

The moving rubber hand illusion revisited: comparing movements and visuotactile stimulation to induce illusory ownership

Article

Creative Commons: Attribution-Noncommercial-No Derivative Works 4.0

Open Access

Kalckert, A. and Ehrsson, H. (2014) The moving rubber hand illusion revisited: comparing movements and visuotactile stimulation to induce illusory ownership. *Consciousness and Cognition*, 26. pp. 117-132. ISSN 1053-8100 doi: <https://doi.org/10.1016/j.concog.2014.02.003> Available at <https://centaur.reading.ac.uk/69608/>

It is advisable to refer to the publisher's version if you intend to cite from the work. See [Guidance on citing](#).

To link to this article DOI: <http://dx.doi.org/10.1016/j.concog.2014.02.003>

Publisher: Elsevier

All outputs in CentAUR are protected by Intellectual Property Rights law, including copyright law. Copyright and IPR is retained by the creators or other copyright holders. Terms and conditions for use of this material are defined in the [End User Agreement](#).

www.reading.ac.uk/centaur

CentAUR

Central Archive at the University of Reading

Reading's research outputs online



ELSEVIER

Contents lists available at ScienceDirect

Consciousness and Cognition

journal homepage: www.elsevier.com/locate/concog

The moving rubber hand illusion revisited: Comparing movements and visuotactile stimulation to induce illusory ownership



Andreas Kalckert*, H. Henrik Ehrsson

Brain, Body & Self Laboratory, Department of Neuroscience, Karolinska Institutet, Stockholm Sweden, Retzius väg 8, SE-171 77 Stockholm, Sweden

ARTICLE INFO

Article history:

Received 27 September 2013

Available online 2 April 2014

Keywords:

Ownership

Agency

Rubber hand illusion

Self-recognition

Body perception

Multisensory integration

Motor control

ABSTRACT

The rubber hand illusion is a perceptual illusion in which a model hand is experienced as part of one's own body. In the present study we directly compared the classical illusion, based on visuotactile stimulation, with a rubber hand illusion based on active and passive movements. We examined the question of which combinations of sensory and motor cues are the most potent in inducing the illusion by subjective ratings and an objective measure (proprioceptive drift). In particular, we were interested in whether the combination of afferent and efferent signals in active movements results in the same illusion as in the purely passive modes. Our results show that the illusion is equally strong in all three cases. This demonstrates that different combinations of sensory input can lead to a very similar phenomenological experience and indicates that the illusion can be induced by any combination of multisensory information.

© 2014 The Authors. Published by Elsevier Inc. This is an open access article under the CC BY-NC-ND license. Open access under [CC BY-NC-ND license](http://creativecommons.org/licenses/by-nc-nd/3.0/).

(<http://creativecommons.org/licenses/by-nc-nd/3.0/>).

1. Introduction

The rubber hand illusion is a perceptual illusion in which participants experience a fake model hand as being part of their own body. In the classical version, a rubber hand is placed in front of the participant and synchronous touches are applied to the rubber hand and the participant's real hand, which is hidden from view (Botvinick & Cohen, 1998; Ehrsson, Spence, & Passingham, 2004; Tsakiris & Haggard, 2005). After a short period, within less than a minute and often as quickly as 10 s (Ehrsson et al., 2004; Lloyd, 2007), participants start to feel as if the touch they sense originates from the location on the rubber hand where they see the brush touching the rubber hand, rather than from their real hand. They also start to experience the feeling that the rubber hand is their own hand (*sense of body ownership*), a feeling that can be quite vivid in many participants. The illusion is often explained as a result of the elimination of the initial conflict between visual and somatosensory representations of the hand and the integration of visual, tactile and proprioceptive signals, that leads to a coherent multisensory perception of the model hand as one's own hand receiving the touches (Ehrsson, 2012; Makin, Holmes, & Ehrsson, 2008). Because the illusion involves consciously felt changes in ownership of the model hand, it has become a very popular model system to study issues related to bodily self-consciousness (Blanke, 2012), subjective embodiment (Tsakiris, 2009), and how the brain makes the perceptual distinction between the physical self and the external environment (Ehrsson, 2012; Petkova et al., 2011).

* Corresponding author. Address: Department of Neuroscience, Karolinska Institutet, Retzius väg 8, 17177 Stockholm, Sweden. Fax: +46 (0) 8 524 87126. E-mail address: andreas.kalckert@ki.se (A. Kalckert).

Recent behavioral experiments have demonstrated that the rubber hand illusion can be elicited by finger movements alone rather than by combined tactile and visual stimulation with an external probe, as in the classical version (Dummer, Picot-Annand, Neal, & Moore, 2009; Kalckert & Ehrsson, 2012; Tsakiris, Prabhu, & Haggard, 2006; Walsh, Moseley, Taylor, & Gandevia, 2011). In our version of the moving rubber hand illusion (Kalckert & Ehrsson, 2012), every time the participant moves his index finger, which is hidden from view under a box, the index finger of a wooden model hand moves synchronously in the same way. This elicits a strong sense of ownership of the model hand and finger, regardless of whether the finger movements are actively produced by the participants or passively by the experimenter. In the case of active movements, the participants also experience a vivid sense of being in voluntary control of the model hand's actions; that is, they experience a *sense of agency* of the model hand (David, Newen, & Vogeley, 2008). This happens because, unlike in passive conditions, the participants form motor intentions to move the model hand. Once the predicted sensory consequences of the movements also match the actual sensory feedback, one experiences the movement as self-produced as opposed to being produced by an external force (Crapse & Sommer, 2008; Holst & Mittelstaedt, 1950). The information related to the sense of agency can serve as another source of information for the process of self-recognition, complementing the sense of ownership (Gallagher, 2000; Kalckert & Ehrsson, 2012).

The moving rubber hand illusion raises several important questions. First, one can ask whether movements lead to a stronger illusion because more channels of sensory information are available than in the classical rubber hand illusion (Botvinick & Cohen, 1998). During movement, not only are cutaneous afferents signaling skin stretching engaged (Edin & Johansson, 1995) but also muscle spindle receptors and joint receptors are engaged (Proske & Gandevia, 2012). None of these are stimulated by the tactile stimulation used in the classical rubber hand illusion. Second, one can ask whether efferent signals from the motor commands contribute to the feeling of ownership when the finger is moved voluntarily. We know that visual perception is influenced by efferent copy signals from oculomotor areas, and the possible role of efferent signals in kinesthesia has been discussed for over a century (Gandevia, Smith, Crawford, Proske, & Taylor, 2006; Matthews, 1982); thus, similar effects on body ownership by efferent signals might be expected. However, these questions have not been resolved in previous literature. The earlier studies investigating moving rubber hand paradigms have used different setups and found apparently conflicting results when comparing active movements, passive movements and visuotactile stimulation. Tsakiris and colleagues (2006), using a video-screen-based setup, found no difference in the strength of the proprioceptive drift between conditions in which the illusion was elicited by active movements, passive movements or visuotactile stimulation. Dummer and colleagues (2009), using whole hand movements, measured the subjective strength of the illusion and found stronger ratings of ownership during active movements than during passive movements, but ratings during visuotactile stimulation were again higher than during active movements (in a between-group design). Finally, Longo and Haggard (2009), using a setup in which a video image of the hand was presented on a screen, analyzed questionnaire data that revealed a main effect of induction type across active, passive, and visuotactile stroking conditions, without specifying the exact relationship among the different types. Kammers and colleagues (2009) also used a video screen based setup to compare proprioceptive drift after active and passive movements and found that the drift was pronounced when testing using a manual pointing response, but not when using a perceptual judgment procedure. More recently, Riemer and colleagues (2013) compared active movements and visuotactile stimulation and found equally strong subjective ratings. However, when testing proprioceptive drift with a perceptual judgment or manual pointing procedure they found that a significant proprioceptive drift associated with the moving rubber hand illusion could only be detected when using the manual pointing procedure. Finally, experiments with fully simulated moving hands in virtual reality have also been performed (Sanchez-Vives, Spanlang, Frisoli, Bergamasco, & Slater, 2010; Slater, Perez-Marcos, Ehrsson, & Sanchez-Vives, 2008) but these do not directly resolve the issues discussed in the literature.

In our previous study (Kalckert & Ehrsson, 2012), we systematically manipulated the spatial orientation of the model hand (aligned with the participant's hand or rotated 180°) and the timing of the visual feedback and somatosensory feedback (synchronous or asynchronous). This allowed us to show that the moving rubber hand illusion depends on the same temporal congruency and anatomic plausibility rules as the classical rubber hand illusion (Ehrsson et al., 2004; Tsakiris & Haggard, 2005), that is, that asynchronous feedback or rotating the model hand 180° breaks the illusion of ownership (Kalckert & Ehrsson, 2012). Moreover, with this design, we were able to dissociate sense of ownership and agency and show that agency could be experienced for the rotated model hand placed in the anatomically implausible position during which participants explicitly rejected feeling ownership. Interestingly, we also noted a small but significant increase in ownership ratings when we directly compared active synchronous movements to passive synchronous movements, although no difference was observed in proprioceptive drift measurements. Thus, given the heterogeneity in the methodology and results of earlier studies, our own included, it is not clear what effect the type of induction has on the rubber hand illusion.

