand. The rubber hand as well as the participant's own hand are stroked synchronously, creating the multisensory conflict of seeing a touch that is felt at a different location. This multisensory conflict is resolved by incorporation of the rubber hand in one's own body representation, as well as by relocation of the felt position of one's own hand towards the rubber hand. The general idea is that the illusion is based on visual capture of proprioceptive information. Proprioception drifts rapidly in the absence of vision, and in the RHI set-up this results in overwriting the proprioceptive location information of one's own hand with the visual location information of the rubber hand. On average 80% of participants report the RHI within 15 s of synchronous stroking (Ehrsson, Holmes, & Passingham, 2005; Lloyd, 2007).

Although synchrony between visual and proprioceptive information is necessary for the RHI to occur, this has proven not to be sufficient. The effect of the illusion is reduced or even eliminated when the posture or laterality of the rubber hand is incongruent with the unseen real hand (Armel & Ramachandran, 2003; Tsakiris & Haggard, 2005). This has led to the suggestion that prior representations about the body also play an important role (Costantini & Haggard, 2007; Tsakiris & Haggard, 2005). If this is indeed the case, the extent of the RHI should depend on the type of body representation that is recruited by the response.

So far the RHI has been assessed mainly through questionnaires – to investigate the sense of ownership over the rubber hand, and perceptual judgments – to measure proprioceptive drift (Durgin, Evans, Dunphy, Klostermann, & Simmons, 2007; Ehrsson et al., 2005; Ehrsson, Spence, & Passingham, 2004; Farne, Pavani, Meneghello, & Ladavas, 2000; Lloyd, 2007). The possible existence of multiple body representations has however been neglected, although it may differently influence the illusion depending on the type of task (de Vignemont, 2007; Gallagher, 2005; Paillard, 1999; Schwoebel & Coslett, 2005; Sirigu et al., 1991). In parallel with the task dependency found for several visual illusions (Aglioti, DeSouza, & Goodale, 1995; Goodale & Milner, 1992; Haffenden & Goodale, 2000; Kroliczak, Heard, Goodale, & Gregory, 2006), and in line with the dissociation between the body image and the body schema, we expected perceptual judgments to be more susceptible to bodily illusions than actions.

In the present study we therefore asked participants to indicate the felt position of their unseen stimulated hand by providing both perceptual judgments and motor responses (please see Fig. 1 for an example of RHIset-up). We conducted two experiments which both involved different types of action and perceptual responses to investigate the generality of a possible RHI task-dependency effect. All perceptual judgments are hypothesized to be predominantly based on the body image, whereas actions are thought to be governed primarily by the body schema (Kammers et al., 2006). While numerous studies have demonstrated that perceptual judgments are affected by the RHI, it is unknown whether this is true for motor responses. Botvinick and Cohen (1998) asked participants to point to the felt location of the occluded stimulated hand and found an endpoint bias towards the rubber hand. However, non-ballistic pointing movements display specific properties that differ from other types of actions (Kroliczak et al., 2006). Here we measured the kinematics of ballistic motor responses and investigated the effect these actions have on subsequent perceptual location judgments. The latter is of interest for two reasons. First, the general idea is that the RHI can arise because of drifting proprioceptive signals, active movements provide an update of this proprioceptive information, which is presumed to cancel out the RHI. However, this has not been tested. Second, if the motor and perceptual responses are indeed based on dissociable body representations, an effect of a preceding motor response on a subsequent perceptual judgment would shed light on the possible interaction between the two body representations.

2. Methods

2.1. Participants

Fourteen naïve right-handed participants (mean age = 22.9 years, S.D. = 4.01) gave informed consent and participated in Experiment 1. Another fourteen participants participated in Experiment 2 (mean age = 22.7 years, S.D. = 3.67, six of whom also participated in Experiment 1—These participants were not de-briefed after Experiment 1, and remained naïve to the purpose of Experiment 2). Right-handedness was assessed with the Van Strien Dutch Handedness questionnaire (Van Strien, 1992) (overall mean = 9.96, S.D. = 0.26, where 7 or higher indicates a strong right-handedness preference in daily activities). Participants received a small fee for participation. The study was approved by the local ethical advisory committee of the Faculty of Social Sciences of Utrecht University, and was conducted in accordance with the declaration of Helsinki (1964).

2.2. General procedure

The participants were asked to remove all jewellery and nail polish from their hands and cut their nails short before the start of the experiment. This was done to keep the visual congruence with the rubber hand as high as possible, and to prevent interference of the magnetic field of the kinematic recording device.

The participants were seated comfortably at a chair behind a desk. On the desk a wooden framework was placed (75 cm × 50 cm × 25 cm). The framework had a removable board that could be placed either vertically, creating two compartments inside the frame (one for the hidden right hand and one for the visible left hand and the rubber hand (Fig. 1)), or horizontally on top of the frame (occluding both hands of the participant and the rubber hand from vision).

In the start/rest position participants placed their forearms on the table with palms down, and the index fingers on two marked caps. The right rubber hand was placed 15 cm to the left of the right arm (measured between the index finger of the rubber hand and the index finger of the right hand). The total distance between the stimulated right and the non-stimulated left index finger was 46.5 cm. The rubber hand and the left hand lay 31.5 cm from each other and the participants were positioned in such a way that their body midline was in the middle of this distance. The proximal end of the rubber hand was not visible to the participant due to the framework and the visible part of the rubber hand was aligned with the participant's right forearm.