In the present study, we re-examined these questions in experiments where we directly compared the rubber hand illusion as elicited by active movements, passive movements, or visuotactile stimulation. In the first experiment, we measured the subjective experience of ownership of the model hand in the three versions of the rubber hand illusion outlined above and quantified the sense of agency in all experimental conditions. In the second experiment, we compared the strength of the illusion induced by active movements or visuotactile stimulation by measuring changes in the felt position of the participant's real hand using a proprioceptive drift measurement. Our results show that all three modes of inducing the illusion – active movements, passive movements, and visuotactile stimulation – elicited a similarly strong rubber hand illusion. Moreover, across individuals, the strength of the ownership illusion was correlated across the three illusion types. These

findings support a model of the rubber hand illusion in which the phenomenological experience of ownership can arise from correlated afferent signals from many different combinations of sensory channels as opposed to certain signals being more important than others.

2. Materials and methods

2.1. Participants

In Experiment 1, we tested 40 healthy participants (22 females; mean age $25.8 \pm SD 5.21$, range 18–39), and in Experiment 2, a different group of 20 healthy participants took part (10 females; mean age $26.3 \pm SD 4.3$, range 19–40). All participants were naïve to the purpose of the experiments. All volunteers provided written, informed consent prior to participation, and no individual exhibited a history of psychiatric or neurological disorders. The Regional Ethical Review Board of Stockholm approved this study.

2.2. Methods

We used a setup previously described in detail in Kalckert and Ehrsson (2012). This setup consists of a wooden box positioned on a table with a life-sized model hand placed on top of the box. The participant sits on a chair and places his/her real hand into the box so that the arm is placed in a relaxed position. A cloth is placed over the participant's right shoulder to cover the space between the model hand and the participant, and creates a perspective for the participant that the model hand is the participant's own outstretched hand. The index finger of the model hand and the index finger of the real hand are connected mechanically via a light stick attached to finger caps placed on the two fingers (see Fig. 1A). When the participant lifts his or her index finger, the model index finger lifts synchronously in the same way (*active synchronous* condition). In the passive movement conditions, the participant relaxes the index finger and the experimenter sitting opposite the box moves the mechanical connection, thereby generating an external force that lifts both the participant's index finger and the index finger of the model hand (*passive synchronous* condition). In the asynchronous conditions (*active asynchronous* condition and *passive asynchronous* condition), the mechanical connection between the participant's index finger and the test person's index finger is disconnected so that the experimenter can lift the model index finger with a temporal delay (approximately half a second) with respect to the participant's right finger movement.

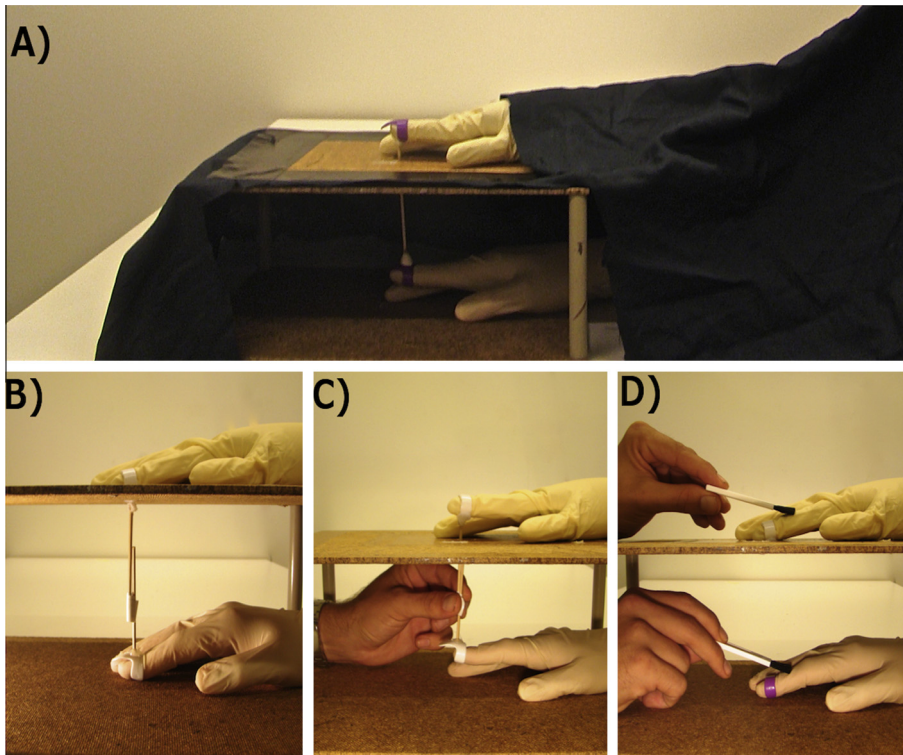


Fig. 1. (A) Setup with the occluding cloth as used in the experiment. (B–D) Illustration of the three conditions: (B) Active movement: the participant taps the finger. (C) Passive movement: the experimenter moves both the rubber hand's and participant's fingers by moving the connecting stick. (D) Visuotactile stimulation: the experimenter strokes both fingers with a small brush.

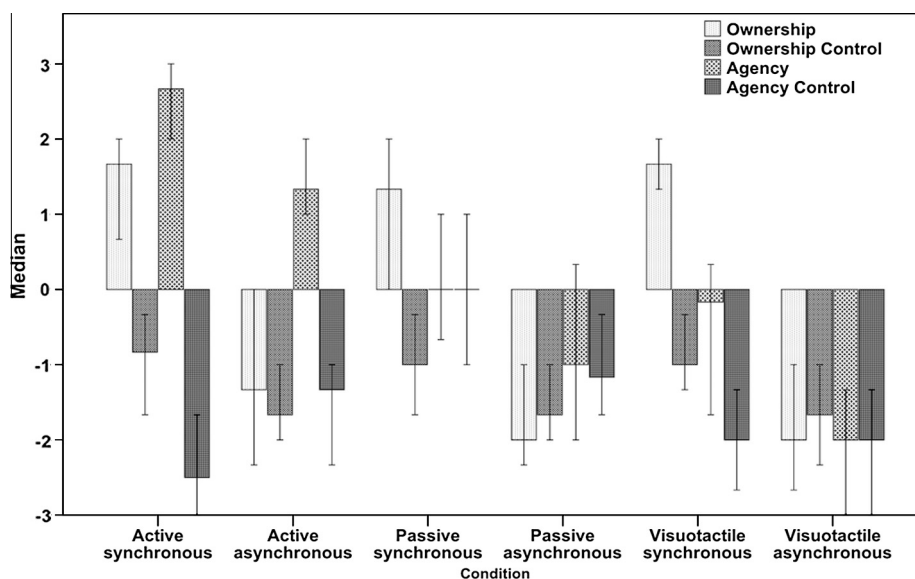


Fig. 2. Experiment 1: Results of the questionnaire data. We computed a mean score for each category (Ownership, Ownership Control, Agency and Agency Control). Median values and 95% CI are shown for each rating in the six conditions. When the median rating is equal or greater +1, we interpret this rating to be agreed and tested for further statistical differences, see Section 3.1.1.

To directly compare the moving rubber hand illusion to the classical version, we used the setup with the wooden model hand placed on top of the box and the participant's real hand placed inside the box (see Fig. 1D). Although this vertical arrangement of hands is a deviation from the classical setup introduced by Botvinick and Cohen (1998), this arrangement with the rubber hand placed above the hidden real hand has been used previously to induce the illusion (Bekrater-Bodmann, Foell, Diers, & Flor, 2012; Ehrsson et al., 2004; Heed et al., 2011).

Each trial lasted 90 s. The participant's task was to either make repetitive index finger tapping movements with the right hand while looking at the model hand, or remain passive while both the participant's finger and the rubber hand's finger were moved passively by the experimenter (i.e., active and passive movement conditions, respectively), or relax and just look at the model hand while both the model hand and the participant's finger were touched with a short brush stroke (i.e., classical visuotactile stimulation conditions). The tactile stimulation in the visuotactile stimulation conditions consisted of repetitive touches applied to the proximal phalanx of the index finger while the participant saw the rubber hand's index finger being touched at the same place (see Fig. 1D). Both the finger taps and the brush strokes occurred at approximately 1 Hz, and to avoid a steady regular rhythm (which is known to produce a slightly weaker illusion), we also included random "double taps" or "double strokes," where the participant made two quick movements in rapid succession or two very rapid strokes were delivered. Importantly, the number of sensory or motor events within each 90 s trial (finger taps in the moving conditions or brush strokes in the visuotactile conditions) was matched across conditions. In the asynchronous conditions, the model hand moved with an approximately 500-ms delay with respect to the participant's index movement (i.e., active asynchronous and passive asynchronous) or the participant viewed the brush touching the model index finger with an approximately 500-ms delay with respect to the tactile stimulation on the participant's real right index finger (i.e., visuotactile asynchronous). In the passive movement conditions, the participant relaxed the index finger while the experimenter moved both the participant's finger and the model hand's finger by pulling the mechanical connections inside the box (see Fig. 1C) that the participant could not see (i.e., passive synchronous and passive asynchronous). Between each trial, the participants had an approximately 30-s rest period to move and stretch the arms and hands to relax. These pauses also served to eliminate potential carry-over effects between trials because moving and stretching the hand like this eliminates the illusion.

2.2.1. Experiment 1

In Experiment 1, we quantified the subjective experience of the illusion using questionnaires. The participants rated their experience on a 7-point Likert scale ranging from -3 (totally disagree) to +3 (totally agree), with 0 indicating "uncertainty." The experimental design consisted of six different conditions presented in a randomized order. We tested three induction types: active movements, passive movements, and visuotactile stimulation. We compared each induction type with synchronous feedback (i.e., active synchronous, passive synchronous and visuotactile synchronous) to the corresponding asynchronous control condition (i.e., active asynchronous, passive asynchronous and visuotactile asynchronous; see above for further details about the six conditions). After each trial (lasting 90 s, see above), participants completed a questionnaire with three ownership statements (related to the experience of perceiving the hand as the "own" hand), three agency statements (related to the experience of voluntary control), three control statements for the ownership statements, and three control statements for the agency statements. The control statements served as controls for task compliance and suggestibility

effects. To analyze the results, we computed one average score from each of the three ownership statements and one average score from the three agency statements. We refer to these average statement scores as the “ownership rating” and “agency rating.” Similarly, we computed the average scores of the corresponding control statements and refer to them as the “ownership control rating” and “agency control rating.” The statements included in the questionnaires were adopted from our previous experiment (see Kalckert & Ehrsson, 2012) and were modified to apply to both induction types, both movements and visuotactile stimulation (see Table 1).

To test for the elicitation of the rubber hand illusion, we compared the category of ownership statements and the category of agency statements to the respective control category of statements for each condition separately (e.g., in the active synchronous condition, we compared ownership ratings vs. ownership control ratings). We also directly compared the ownership ratings of the synchronous condition to those of the corresponding asynchronous condition (i.e., ownership rating of the synchronous active movements vs. ownership rating of the asynchronous active movements). In the same manner, we directly compared the agency ratings across the synchronous and asynchronous conditions. Our a priori-defined criterion for experiencing illusory ownership or agency in a given condition was a median group score on the ownership or agency ratings higher or equal to +1. This requires that the majority of the participants give a positive rating of the statements for us to conclude successful induction of illusory ownership or sense of agency of the model hand. The data were tested for normality with a Shapiro–Wilk test ($p > .05$). For further statistical analysis, we used the non-parametric Wilcoxon signed rank test for pairwise comparisons and a Friedman test for multiple comparisons between conditions for the questionnaire data. All tests are reported two-tailed, if not otherwise stated. In the instances where we had strongly directional hypotheses on the basis of our previous study (Kalckert & Ehrsson, 2012), we used one-tailed tests, as clearly indicated in those cases.

2.2.2. Experiment 2

In the second experiment, we tested the degree to which the participants felt their right hand was located closer to the model hand after the illusion – the so-called “proprioceptive drift” – a commonly used objective measure for the rubber hand illusion. With their eyes closed, participants pointed before and after each 90-s stimulation period to indicate the felt position of the right index finger with their left index finger. Participants were asked to make a single brisk but accurate pointing movement by touching a board attached to the side of the model hand box on which the experimenter could mark the end-point of each pointing movement. The proprioceptive drift in the vertical plane was then calculated by subtracting the two position measurements from each other (Post-pointing minus Pre-pointing). Positive values indicated an upward drift in hand position sense towards the model hand.

In this experiment, we compared the two induction types (active movements and visuotactile stimulation) to their respective asynchronous control conditions, thus having four different conditions (i.e., active synchronous, active asynchronous, visuotactile synchronous and visuotactile asynchronous). We did not include the passive movement condition to avoid this experiment being too long and because a comparison of active and passive conditions was performed in our earlier study, demonstrating similar proprioceptive drift (Kalckert & Ehrsson, 2012, see Fig. 7). Each condition was repeated three times in a pseudo-randomized order (12 trials in total). We calculated an average drift score across the three trials for each condition and used this score in the statistical analysis. The data were tested for normality (Shapiro–Wilk, $p < .05$), and the appropriate parametric or non-parametric tests were used in this analysis. All tests are two-tailed, if not otherwise stated.

3. Results

3.1. Experiment 1: Questionnaire

3.1.1. Ownership and agency in each induction type

3.1.1.1. Ownership and agency during active movements. Participants experienced ownership after the synchronous active movements (Median: +1.7) but not after the asynchronous active movements (Median: –1.3). This difference was significant

Table 1

Statements used in the experiment to measure the experience of ownership and agency with their respective control categories.

Ownership	1	<i>I felt as if I was looking at my own hand</i>
	2	<i>I felt as if the rubber hand was part of my body</i>
	3	<i>I felt as if the rubber hand was my hand</i>
Ownership control	1	<i>It seems as if I had more than one right hand</i>
	2	<i>It felt as if I had no longer a right hand, as if my right hand had disappeared</i>
	3	<i>I felt as if my real hand was turning rubbery</i>
Agency	1	<i>I felt as if I could cause movements of the rubber hand</i>
	2	<i>I felt as if I could control movements of the rubber hand</i>
	3	<i>The rubber hand was obeying my will and I can make it move just like I want it</i>
Agency control	1	<i>I felt as if the rubber hand was controlling my will</i>
	2	<i>It seemed as if the rubber hand had a will of its own</i>
	3	<i>I felt as if the rubber hand was controlling me</i>

(ownership ratings in active synchronous vs. ownership ratings in active asynchronous: $z = -4.706, p < .001$). Additionally, after the synchronous active movements, the ownership statements were rated significantly higher than the respective category of control statements (ownership rating vs. ownership control rating: $z = -4.936, p < .001$).

After synchronous active movements, the agency statements were rated significantly higher than control statements (agency rating vs. agency control rating: $z = -5.46, p < .001$). This was also the case for the asynchronous active movements (agency rating vs. agency control rating: $z = -4.326, p < .001$). It is noteworthy that although the participants gave higher ratings of agency in the synchronous condition (Median: +2.7) compared to the asynchronous condition (Median: +1.3) (agency rating in active synchronous vs. agency rating in active asynchronous: $z = -5.127, p < .001$), participants still experienced agency in the asynchronous condition (agency rating $\geq +1$). Taken together, these results show that active and synchronous movements result in a strong sense of ownership and agency of the model hand.

3.1.1.2. Ownership and agency during passive movements. Participants experienced ownership in the synchronous passive condition (Median: +1.3), but not in the asynchronous passive condition (Median: -2.0). The difference in ownership ratings between the conditions was significant (ownership rating in synchronous passive vs. ownership rating in asynchronous passive: $z = -5.308, p < .001$). Additionally, after the synchronous passive condition, participants gave significantly higher ownership ratings than to the corresponding control category (ownership rating in synchronous passive vs. ownership control rating synchronous passive: $z = -4.560, p < .001$). The agency statements were not positively rated in synchronous (Median: 0) or asynchronous movements (Median: -1.0). Thus, after passive and synchronous movements, participants experienced a sense of ownership of the model hand but not agency.

3.1.1.3. Ownership and agency during visuotactile stimulation. Participants experienced ownership in the visuotactile synchronous condition (Median: +1.7) but not in the asynchronous condition (Median: -2.0), and this difference was significant (ownership rating in visuotactile synchronous vs. ownership rating in visuotactile asynchronous: $z = -5.275, p < .001$). The ownership rating of the visuotactile synchronous condition was also significantly higher than the ownership control rating of the same condition (ownership rating vs. ownership control rating: $z = -5.308, p < .001$). Agency was positively rated in the synchronous condition (Median: -0.2) or asynchronous condition (Median: -2.0). Thus, as in the case of the passive movement condition (see above), the participants experienced only a sense of ownership of the model hand but not of agency.