In both experiments a marker of the kinematic recording device was attached to the tip of the two index fingers and a dummy marker was attached to the index finger of the rubber hand. The experimenter induced the illusion with two identical brushes during a 90 s stimulation period. Stimulation on the index fingers of the right hand and the rubber hand was either synchronous (Illusion) or asynchronous (Control). The direction of the stroking was always from knuckle to fingertip. The speed and length of the stroking was unpredictable in both conditions. In the asynchronous condition, the difference between the stroking on the participant's own hand and on the rubber hand was also unpredictable.

After the stimulation period the responses were collected. The general order of the types of response in both experiments was: first perceptual response, motor response(s), and finally a repetition of the first perceptual response (please see Fig. 2 for time-line Experiment 1).

2.3. Experiment 1

In Experiment 1 the perceptual response consisted of a verbal localization task whereby the experimenter mirrored the felt location of the participant's two index fingers. The verbal localization task was then followed by two reaching movements whereby the target was the participant's other hand. Finally, participants were asked again to perform the verbal localization task. The experiment therefore consisted of a 2 × 4 × 2 design, with factors Perceptual response (for the stimulated right as well as the non-stimulated left hand), Motor response (with four different combination of reaching responses (please see Section 2.3.2) and Type of stroking (which could be either synchronous or asynchronous). Responses were obtained for both left and right hand in each trial, such that trials were run in one of 8 different conditions. Trials were presented in randomised order and repeated three times, making a total of 24 trials.

2.3.1. Perceptual response

After stimulation the participants were instructed to close their eyes so that the board could be placed on top of the framework, occluding the participant's forearms and the rubber hand from vision. Subsequently, the participants were asked to open their eyes. The experimenter sat in front of the participant and placed his index fingers on the edge of the framework. Next, the experimenter moved his index fingers along the edge of the board starting either from the midline to the edges of the board, or vice versa. The two starting positions were counterbalanced. The participant was asked to mentally draw a line from the location of the experimenter's index fingers to felt location of their own fingers, and to verbally report when the experimenter mirrored the perceived position of their own index fingers. The difference between the participant's index fingers and the index fingers of the experimenter formed the dependent variable for the perceptual response. On average the perceptual response for the left and the right hands together took about 1 min, after which the motor responses were collected.

2.3.2. Motor response

Next, the participants were asked to perform two ballistic reaching movements. This could be done in one of four conditions: either twice with the non-stimulated left index finger towards the stimulated right index finger (condition 1), once with the stimulated and once with the non-stimulated hand (counterbalanced; conditions 2 and 3), or twice with the stimulated right hand towards the non-stimulated left index finger (condition 4). In order to prevent proprioceptive location feedback from skin contact between the index fingers a small board was placed over the hand to which the participants were asked to reach. This board was placed inside the framework directly above the hand (6 cm) to prevent the action terminating too soon. Participants were asked to reach directly with one hand to the tip of the index finger of the other hand in a single smooth movement. They were not allowed to make any corrections once the pointing hand had reached the board above the target hand. Participants did not see their hands, since

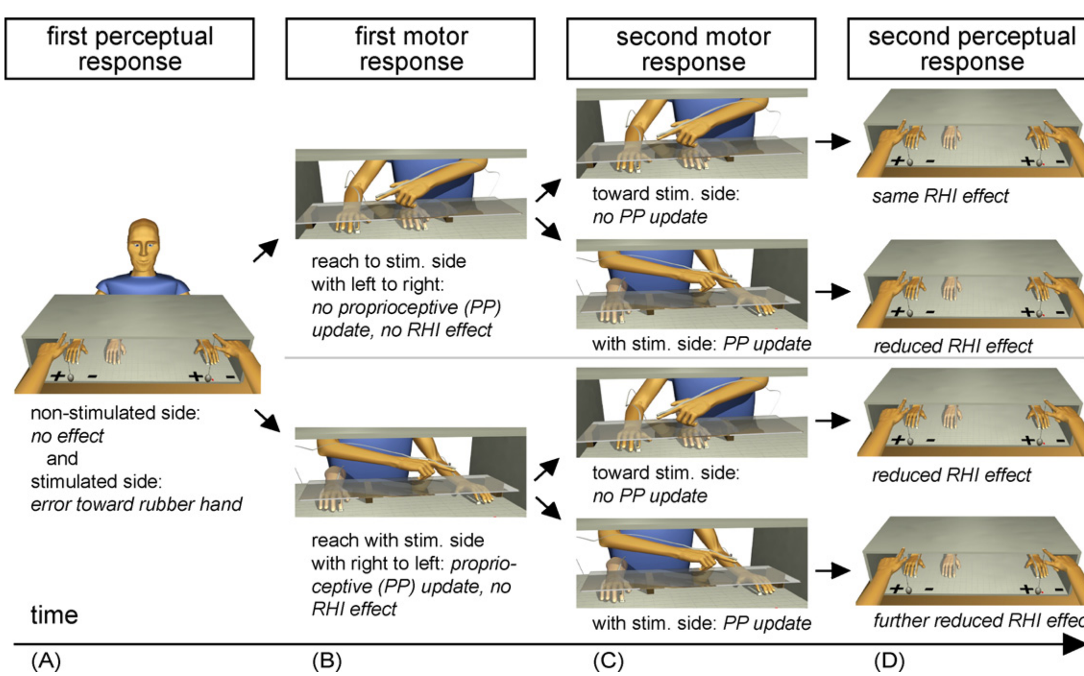


Fig. 2. Time line and hypotheses Experiment 1. (A) First perceptual response, followed by (B) either reaching with or towards the stimulated hand. Next, (C) second reaching movement, and finally (D) the second perceptual response. Hypotheses are in italics.

(A) **Instructions:**
Please keep the last trial in mind when rating the questions according to a scale from 1 till 10, whereby 1 means 'I strongly disagree' and 10 means 'I strongly agree'

During the last trial there were times when:
1. It seemed as if I was feeling the touch at the location where I saw the rubber hand being touched
2. It seemed as though the touch I felt was caused by the stimulation on the rubber hand
3. I felt as if the rubber hand was my own hand
4. It felt as if my real right hand was drifting toward the left (toward the rubber hand)
5. It felt as if I had more than one right hand or arm
6. It seemed as if the touch I was feeling came from somewhere between my own hand and the rubber hand
7. It felt as if my real right hand was turning 'rubbery'
8. It appeared (visually) as if the rubber hand was drifting toward my own right hand
9. The rubber hand began to resemble my own real hand, in terms of shape, skin tone, freckles, etc
10 It felt as if the rubber hand and my own right hand lay closer to each

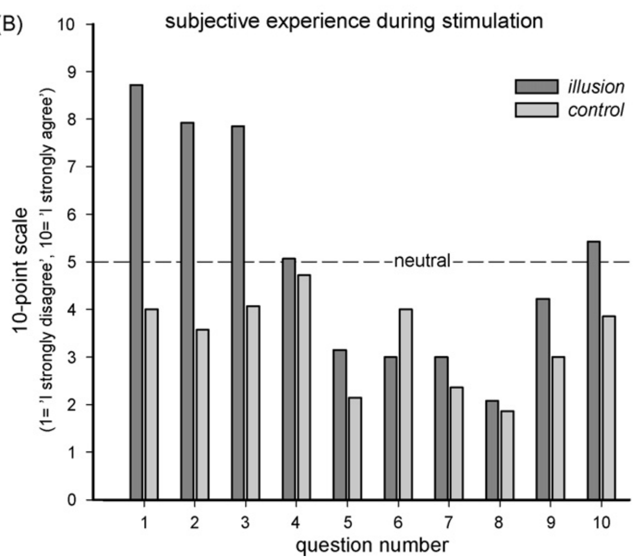
(B)


Fig. 3. Rubber Hand Illusion Questionnaire. (A) The 10 RHI-related questions. (B) Mean questionnaire ratings for the Illusion and the Control condition.

their forearms remained in the framework which was covered by the horizontal board.

Finally, after the reaching movements a second perceptual response was recorded that was identical to the first perceptual task.

2.3.3. Questionnaire

The participants were asked to fill in a Rubber Hand Illusion Questionnaire (based on Botvinick and Cohen (1998) and Ehrsson et al. (2005)) once midway through and once at the end of the experiment. Participants were asked to keep the last trial in mind while completing the questionnaire. This was manipulated in such a way that the questionnaire followed an illusion as well as a control trial. This was done on both testing sessions, making a total of 4 questionnaires (two per condition) (please see Fig. 3A for questionnaire).

2.4. Experiment 2

In Experiment 2 the perceptual response consisted of choosing one stick out of 8 that was the most similar in length to the perceived distance between the participant's index fingers. Participants were then asked to grasp a stick. Finally, they were asked to perform again the verbal stick selection. The experiment therefore consisted of a 3×2 design with three possible motor responses (three different sticks of different lengths were presented) and either synchronous or asynchronous stroking, for a total of 6 different conditions. These were presented in randomised order and repeated twice, making a total of 12 trials.

2.4.1. Perceptual response

After the stimulation period the board was placed on top of the framework to occlude both forearms and the rubber hand. On top of the board eight sticks were presented, increasing in length with steps of 2.5 cm. The participant was told that one of the sticks resembled the actual distance between his left and right index fingers (46.5 cm), and was instructed to indicate verbally which stick resembled the perceived distance between the two index fingers. There were three different groups of sticks with different lengths, which were counterbalanced. Each group included sticks identical in length to the distance between both index fingers (46.5 cm) and to the distance between the non-stimulated left index finger and rubber hand (31.5 cm). The difference between the indicated length and the actual distance formed the dependent variable.

2.4.2. Motor response

One stick (this could be either large 56.5 cm, medium 46.5 cm (actual distance) or small 26.5 cm) was presented horizontally at the edge of the framework, just within the visual field of the participant. The participants were asked to grasp the stick at the two ends between both index fingers. In other words, to grasp simultaneously the left and right end of the stick with their left and right index finger, respectively. As the body midline was midway between the rubber hand and the left hand, the grasping movement was asymmetrical so that the participants could not rely just on the position of the non-stimulated left hand. This was done three times for each stick length. The presentation order of the different sticks was counterbalanced. Finally, after the grasping movement a second perceptual response was recorded.

2.4.3. Kinematic measurement parameters

Kinematic data of the two index fingers was acquired using the miniBIRD tracking system (Ascension Technology Ltd.), with a sampling rate of 86 Hz. To keep the visual information constant a dummy marker was attached to the index finger of the rubber hand. Data was low-passed filtered (fourth order Butterworth filter at 10 Hz), after which the tangential speed of the two markers was calculated. The onset of the movement was determined when velocity exceeded 0.1 m/s, for over 0.02 s. The offset of the movement was set at the moment the velocity remained below 0.1 m/s, for over 0.02 s. If two movements followed each other within 0.1 s they were regarded as one. Only movements with durations exceeding 0.2 s were considered valid. Using these parameters two movements (one forward to the perceived target and one back to the starting position) were detected in all trials for all participants (checked visually).