3.1.1.4. Comparing ownership and agency across the three synchronous conditions. To compare the strength of the rubber hand illusion across the three induction types, which induce the illusion of ownership, we directly compared the ownership ratings across the active synchronous, passive synchronous and visuotactile synchronous conditions. We found no significant difference in ownership ratings across the three synchronous conditions (Friedmann: $\chi^2 = 3.714$ ($df = 2, n = 40$), $p = .156$). Likewise, the individual pairwise comparisons were not significant ($p > .05$). Thus, none of the illusion induction types produced a stronger ownership illusion than any of the others.

Not surprisingly, as agency was experienced only during active movements (see also [Longo & Haggard, 2009](#)), we found a significant difference in the agency category ratings across the three induction types (*active synchronous, passive synchronous and visuotactile synchronous*) (Friedmann: $\chi^2: 51.294, df = 2, n = 40, p < .001$). We performed post hoc pairwise comparisons and found that the active condition was associated with significantly stronger agency ratings than the passive condition ($z = -5.127, p < .001$), and the same difference was observed with respect to the visuotactile condition ($z = -5.446, p < .001$). The passive movement condition and the visuotactile condition did not significantly differ ($z = -1.141, p = .254$).

3.1.2. Correlation of ownership and agency across the three illusion types

3.1.2.1. Correlations of ownership and agency across conditions. Next, we sought to determine whether ownership ratings were correlated across the three versions of the rubber hand illusion. Such correlations would support the hypothesis that essentially the same illusion was elicited in the three cases. Thus, we ran three correlation analyses in which we related the ownership rating of each induction type with each other (active synchronous, passive synchronous, visuotactile synchronous). We found highly significant correlations among all three conditions in the three pairwise comparisons (active synchronous and passive synchronous: $r = .76, n = 40, p < .001$; active synchronous and visuotactile synchronous: $r = .633, n = 40, p < .001$; passive synchronous and visuotactile synchronous: $r = .473, n = 40, p = .002$; Spearman); see [Fig. 3](#).

We also investigated whether the agency ratings were correlated across the three synchronous conditions and found (not surprisingly, as agency was only experienced in the active movement conditions) that there were no significant correlations (active synchronous and passive synchronous: $r = .259, n = 40, p = .106$; active synchronous and visuotactile synchronous: $r = .054, n = 40, p = .742$; passive synchronous and visuotactile synchronous: $r = .015, n = 40, p = .928$); see [Fig. 3](#).

3.1.2.2. Correlations between ownership and agency. To re-examine the expected systematic relationship between ownership and agency we observed previously ([Kalckert & Ehrsson, 2012](#)) we also correlated the ownership and agency ratings in each of the three synchronous conditions eliciting the illusion. Ownership and agency were significantly correlated in all conditions (ownership rating and agency rating during active synchronous: $r = .290, n = 40, p = .035$; ownership rating and agency rating in passive synchronous: $r = .321, n = 40, p = .022$; ownership rating and agency rating in visuotactile synchronous: $r = .538, n = 40, p < .001$; Spearman one-tailed). These observations fit with the idea that when one experiences

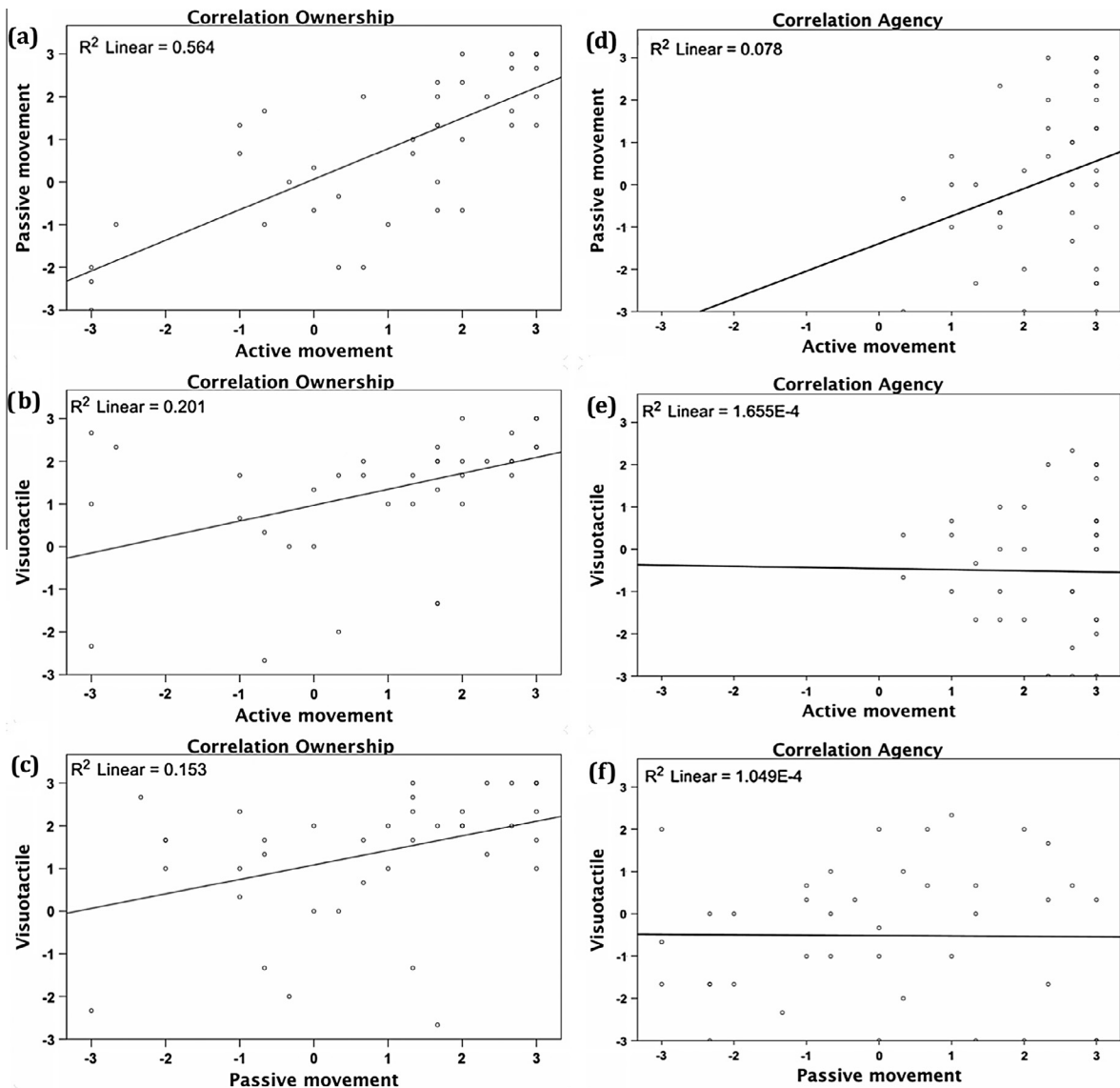


Fig. 3. Correlations of the ownership (Fig 3a–c, left panel) and agency (Fig. 3d–f, right panel) ratings between synchronous conditions. There are significant correlations between ownership ratings across the three synchronous conditions (a–c), which suggests a similar underlying mechanism. The agency ratings for the synchronous conditions (d–f) showed no significant correlations.

ownership of the model hand, the tendency to report a certain feeling of agency over the model hand automatically increases (see Section 4); see Fig. 4.

3.1.3. Number of illusion responders

As in previous studies, we counted the number of responders in the synchronous conditions using a cut-off score for the ownership rating ≥ 1 (Kalckert & Ehrsson, 2012; Petkova & Ehrsson, 2009). Using this approach, we found that in the present sample, 25 of 40 (63%) participants were classified as responders during the active synchronous condition, 23 (58%) during the passive synchronous condition, and 31 (78%) during the visuotactile synchronous condition. Of our participants, 19 (48%) showed the illusion for all three illusion induction types (i.e., displayed ownership rating ≥ 1 in active synchronous, passive synchronous, and visuotactile synchronous; see Fig. 5 for further information).

Based on this classification, we performed a McNemar test to determine whether there were significant differences in the number of illusion responders between conditions. This analysis did not show any significant difference between the active synchronous and passive synchronous conditions ($n = 40$, $p = .727$), nor between the active synchronous and visuotactile synchronous conditions ($n = 40$, $p = .109$), but there was a significant difference in the number of responders between the passive synchronous and visuotactile synchronous conditions ($n = 40$, $p = .039$).