The dependent kinematic variables were Movement Time (total time between movement on- and offset), Peak velocity (highest velocity between on- and offset of the action), Relative time to peak velocity (the time were the peak in velocity occurred compared to the total movement time), Mean velocity (the average velocity between on- and offset of the movement), and Endpoint error (the distance between the indicated and veridical location of the index finger in the horizontal plane). Endpoint variance was expressed by the area of the 95% confidence ellipses (McIntyre, Stratta, & Lacquaniti, 1998).

2.5. Statistical analyses

In order to investigate *the strength of the illusion* we subtracted the error between the indicated and veridical location in the control condition (asynchronous stroking) from the illusion condition (synchronous stroking). Two-way paired-sample t-tests between conditions were used to investigate the relative strength of the illusion, while one-sample t-tests against zero (the veridical location of the index finger) were administered to investigate the strength of the illusion for the actual location of the index fingers. Normality was checked visually with probability plots and using the Kolmogorov–Smirnov test (Asymp. Sig. (2-tailed), all p-values > 0.40).

2.6. Results Experiment 1

2.6.1. Questionnaire

Participants completed the RHI questionnaire a total of four times: twice after asynchronous stroking and twice after synchronous stroking. The mean per condition for all participants is shown in Fig. 3B. Results show that for the first ten statements, participants only rated the first three illusion-related questions and question 10 above 5 (neutral). The remaining seven statements were included as control. This confirms the subjective experience of the feeling of ownership over the rubber hand. The final question shows that participants rated the experience of the rubber hand illusion to be more vivid, i.e. more intense, after synchronous stimulation (Fig. 3).

2.6.2. First perceptual response

The results for Experiment 1 were threefold. First, we replicated the classic RHI using perceptual judgments (One sample t-test, mean error = −5.93 cm, $t(13) = -28.14$, $p < 0.001$) (Fig. 4A, left bar).

It is interesting to note here that the illusion only significantly affected the stimulated right hand, and not the contralateral non-stimulated left hand (mean error = −0.15 cm, $t(13) = -1.48$, $p = 0.16$).

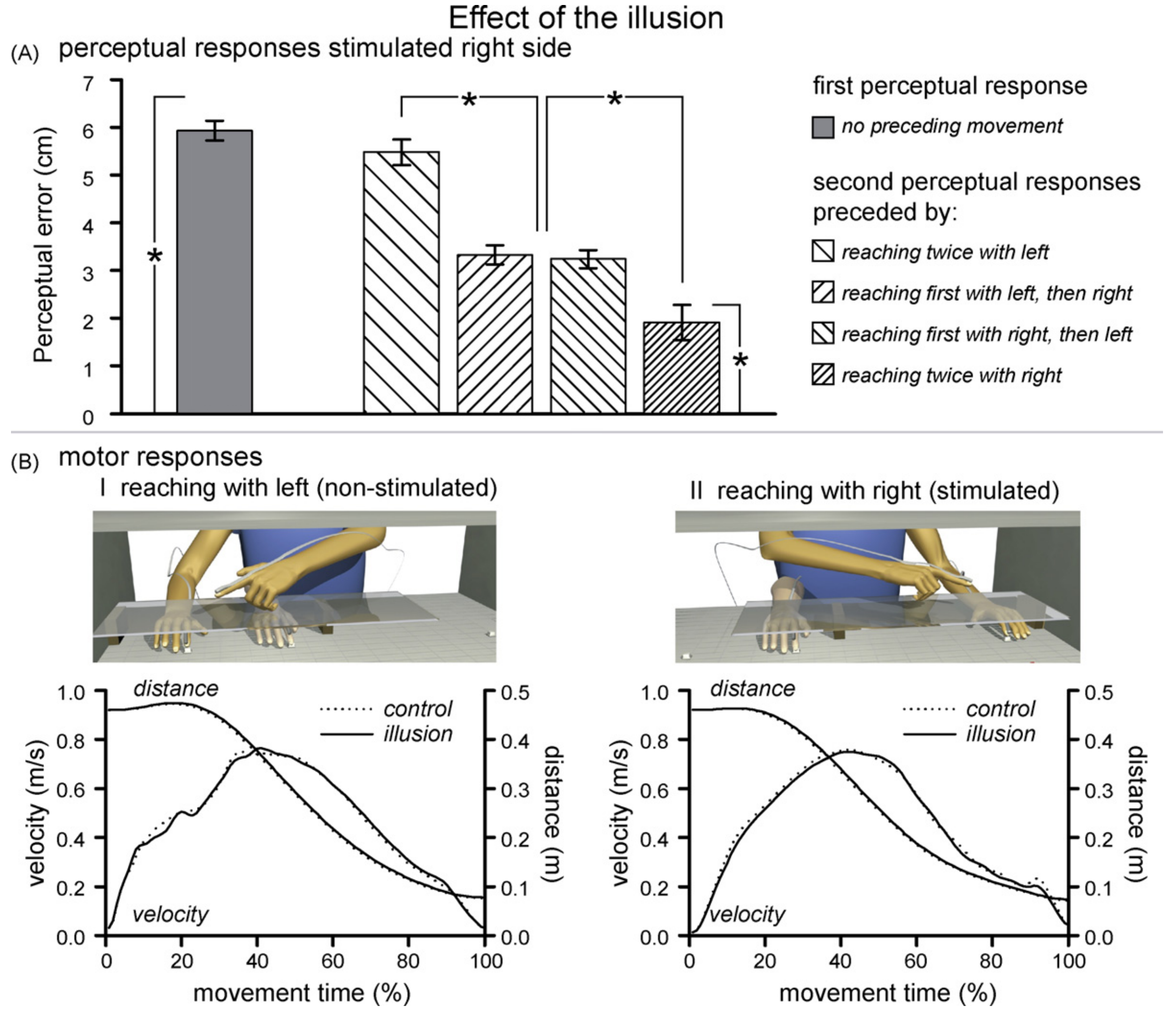


Fig. 4. Results Experiment 1. (A) Strength of the illusion on perceptual judgments for the stimulated right side. Significant illusion effects were found for all perceptual judgments compared against the actual location of the index finger (zero). (B) Mean distance and velocity trajectories for the first reaching response for the Illusion and Control conditions, for reaching with the non-stimulated left hand towards the stimulated right index finger (I), and for reaching with the stimulated right hand towards the non-stimulated left index finger (II).