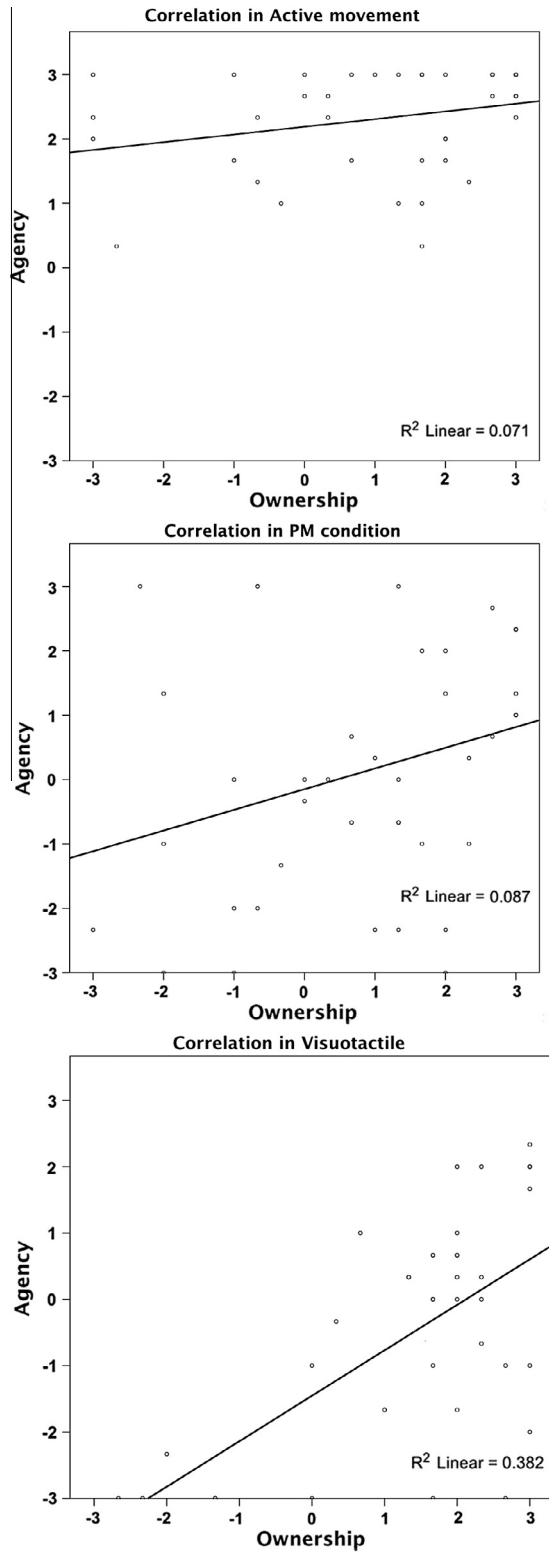


Fig. 4. Correlations between ownership and agency ratings: we correlated the ownership and agency ratings of the three synchronous conditions and found significant correlations in all three induction types.

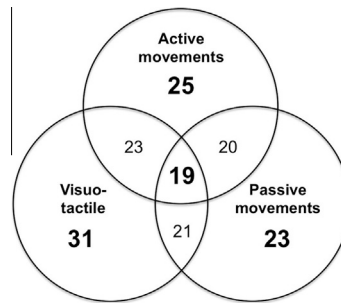


Fig. 5. Venn diagram illustrating the distribution of illusion responders in the visuotactile synchronous, active synchronous and passive synchronous condition: when the ownership rating is ≥ 1 , we categorized the participant as an “illusion responder”: the majority of participants ($n = 40$) experience the illusion, but interindividual differences can also be observed; 48% ($n = 19$) experience the illusion of ownership in all three synchronous conditions.

Notably, only 1 of the 40 participants denied the illusion in all three types (ownership rating ≤ -1 on all three of the synchronous conditions). Using the same logic that we used to classify people as “responders” we classified participants as “rejecters”, when they showed an ownership rating ≤ -1 , only five participants have no illusion of ownership in the active synchronous condition, only three in the passive synchronous condition, and only five in the visuotactile synchronous condition.

3.2. Experiment 2: Proprioceptive drift

3.2.1. Proprioceptive drift in active movement vs. visuotactile stimulation

We observed a significant difference between the active synchronous and active asynchronous conditions ($t = 3.406$, $df = 19$, $p = .003$). Similarly, we also observed a significant difference between visuotactile synchronous and visuotactile asynchronous ($z = -2.501$, $p = .012$). Thus, as can be seen in Fig. 6, both active movements and visuotactile stroking produced a significant proprioceptive drift towards the model hand, providing objective evidence of the ownership illusion. We also compared the two synchronous illusion conditions and found no significant difference ($t = -.591$, $df = 19$, $p = .561$). Thus, proprioceptive drift is similarly strong for both active movements and visuotactile stimulation.

3.2.2. Questionnaire

After the proprioceptive drift experiment, the participants also repeated the four conditions (i.e., active synchronous, active asynchronous, visuotactile synchronous and visuotactile asynchronous) and filled in the questionnaire after each condition to measure the subjective strength of the illusion. We performed the same analysis on the questionnaire data as described above for Experiment 1 (see Section 3.1.). The purpose was to obtain subjective data to use in the correlation analysis with the proprioceptive drift data.

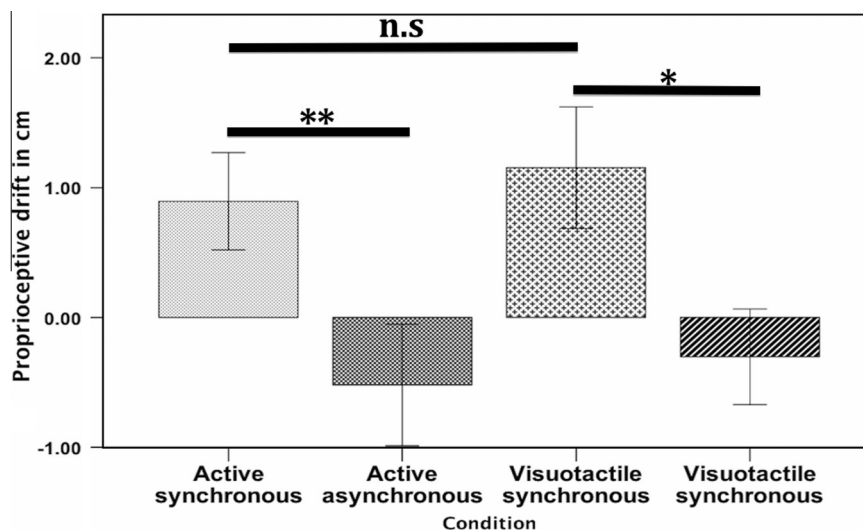


Fig. 6. Proprioceptive drift data. A significant positive drift towards the rubber hand was observed in the active synchronous and visuotactile synchronous conditions. There was no significant difference in the degree of proprioceptive drift between these two synchronous conditions, which suggests an equally strong illusion in these two conditions. Error bars show $+1SE$.

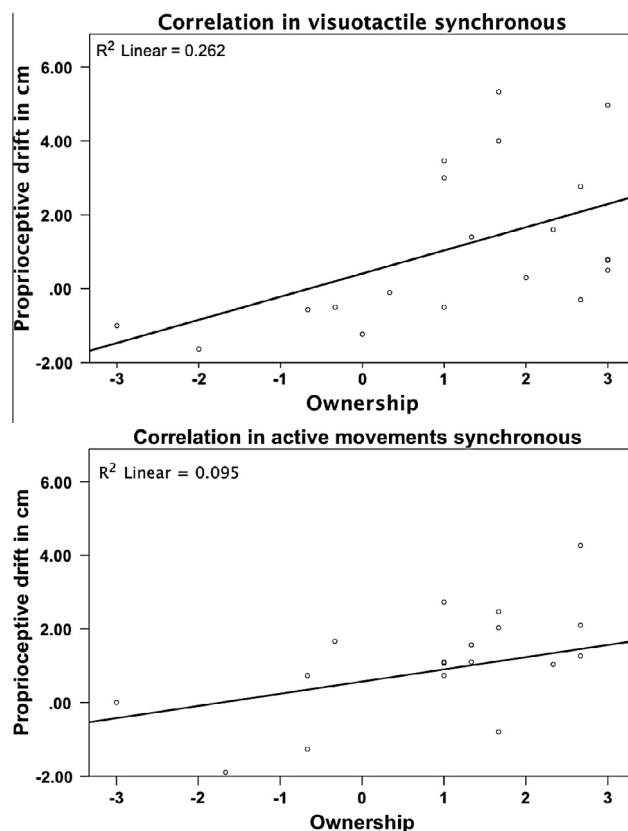


Fig. 7. In the active synchronous condition, proprioceptive drift showed a statistical trend toward a correlation with ownership ratings. In the visuotactile synchronous condition, this correlation was significant. Proprioceptive drift showed no significant correlation to ownership ratings in any of the asynchronous conditions.