2.6.3. Motor response

Second, we analysed the reaching movements made by the stimulated right and non-stimulated left hand, focusing on systematic endpoint errors, the distribution of variable errors, and the trajectory of the reaching movements (van Beers, Sittig, & Gon, 1999). Remarkably, none of the above parameters was significantly affected by the illusion (Fig. 4B and Table 1).

More specifically, the endpoint errors for the first reaching response showed no significant effect of the illusion for either hand (Paired sample *t*-test Control versus Illusion reaching with non-stimulated left hand $t(13) = 1.11$, $p = 0.29$; stimulated right hand $t(13) = 0.67$, $p = 0.52$), and did not differ significantly from each other $t(13) = 0.38$, $p = 0.71$). There was a significant overall reaching error towards the body midline in both the illusion and control conditions (Illusion: One sample *t*-test mean error with stimulated right hand = 7.6 cm, $t(13) = 17.67$, $p < 0.001$; mean error with non-stimulated left hand = 7.4 cm, $t(13) = 19.77$, $p < 0.001$, and Control: mean error with stimulated right hand = 8.0 cm, $t(13) = 16.27$, $p < 0.001$; mean error with non-stimulated left hand = 7.6 cm, $t(13) = p < 0.001$). However, there was no significant difference between the control and the illusion condition for either hand, indicating a bias towards the body midline independent of the RHI (Paired sample *t*-test stimulated right hand, $t(13) = -1.88$, $p = 0.82$; non-stimulated left hand, $t(13) = -1.30$, $p = 0.22$).

Furthermore, there was no significant effect of the illusion (control minus illusion) for the endpoint bias of the reaching responses, compared to the veridical location of the index finger (zero) (One sample *t*-test; First reaching response; with non-stimulated left side $t(13) = 1.53$, $p = 0.15$; with stimulated right side $t(13) = 0.62$, $p = 0.55$; Four types of second response; Twice with non-stimulated left side $t(13) = -0.20$, $p = 0.88$, Twice with stimulated right side $t(13) = 1.33$, $p = 0.21$; with the non-stimulated left side preceded by reaching with the stimulated right side $t(13) = -1.19$, $p = 0.25$; with the stimulated right side preceded by reaching with the

Table 1
Effect of the illusion for the first reaching responses of Experiment 1

Variable	Unit	Reaching with non-stimulated left hand Mean	Reaching with stimulated right hand Mean	*F*-value	*p*-Value
Movement Time	ms	4.00	−40.82	0.695	0.420
Peak velocity	cm/s	4.01	0.02	1.290	0.277
Relative time to Peak velocity	%	2.24	0.86	0.350	0.564
Mean velocity	cm/s	0.47	0.42	0.002	0.962
Endpoint error	cm	−0.33	−0.15	0.040	0.845

Table displays the means for the different kinematic parameters for reaching with the non-stimulated, as well as the stimulated hand for the first reaching response. Shown are the *F*-values and the *p*-values for the Stimulation × Hand interaction ($N = 14$). The reaching was resistant to the RHI for all the measured parameters.

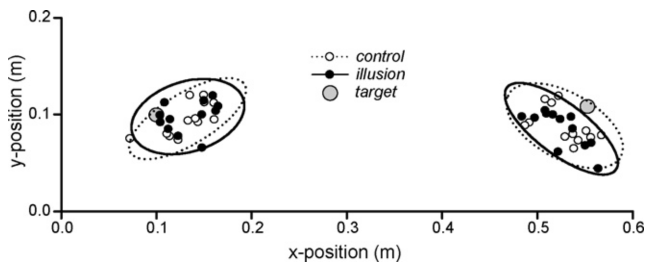


Fig. 5. End point bias of the reaching responses for one representative participant. The ellipses depict 95% multivariate confidence intervals.

non-stimulated left side $t(13) = 0.06$, $p = 0.96$). Finally, the ellipses in Fig. 5 showed no significant effect of the illusion for the distribution of the variable errors ($p > 0.1$). Here we only show the results of one 'representative' participant.

In short, the calibration of the reaching movements is impervious to the RHI, whether the stimulated hand is the goal or the means of the movement. As predicted, there was a significant difference for the felt location of the index finger between the perceptual response and the motor response for the stimulated right hand (Paired sample *t*-test; mean = −5.93 cm, $t(13) = -28.27$, $p < 0.001$), but not for the non-stimulated left hand (mean = −0.02 cm, $t(13) = -1.45$, $p = 0.17$).