The post-drift-test questionnaire results reproduced the findings of Experiment 1 (see Table 3). Ownership was experienced during active synchronous and visuotactile synchronous conditions, but not during the asynchronous control conditions. In the active synchronous condition, the ownership rating was rated significantly higher than the ownership control rating ($Z = -3.748, p < .001$). The ownership rating in the active synchronous condition was also significantly higher than the ownership rating in the active asynchronous condition ($Z = -3.315, p = .001$). In the visuotactile synchronous condition, the ownership rating was significantly higher than the ownership control ratings for the same condition ($Z = -3.768, p < .001$). The ownership rating in this visuotactile condition was also significantly higher than the ownership ratings in the visuotactile asynchronous condition ($Z = -3.522, p < .001$). Agency was experienced only in the active movement conditions, with higher ratings during active synchronous than during active asynchronous movements ($Z = -2.281, p = .023$). In the active synchronous condition, the agency rating was significantly higher than the agency control rating in the same condition ($Z = -3.928, p < .001$). As in Experiment 1, the agency rating in the active asynchronous condition was higher than +1 and was significantly higher than the agency control rating in the same condition ($Z = -3.310, p = .001$). In sum, these results are similar to the results obtained with fully naïve participants in Experiment 1 (compare Table 2) and are in line with our previous observations (Kalckert & Ehrsson, 2012). Furthermore, this shows that we can use the subjective data collected after the proprioceptive drift experiment to look for correlations between questionnaire items and the proprioceptive drift data (see below).

3.2.3. Correlations between proprioceptive drift and ownership ratings

Finally, we tested for the hypothesized correlations between the proprioceptive drift towards the model hand and the questionnaire reports of ownership for each of the two versions of the illusion. We also looked for correlations between proprioceptive drift and the agency ratings, although we did not expect to find a relationship (Kalckert & Ehrsson, 2012). In the active synchronous condition, the proprioceptive drift showed a statistical trend for correlation with the ownership ratings (Spearman: $r = .356, n = 20, p = .062$, one-tailed), which is in line with the significant correlation we reported in our previous study (Kalckert & Ehrsson, 2012). In the visuotactile synchronous condition, drift was significantly correlated to ownership rating (Spearman: $r = .580, n = 20, p = .004$, one-tailed) (see Fig. 7), in line with many earlier studies on the classical rubber hand illusion. There was no such correlation between the ownership rating and the proprioceptive drift in the

Table 2

Overview of the rating results: Participants experienced the illusion of ownership in all three synchronous conditions (≥ 1), whereas agency was only experienced in the active movement conditions. None of the control ratings were positively rated in any of the conditions. Median values in bold.

	Synchronous				asynchronous			
	Ownership	Ownership Control	Agency	Agency Control	Ownership	Ownership Control	Agency	Agency Control
<i>Active movement</i>								
Median	1.7	-0.8	2.7	-2.5	-1.3	-1.7	1.3	-1.3
Quartiles	25	0.0	-2.3	1.7	-3.0	-2.7	0.4	-2.6
	75	2.7	-0.1	3.0	-1.3	0.9	2.3	-0.7
<i>Passive movement</i>								
Median	1.3	-1.0	0.0	0.0	-2.0	-1.7	-1.0	-1.2
Quartiles	25	-0.7	-1.9	-1.3	-1.9	-2.7	-2.6	-2.0
	75	2.3	0.0	1.8	1.3	-0.2	-0.4	0.3
<i>Visuotactile</i>								
Median	1.7	-1.0	-0.2	-2.0	-2.0	-1.7	-2.0	-2.0
Quartiles	25	1.0	-1.7	-1.7	-3.0	-3.0	-2.8	-3.0
	75	2.3	0.3	0.7	-0.8	0.0	-0.3	-1.0

Table 3

Results of the subjective data from the questionnaire conducted after the proprioceptive drift test procedures of Experiment 2. The results are very similar to the results of Experiment 1; see Table 2. Median values in bold.

	Synchronous				Asynchronous			
	Ownership	Ownership control	Agency	Agency control	Ownership	Ownership control	Agency	Agency control
<i>Active movement</i>								
Median	1.2	-1.3	1.7	-2.0	-1.7	-1.8	1.2	-1.5
Quartiles	25	0.0	-2.3	1.3	-3.0	-2.3	0.7	-2.6
	75	2.2	-0.3	2.6	-1.3	0.6	-0.8	1.7
<i>Visuotactile</i>								
Median	1.5	-1.2	0.7	-1.7	-1.7	-2.0	-1.8	-0.8
Quartiles	25	0.1	-2.3	-1.0	-2.7	-2.6	-3.0	-2.3
	75	2.7	0.0	1.3	-1.0	-0.3	-0.7	0.8

asynchronous conditions (active asynchronous: $r = .202$, $n = 20$, $p = .196$; visuotactile asynchronous: $r = .193$, $n = 20$, $p = .207$; all one-tailed, not shown).

For agency, as we expected and in agreement with our earlier study (Kalckert & Ehrsson, 2012), we did not find a correlation between the agency ratings and the proprioceptive drift, either in the active synchronous condition (Spearman: $r = .172$, $n = 20$, $p = .234$, one-tailed) or in the visuotactile synchronous condition (Spearman: $r = .292$, $n = 20$, $p = .106$, one-tailed). Similarly we found no correlation between the agency ratings and the drift in the visuotactile asynchronous condition: $r = -.091$, $n = 20$, $p = .352$; one-tailed, not shown). Unexpectedly we found a statistical trend for the active asynchronous condition ($r = -.373$, $n = 20$, $p = .052$, one-tailed), which is in contrast to our previous observations and for which we have no explanation.

4. Discussion

In the present study, we found that participants experienced the rubber hand illusion irrespective of whether it was elicited by active or passive index finger movements or by brushstrokes applied to the fingers. The number of participants experiencing the illusion was similar in three versions. The strength of the illusion, as rated in the questionnaires, was not significantly different and was correlated across the different illusion paradigms. Similarly, proprioceptive drift was equally strong in the active movement and the classical version of the paradigm. These observations suggest that essentially the same illusion was elicited in the three versions of the rubber hand illusion. This suggests that different types of somatosensory and visual information can be combined to elicit the same changes in ownership perceptions. Moreover, the observation that the active movements did not further enhance the illusion speaks against the hypothesis that efferent signals associated with the voluntary motor commands play a significant role in the ownership feelings during the rubber hand illusion. Finally, we observed that questionnaire ratings of ownership and agency were correlated across individuals, even in the passive versions (passive movement and visuotactile) of the illusion. This result suggests that ownership modulates agency and, in the absence of voluntary motor commands and intentions, produces a weak tendency for agency, even in the passive conditions.

When comparing the strength of the illusion in the three conditions, we did not observe a significant difference in the subjective ratings of ownership, nor did we observe any differences in the proprioceptive drift between the active movements and the classical version tested here. The latter observation is in line with Tsakiris and colleagues' finding of no

significant difference in proprioceptive drift (Tsakiris et al., 2006) and with our earlier observation of similar drift in active and passive movement conditions (Kalckert & Ehrsson, 2012). In line with these observations and consistent with the present questionnaire results, the recent study by Riemer, Kleinböhl, Hölzl, & Trojan, 2013 also found no differences in the subjective strength of the ownership illusion (albeit they observed relatively low ratings overall) when induced by active movements or visuotactile stimulation. However, the study by Riemer and colleagues found that the proprioceptive drift was stronger for the actively moving rubber hand illusion compared to the classical version, when tested with a manual pointing procedure similar to the present one. Dummer and colleagues (Dummer et al., 2009) found higher ownership ratings for the active movement condition compared to the passive condition, which could be due to the particular design of the study which used a between-group comparison and was therefore subject to potential individual differences. In a previous study, we also observed indications of higher ownership ratings during active movements (average score of 2.12 on the seven-point Likert scale) compared to passive movements (average score of 1.57) (Kalckert & Ehrsson, 2012). In direct contrast with this observation, Walsh and colleagues (Walsh et al., 2011) found even higher ratings in the passive condition than in the active one. Thus, the picture that emerges from the earlier literature and the present data is that active and passive movements elicit equally vivid rubber hand illusions, and this illusion is as vivid as the classical version induced by stroking. These findings do not support the notion that efferent signals or efference copy mechanisms play an important role in the ownership illusion (in contrast to agency).