2.6.4. Second perceptual response

Finally, we were interested in the dynamics of the RHI on the perceptual judgment and its modulation by the preceding motor responses. The second perceptual judgment, preceded by two reaching movements with the non-stimulated left hand, did not differ significantly from the first (Paired sample *t*-test $t(13) = -1.92$, $p = 0.78$). Thus when participants made reaching movements with their non-stimulated left hand, the strength of the illusion remained the same from the first perceptual response to the second. Hence, when no additional proprioceptive update from the stimulated side was provided, the illusion remained unattenuated. This suggests that the passing of time (over this time scale) does not influence the strength of the RHI. When participants performed a single reaching movement with the stimulated right hand, there was a significant decrease in the strength of the illusion on the subsequent perceptual judgment (mean reaching first with left followed by right = −3.33, $t(13) = -16.61$, $p < 0.001$; mean reaching first with right followed by left = −3.24, $t(13) = -16.27$, $p < 0.001$) (Fig. 4A, right bars). This was independent of the order of the reaching movements made with the stimulated and non-stimulated hand (Paired sample *t*-test, $t(13) = -0.38$, $p = 0.71$).

Finally, after two reaching responses with the stimulated right hand, the strength of the illusion on the perceptual judgment was further reduced (mean reaching twice with right = −1.91, $t(13) = -5.14$, $p < 0.001$), but remained significantly different from the actual location of the hand (zero) (One sample *t*-test, mean = −1.92 cm, $t(13) = -5,14$, $p < 0.001$).

2.7. Results Experiment 2

2.7.1. First perceptual response

The results of Experiment 2 were consistent with the differential effect of the illusion found in Experiment 1 (Fig. 6). First, there was a significant effect of the illusion for the first perceptual stick judgment (One sample *t*-test, mean = −3.46 cm, $t(13) = -10.74$, $p < 0.001$). Second, we again found a significant reduction of the strength of the illusion for the second perceptual response after movement with the stimulated right side (Paired sample *t*-test, mean = −1.72 cm, $t(13) = -5.94$, $p < 0.001$). Finally, action did not erase the RHI since the effect of the illusion was still significant for the second perceptual stick judgment (One sample *t*-test, mean = −1.74 cm, $t(13) = -5.32$, $p < 0.001$) (Fig. 6A).

2.7.2. Motor response

Consistently with the results of Experiment 1, there was no significant effect of the illusion on any of the kinematic parameters of the grasping motor response. More specifically, there was no significant effect of the illusion for the kinematic metric distance, which consists of the travelled space between the starting position and the edge of the framework just before the subject received visual information about the hands (Paired sample *t*-test, mean = −0.001 cm, $t(13) = -0.71$, $p = 0.49$) nor for peak velocity of the grasping movement (mean stimulated right hand = −0.00, $t(13) = -0.07$, $p = 0.95$); mean non-stimulated left hand = 0.06, $t(13) = 0.89$, $p = 0.39$). Finally, the grip aperture bias was also RHI independent (Paired sample *t*-test, $t(13) = 0.93$, $p = 0.31$) (Fig. 6B).

3. Discussion

The present results of the two RHI experiments show a strong task-dependency effect. Perceptual bodily judgments are illusion sensitive while ballistic actions are robust against the bodily illusion induced by sensory conflict. The dissociation is consistent with a previous study showing task-dependency using the vibrotactile bodily illusion (Kammers et al., 2006), and is in line with the multiple body representations model, which dissociates the body schema governing motor responses, and the body image underlying perceptual judgments (Gallagher, 2005; Graziano and Botvinick, 1999; Kammers et al., 2006; Paillard, 1991, 1999). Furthermore, we demonstrated the validity of the multiple body representations model in healthy individuals, by measuring for the first time the kinematics of body-oriented motor responses during the Rubber Hand Illusion. The present results are also in line with the immunity of action to visual illusions that has been already shown (Aglioti et al., 1995). However, further studies on visual illusions have challenged the dissociation between perception and action within the visual system (Franz, Gegenfurtner, Bulthoff, & Fahle, 2000). One possible explanation is that early visual illusions affect action (dorsal stream) whereas higher order visual illusions do not (ventral stream) (Kroliczak et al., 2006). Here, we showed a task dependency effect for a higher order bodily illusion based on multimodal sensory integration, already found for the (lower order) kinaesthetic illusion induced by vibrotactile stimulation. Only the perceptual responses, and not the motor responses, were susceptible to the bodily illusion. Even though participants did not know where their hand was, they knew how to reach it.

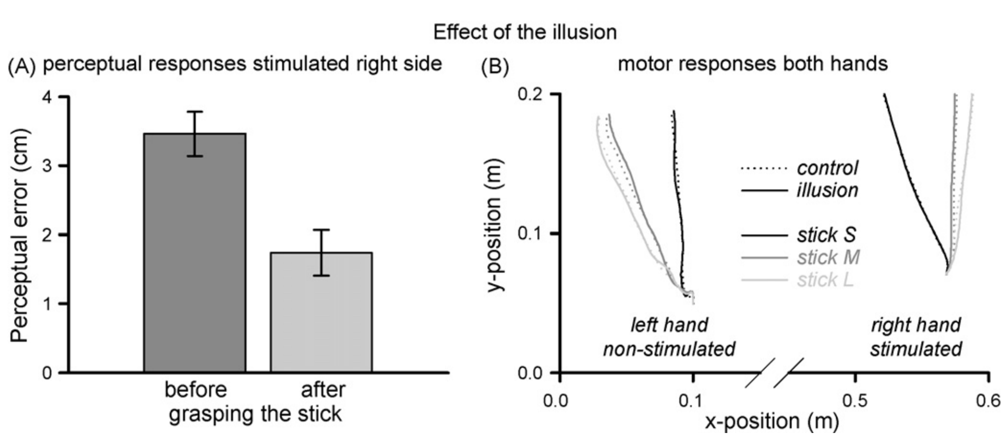


Fig. 6. Results of Experiment 2. (A) Significant effect of the illusion for the first as well as the second perceptual judgments compared with the actual location (zero), and between conditions. (B) Panel B shows the grasping trajectories for each stick length, small (S) 26.5 cm, medium (M) 46.5 cm (actual distance between both index fingers), or large (L) 56.5 cm. No significant effect of the illusion was found for the grasping trajectories for the non-stimulated left hand, nor the stimulated right hand.