The differences in the earlier literature might reflect an inherent difficulty in measuring the illusion. Despite the fact that the illusion is vivid and can be readily demonstrated in classrooms and to the general public, the question of how best to quantify it in laboratory settings has not been fully settled. However, there is more or less a consensus in the field that subjective ratings should be complemented with an objective measure, and the most commonly used measures are proprioceptive drift (as used in the present study) or the skin conductance response elicited by threatening or injuring the rubber hand (Armel & Ramachandran, 2003; Guterstam, Petkova, & Ehrsson, 2011; Petkova & Ehrsson, 2008), but see also recent investigations in using other objective measures such as the cross-modal congruency task (Zopf, Savage, & Williams, 2009, 2013). The recent critique of proprioceptive drift as a single measure of the illusion (Holle, McLatchie, Maurer, & Ward, 2011; Rohde, Di Luca, & Ernst, 2011), see also (Holmes & Spence, 2005), highlights the importance of complementary measures to assess the presence of the illusion. The concern is that proprioceptive drift is not always related to the illusion but can occur in situations in which the subjective illusion is abolished, such as when the rubber hand is presented to the participant in the 180° rotated position (Holle et al., 2011) or in the asynchronous condition (Rohde et al., 2011). Thus, the divergent results observed in the earlier studies may partly relate to the measures used in different studies (questionnaires, drift measurement using different test procedures), adding to differences in the setups and types of finger or hand movements employed (such as full hand movements vs. finger movements or real model hand vs. recorded hand on a computer screen). As already mentioned, some groups used only the drift measure (Kammers, Longo, Tsakiris, Dijkerman, & Haggard, 2009; Tsakiris et al., 2006), some only questionnaires (Dummer et al., 2009; Longo & Haggard, 2009) and some employed both but obtained somewhat discrepant results across the two measures (Kalckert & Ehrsson, 2012; Riemer et al., 2013). For example, Riemer et al. (2013) found that proprioceptive drift was stronger for the moving rubber hand illusion than the classical version, but only when drift was measured using a manual pointing procedure, and not when it was assessed with a perceptual judgment procedure. The latter is in line with the observations made by Tsakiris and colleagues who introduced the perceptual judgment approach to measure drift (Tsakiris et al., 2006). However the former finding by Riemer and colleagues (2013) of greater drift after their active movement condition as assessed with the manual pointing response is in apparent direct contrast with the present results. A difference in results between these studies may be due to the different procedures used: Kammers and colleagues (2009) inferred the proprioceptive drift from a pointing movement performed towards an external target using the illusion-affected hand. Thus the participants performed a goal-directed hand action with their affected hand, which is quite different from the inter-manual pointing task employed in the present study. The drift procedure of Riemer, Kleinböhl, Hölzl, and Trojan (2013) is more similar to the one we used in the present study, where participants used their unaffected left hand to point towards the location of their occluded (illusion-affected) right hand. However, in contrast to our study, they compared the individual pointing performances after each illusion induction trial to a baseline measurement obtained before the main experiment, whereas we compared pointing performance before and after each illusion induction trial individually, which in our opinion produces more reliable results. In sum, the present data suggests that both the moving and classical rubber hand illusion result in a similar pointing bias towards the rubber hand, which is in line with the questionnaire result of similar subjective experience of the illusions.

The strongest results are clearly those that are obtained by consistently using multiple measures, as in the present study in which a coherent picture emerges from the questionnaire and drift data. Moreover, in defense of the proprioceptive drift measure, we observed significant correlations between proprioceptive drift and the subjective strength of the illusion when stimulation occurred synchronously but not when it was delivered asynchronously. Similar correlations between drift and questionnaire ratings have been described before (Bekrater-Bodmann et al., 2012; Botvinick & Cohen, 1998; Kalckert & Ehrsson, 2012; Longo, Schüür, Kammers, Tsakiris, & Haggard, 2008). Thus, the detection of visuotactile synchrony leading to a sensation of ownership may drive the recalibration of proprioceptive information towards the visually observed hand (Botvinick & Cohen, 1998; Makin et al., 2008). That is, drift arises as a consequence of the illusion and can thus be used as an indirect measure of the illusion.

It is interesting to note that, unlike ownership, there seems to be no relationship between proprioceptive drift and sense of agency. Thus, in the presence of an illusory feeling of ownership of the rubber hand, proprioceptive drift can be expected,

but not in all cases when agency over a model hand or sensory event is experienced. This is consistent with the view that a sense of agency can develop related to not only a bodily action but also to distant effects in the external world (Sato & Yasuda, 2005). Considering that agency can be experienced over events in the external world, it makes sense that a recalibration of the perceived position of the body does not need to be triggered by agency sensations in general. Further support for this hypothesis comes from our previous study where we dissociated sense of ownership and agency by manipulating the position of the rubber hand (aligned vs. rotated). A 180° rotation eliminates the ownership illusion but not sense of agency. Indeed, we observed a proprioceptive drift only in the aligned position (Kalckert & Ehrsson, 2012). Similarly, Longo and colleagues found no correlation between drift and the subjective experience of agency, but found a correlation of drift and ownership (Longo et al., 2008).

It is interesting to consider the finding of equally strong illusions in the three versions of the rubber hand illusion in relation to the different sensory modalities involved in each paradigm. In the classic rubber hand illusion, only tactile and visual information is available from the object touching the hand and the hand itself. In the passively moving rubber hand illusion, information from skin receptors, muscle spindles, joint receptors and visual feedback provide kinesthetic information (Edin & Abbs, 1991; Edin & Johansson, 1995; Goodwin, McCloskey, & Matthews, 1972; Proske & Gandevia, 2012). During the active moving rubber hand illusion, this is accompanied by efferent information from voluntary motor commands and the central sensory predictions they produce (i.e., efference copy mechanism) (Bays & Wolpert, 2006; Wolpert & Ghahramani, 2000). Despite these differences in available sensory and motor information between the three induction types, a very similar illusion was triggered. This suggests that the rubber hand illusion does not depend on specific types of sensory signals, such as vision or proprioceptive afferents, but that it is the spatiotemporal relationship of the available signals that matters (Ehrsson, 2012). Ehrsson, Holmes, and Passingham (2005) have shown that vision can be eliminated in this illusion by blindfolding the participant and instead letting the participant touch a rubber hand using the left index finger while he or she feels a touch on their own right hand at the corresponding location. In this “somatic version” of the rubber hand illusion, the participant thus experiences touching his or her own right hand directly with the left hand when in fact he or she is touching a rubber hand and being touched by the experimenter (Aimola Davies, White, Thew, Aimola, & Davies, 2010; Ehrsson et al., 2005; Petkova, Zetterberg, & Ehrsson, 2012). Finally, Walsh and colleagues (Walsh et al., 2011) used a rubber hand illusion based on movements and anaesthetized the finger with lidocaine, thus eliminating the somatosensory information from the superficial skin. Nevertheless, in this situation where only proprioceptive and visual information is available, participants have an illusion of ownership and experience the rubber hand as part of their own body. Thus, very different types of sensory feedback can trigger the illusion, but correlated visual and tactile stimulation of an external object moving in peripersonal space is not necessary to trigger the illusion. Matching feedback from finger movements is equally efficient in eliciting the illusion.

Most of our participants experienced the illusion in the moving (63%) and/or classical visuotactile rubber hand illusion (78%) during synchronous conditions. There were no significant differences in the proportion of participants that experienced or denied the illusion in the three paradigms tested. These numbers are consistent with earlier studies of the classical rubber hand illusion reporting that approximately 70% of participants experience the illusion of ownership (Ehrsson, 2012; Ehrsson et al., 2004; Lloyd, 2007) and with our previous moving rubber hand study (75%) (Kalckert & Ehrsson, 2012). The factors that determine the individual differences in the illusion are not fully understood (Haans, Kaiser, Bouwhuis, & IJsselstein, 2010) but may be related to differences in how different types of signals in different modalities are weighted in the dynamic process of integration (Hagura, Hirose, Matsumura, & Naito, 2012; van Beers, Wolpert, & Haggard, 2002). Interestingly, when looking at the number of “illusion rejecters,” i.e., those participants who reported an ownership score of -1 or lower, we see that only 1 of 40 participants strongly denied the illusion in all three cases. Thus, those who experienced the illusion in one condition were also more likely to experience the illusion in the other conditions. Replicating the earlier observation made by Riemer and colleagues, we observed that the ownership illusion scores in the moving and classical rubber hand illusion were highly correlated (Riemer et al., 2013). This again points towards a very similar mechanism for ownership across the active movement, passive movement, and visuotactile stimulation conditions.