In addition to this dissociation, the present study also sheds new light on the specific features of the interaction between these body representations. First, it is interesting to note that both action movements towards the stimulated right hand with the non-stimulated left hand as well as actions with the stimulated right hand were insensitive to the illusion. If the illusion distorted the underlying body schema, biases in reaching either with or towards the stimulated hand would have been expected, comparable to those observed with perceptual judgments. Contrary to some predictions (Frith, 2005), this was not the case. This suggests that the body schema includes all the information relevant for acting, representing both the body as the goal and the body as the means to get to a goal. Second, the specific task demands (accurate guidance of a reaching movement or perceptual indication of a location) determine the type or amount of input sources that are included in the body representation. We suggest that the distinction between the body schema and the body image can be accounted for by differences in the rules governing multisensory integration (Ernst & Bulthoff, 2004). The relative weighting of proprioception and vision depends on what information is the most 'reliable' for each type of body representation (Welch & Warren, 1986). Most of the time, there is a dominance of vision over the other modalities. The RHI illustrates this general principle of visual capture of the felt location of one's occluded own hand and the visible location of the rubber hand. The absence of relocation for the motor responses suggests that capture of proprioceptive information by vision is only present for the perceptual responses. When acting, one rarely sees all moving body parts, and one relies on proprioception first. In its absence, planning and controlling movements become difficult, as illustrated by deafferented patients before they learn to use vision alone.

However, it has been shown that proprioception can dominate when it is more reliable than vision (van Beers, Wolpert, & Haggard, 2002). Here, we showed that the relative weighting depends not only on the property processed, but also on the type of task that is being performed. In other words, we suggest that, in healthy individuals, proprioception is weighted more heavily than vision for the body schema used for action. In contrast, this is reversed for the body image used for perceptual judgments.

Our action results may seem in contradiction with some recent results. Holmes, Snijders, and Spence (2006) showed that the mere visual display of a fake hand can affect reaching movements. However, there was no tactile stimulation in that study and the effect was independent of the RHI itself (asynchronous versus synchronous stimulation). In contrast, we compared the difference of kinematics between synchronous and asynchronous tactile stimulation, and therefore looked at the possible affects of RHI-specific relocation of one's own hand.

More surprising is the strength of the RHI on pointing responses observed by Botvinick and Cohen (1998). They asked their participants to run their non-stimulated hand along a small line below the table top and were asked to mirror the felt location of the occluded stimulated hand resting on the table top with the non-stimulated hand below the table top. We suggest that the motor response asked in their study involves different motor subsystems than the one we used in the present study. The main difference between the two types of action is the nature of the non-ballistic pointing movement versus the ballistic reaching movement. Ballistic movements are executed in such a fast manner that there are no on-line adjustments, i.e. they are executed within a closed loop (Kroliczak et al., 2006). It has been shown in vision that fast movements depend on the dorsal stream whereas slow pointing movements involve the ventral stream as well. Neuropsychological studies have shown that patients with lesions of the dorsal stream are still able to make fairly accurate pointing movements after being instructed to slow down (Rossetti et al., 2005). Consequently, the motor responses used here recruited the somatosensory equivalent of the dorsal stream (Dijkerman & de Haan, 2007), in contrast to Botvinick and Cohen's pointing response. Based on our results, we can conclude that the ballistic fast actions are robust to the RHI. Another explanation for the apparent contradiction might lie in the instruction for the pointing responses. In Botvinick and Cohen's RHI study, participants were asked to point to where they "felt" or perceived their hand to be, relying thus on a perceptual judgment. In the present experiment participants were asked to reach directly with one hand to the other, without referring to the RHI. As a result, the Botvinick and Cohen's pointing task seems to be more a perceptual localization task than a true action response.

In conclusion, fifty years ago, Merleau-Ponty asked, "If I know where my nose is when it is a question of holding it, how can I not know where it is when it is a matter of pointing to it?" (Merlau-Ponty, 1945, p. 103). Evidence from patients indicated that such a dissociation was possible. Our study argues in favour of the distinction between body schema and body image in healthy individuals as well. The robustness of the illusion indicates the stability of the body image: once triggered, the bodily illusion is maintained despite evidence to the contrary. As a consequence, our results go against the general view that the dominance of visual information is explained by the weakness of the proprioceptive signal after a period of rest (Frith, 2005). If this were true, new proprioceptive information should erase the RHI completely. However, in the current study it was only reduced. More importantly, this reduction shows that interaction between these different body representations is possible in healthy individuals.

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References

Aglioti, S., DeSouza, J. F., & Goodale, M. A. (1995). Size-contrast illusions deceive the eye but not the hand. *Current Biology*, *5*(6), 679–685.

Armel, K. C., & Ramachandran, V. S. (2003). Projecting sensations to external objects: Evidence from skin conductance response. *Proceedings of Biological Sciences*, *270*(1523), 1499–1506.

Belin, P., & Zatorre, R. J. (2000). 'What' 'where' and 'how' in auditory cortex. *Nature Neuroscience*, *3*(10), 965–966.

Botvinick, M., & Cohen, J. (1998). Rubber hands 'feel' touch that eyes see. *Nature*, *391*(6669), 756.

Buxbaum, L. J., & Coslett, H. B. (2001). Specialised structural descriptions for human body parts: Evidence from autotopagnosia. *Cognitive Neuropsychology*, *18*(4), 289–306.

Costantini, M., & Haggard, P. (2007). The rubber hand illusion: Sensitivity and reference frame for body ownership. *Consciousness and Cognition*, *16*(2), 229–240.

de Vignemont, F. (2007). When do we empathize? *Novartis Foundation Symposium*, *278*, 181–190 (discussion 190–196, 216–221).

Dijkerman, H. C., & de Haan, E. H. (2007). Somatosensory processes subserving perception and action. *The Behavioral and Brain Sciences*, *30*(2), 189–201.

Durgin, F. H., Evans, L., Dunphy, N., Klostermann, S., & Simmons, K. (2007). Rubber hands feel the touch of light. *Psychological Science*, *18*(2), 152–157.

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. *The Journal of Neuroscience*, *25*(45), 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*(5685), 875–877.

Ernst, M. O., & Bulthoff, H. H. (2004). Merging the senses into a robust percept. *Trends in Cognitive Sciences*, *8*(4), 162–169.

Farne, A., Pavani, F., Meneghello, F., & Ladavas, E. (2000). Left tactile extinction following visual stimulation of a rubber hand. *Brain*, *123*(Pt 11), 2350–2360.

Franz, V. H., Gegenfurtner, K. R., Bulthoff, H. H., & Fahle, M. (2000). Grasping visual illusions: No evidence for a dissociation between perception and action. *Psychological Science*, *11*(1), 20–25.

Frith, C. (2005). The self in action: Lessons from delusions of control. *Consciousness and Cognition*, *14*(4), 752–770.

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

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, *15*(1), 20–25.

Graziano, M. S. A., & Botvinick, M. M. (1999). How the brain represents the body: Insights from neurophysiology and psychology. In D. Gopher & A. Koriat (Eds.), *Attention and performance XVII—Cognitive regulation of performance interaction of theory and application* (pp. 136–157).

Haffenden, A. M., & Goodale, M. A. (2000). Independent effects of pictorial displays on perception and action. *Vision Research*, *40*(10–12), 1597–1607.

Head, H., & Holmes, H. G. (1911–1912). Sensory disturbances from cerebral lesions. *Brain*, *34*, 102–254.

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 & Psychophysics*, *68*(4), 685–701.

Jacob, P., & Jeannerod, M. (2003). *Ways of seeing. The scope and limits of visual cognition*. Oxford: Oxford University Press.

Kammers, M. P. M., van der Ham, I. J., & Dijkerman, H. C. (2006). Dissociating body representations in healthy individuals: Differential effects of a kinaesthetic illusion on perception and action. *Neuropsychologia*, *44*(12), 2430–2436.

Kroliczak, G., Heard, P., Goodale, M. A., & Gregory, R. L. (2006). Dissociation of perception and action unmasked by the hollow-face illusion. *Brain Research*, *1080*(1), 9–16.

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*(1), 104–109.

McIntyre, J., Stratta, F., & Lacquaniti, F. (1998). Short-term memory for reaching to visual targets: Psychophysical evidence for body-centered reference frames. *The Journal of Neuroscience*, *18*(20), 8423–8435.

Merlau-Ponty, M. (1945). *La Phenomenologie de la Perception*. (Paris: Gallimond, 2nd ed, 1945).

Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*. Oxford University Press.

Paillard, J. (1991). Knowing where and knowing how to get there. In J. Paillard (Ed.), *Brain and space* (pp. 461–481).

Paillard, J. (1999). Body schema and body image: A double dissociation in deafferented patients. In G. N. Gantchev, S. Mori, & J. Massion (Eds.), *Motor control, today and tomorrow* (pp. 197–214).

Rossetti, Y., Revol, P., McIntosh, R., Pisella, L., Rode, G., Danckert, J., et al. (2005). Visually guided reaching: Bilateral posterior parietal lesions cause a switch from fast visuomotor to slow cognitive control. *Neuropsychologia*, *43*(2), 162–177.

Schwoebel, J., & Coslett, H. B. (2005). Evidence for multiple, distinct representations of the human body. *Journal of Cognitive Neuroscience*, *17*(4), 543–553.

Sirigu, A., Grafman, J., Bressler, K., & Sunderland, T. (1991). Multiple representations contribute to body knowledge processing. Evidence from a case of autotopagnosia. *Brain*, *114*(Pt 1B), 629–642.

Tsakiris, M., & Haggard, P. (2005). The rubber hand illusion revisited: Visuotactile integration and self-attribution. *Journal of Experimental Psychology. Human Perception and Performance*, *31*(1), 80–91.

van Beers, R. J., Sittig, A. C., & Gon, J. J. (1999). Integration of proprioceptive and visual position-information: An experimentally supported model. *Journal of Neurophysiology*, *81*(3), 1355–1364.

van Beers, R. J., Wolpert, D. M., & Haggard, P. (2002). When feeling is more important than seeing in sensorimotor adaptation. *Current Biology*, *12*(10), 834–837.

Van Strien, J. W. (1992). Classificatie van links- en rechtshandige proefpersonen. *Nederlands Tijdschrift voor de Psychologie en haar Grensgebieden*, *47*, 88–92.

Welch, R. B., & Warren, D. H. (1986). Intersensory interactions. In K. R. Kaufman & J. P. Thomas (Eds.), *Handbook of perception and human performance Vol. 1: Sensory processes and perception*. New York: Wiley.