Is it not surprising that the ownership illusion is not greater after active movements compared to visuotactile stimulation? Should not information about voluntary motor commands, matching sensory predictions, and afferent feedback facilitate the ownership illusion, at least slightly, just as it triggers the sense of agency? Studies have shown that during active movements, when efference copy mechanisms are engaged, the recognition of an action or body part is enhanced (Farrer, Franck, Paillard, & Jeannerod, 2003; MacDonald & Paus, 2003; Tsakiris, Haggard, Franck, Mainy, & Sirigu, 2005). For example, Tsakiris and Haggard (2005) visually presented active or passive finger movements where the image of the hand was that of the participant's hand or the experimenter's hand, and then varied the delay between the visual and somatosensory feedback. In the active movement condition, the presented hand was recognized more accurately than in the passive movement condition, suggesting that efferent information enhanced self-recognition in this task. Although studies on self-recognition of action have contributed greatly to our understanding of how we identify visually presented actions, these paradigms can provide only indirect evidence for the moving rubber hand illusion and the role of sensory and efferent cues in this paradigm. In most of these studies, visual feedback is manipulated by introducing a temporal delay (or spatial deviation) and the participants are instructed to report the presence of a discrepancy. These studies on action self-recognition are best understood in terms of sense of agency: when the temporal delay or spatial deviation exceeds a certain threshold, the participant notices the discrepancy and feels a mismatch between the intended movement and the actual feedback (Daprati et al., 1997; Farrer,

Bouchereau, Jeannerod, & Franck, 2008; Nahab et al., 2011; Nielsen, 1963). Shimada, Qi, and Hiraki (2009) showed that during active movements, the threshold for the detection of mismatches (i.e., delayed visual feedback) is indeed lower, therefore suggesting improved discrimination ability when efferent information is available. Although many of these studies use an image of the participant's real hand (i.e., Nahab et al., 2011), they do not necessarily imply or manipulate sense of ownership over this hand nor trigger perceptual body illusions. Consequently, it is necessary to carefully distinguish between the delayed feedback detection paradigms mentioned above and studies on agency and ownership in the context of rubber hand illusion paradigms. We believe future studies are needed to combine these two approaches and mix the rubber hand illusion with delayed feedback detection tasks or forced-choice action recognition paradigms under various contexts of spatiotemporal congruency of multisensory feedback and efferent motor signals.

If we put aside the question of a possible contribution of efferent signals, why are the ownership ratings so similar in the moving rubber hand illusion and classical version elicited by brush-strokes? One explanation could be that in the classical rubber hand illusion, the stimulation consists of two very distinct events in perihand space: an object seen touching the model hand and a matching touch sensation on the real hand. Possibly, these cues could be powerful in driving the illusion because of the important role of visuotactile integration in peripersonal space for guiding spatially precise hand action towards external objects (Brozzoli, Gentile, & Ehrsson, 2012; Makin et al., 2008). During movements, many different types of sensory channels provide information about the ongoing finger action, and all these signals might produce a stronger illusion. However, this also means that signals from many separate information channels have to be integrated: signals from cutaneous receptors signaling skin stretch, muscle spindles, joint receptors, visual information, and, in the case of active movements, perhaps efferent signals and sensory predictions (i.e., efference copy). All these different information channels have to be evaluated for congruency. Thus, there are not only more channels to harvest information from but also potentially more channels signaling the initial conflict between the seen and felt positions of the model hand and the real hand. Therefore, one can speculate whether there might be a trade-off between the number of heterogeneous information channels and fewer but more precise and information-rich sensory signals. This could explain the observation by Walsh et al. (2011) of higher ownership ratings during anesthesia of the superficial skin than in the non-anaesthetized condition when the illusion relies purely on a match between visual and proprioceptive cues.

Finally, if one conceptualizes the rubber hand illusion as an “all or nothing” phenomenon, where the brain makes inferences based on actual incoming sensory information, then it is not surprising to see that different types of sensory information can yield the same result (i.e., to incorporate the rubber hand as part of the own body). Once this central process has accumulated enough sensory evidence (meaning spatially and temporally correlated multisensory stimuli), it can make the inference that this visually observed hand (i.e., the rubber hand) is the “own hand”, thereby giving rise to the ownership illusion. Importantly, a match between any two sources of sensory information that can be regarded as independent, be they visual and tactile (in the case of the classical rubber hand illusion), or correlated sensorimotor signals (in the case of the moving rubber hand illusion) might count as important evidence in favor of this dynamic central decision process. Although this explanation emphasizes bottom-up mechanisms in the generation of the illusion, it does not exclude top-down influences, which set important a priori criteria for what types of objects can become part of one's own body (Guterstam et al., 2011; Petkova & Ehrsson, 2009; Tsakiris, Carpenter, James, & Fotopoulou, 2010).

Because we also included statements regarding the feeling of being in voluntary control over the model hand, we were able to make some observations regarding the sense of agency. We found not only that sense of agency was strongly experienced in the active and synchronous movement condition, as one would expect (Synchronous active movement median: 2.7), but also that relatively high agency ratings were noted (Asynchronous active movement median: 1.3) in the active asynchronous condition (but still significantly lower than in the synchronous condition). A possible reason for this rather strong explicit agreement of agency in the active asynchronous condition in this study – more so than in our previous study (Kalckert & Ehrsson, 2012), see Fig. 2) – is the small changes we introduced to the agency statements in the questionnaire to make them applicable to both the moving and classical versions of the rubber hand illusion. This adaptation meant that the statements became slightly more general to include the feelings that the participant could move the hand if they would like to (“I felt as if I *could* movements of the rubber hand”). Thus these observations provide a more indirect measurement of agency, as compared to situations in which participants actually produced finger movements and could claim that they executed these. Furthermore, the small differences in statement formulation might result in slightly higher ratings in the passive and asynchronous condition in the present study compared to our previous one. Nevertheless, it is rather striking that participants reported high agency of the model hand when the feedback was out-of-sync. This result suggests that voluntary intentions (prior to a comparison between efferent copy and actual sensory feedback) play an important part in the sense of agency (Kalckert & Ehrsson, 2012). This finding is in line with earlier observations that participants tend to attribute actions to themselves, sometimes even in cases where a clear spatiotemporal mismatch is present (Nielsen, 1963; Preston & Newport, 2010), which might be dependent on the specific context (Jeannerod, 2003; Synofzik, Vosgerau, & Newen, 2008). Therefore, when an intention is present, participants tend to experience a certain degree of agency and attribute a causal relationship between their actions, regardless whether there is a match between the afferent sensory feedback and the expected sensory feedback or not.

Interestingly, we also noted weaker denial of agency in the passive movement and visuotactile condition when the visuosomatic feedback occurred synchronously compared to asynchronously. Actually, the participants reported that they were uncertain about agency in these instances (see Fig. 2). In other words, when participants experienced the ownership illusion, they less strongly denied agency in the synchronous passive movement and visuotactile conditions. Note that we also

observed significant correlations between ownership and agency in these two conditions although neither of them involves producing or experiencing a voluntary movement. Speculatively, this suggests that whenever the hand was perceived as part of their own body, participants automatically tended to become more uncertain about the level of control they could exhibit over the model hand (see also (Kalckert & Ehrsson, 2012)). Thus, based on our results, one can formulate the interesting hypothesis that ownership may facilitate agency over bodily actions, a notion that deserves further investigation in future studies (Tsakiris, Schütz-Bosbach, & Gallagher, 2007).

5. Conclusion

Active and passive movements or visuotactile stimulation can induce an equally strong rubber hand illusion. The subjective strength of illusory ownership of the model hand does not differ even if the types of sensory stimulation and sensory modalities involved differ. Although active movements elicited a sense of agency of the model hand and active movements are known to engage efference copy mechanisms, median scores of ownership were very similar for the active and passive movement conditions, questioning the role of efferent signals in the perceptual illusion of ownership. Further research is needed to investigate the potential interactions of the sense of ownership and agency for bodily self-recognition and how individual channels of sensory information are integrated to generate the feeling of ownership of the body.

Acknowledgments

This study was funded by the European Research Council (erc.europa.eu), the Swedish Foundation for Strategic Research (www.stratresearch.se/en), the Human Frontier Science Program (www.hfsp.org), Söderbergiska Stiftelsen, and Stockholm Brain Institute (www.stockholmbrain.se). The authors thank all participants for their participation in this study.

References

- Aimola Davies, A. M., White, R. C., Thew, G., Aimola, N. M. V., & Davies, M. (2010). Visual capture of action, experience of ownership, and the illusion of self-touch: A new rubber hand paradigm. *Perception*, 39(6), 830–838. <http://dx.doi.org/10.1068/p6610>.
- Armel, K. C., & Ramachandran, V. S. (2003). Projecting sensations to external objects: Evidence from skin conductance response. *Proceedings Biological Sciences/The Royal Society*, 270(1523), 1499–1506. <http://dx.doi.org/10.1098/rspb.2003.2364>.
- Bays, P. M., & Wolpert, D. M. (2006). Computational principles of sensorimotor control that minimize uncertainty and variability. *The Journal of Physiology*, 578(2), 387–396. <http://dx.doi.org/10.1113/jphysiol.2006.120121>.
- Bekrater-Bodmann, R., Foell, J., Diers, M., & Flor, H. (2012). The perceptual and neuronal stability of the rubber hand illusion across contexts and over time. *Brain Research*, 1452, 130–139. <http://dx.doi.org/10.1016/j.brainres.2012.03.001>.
- Blanke, O. (2012). Multisensory brain mechanisms of bodily self-consciousness. *Nature Reviews Neuroscience*, 13(8), 556–571. <http://dx.doi.org/10.1038/nrn3292>.
- Botvinick, M., & Cohen, J. (1998). Rubber hands “feel” touch that eyes see. *Nature*, 391(6669), 756. <http://dx.doi.org/10.1038/35784>.
- Brozzoli, C., Gentile, G., & Ehrsson, H. H. (2012). That’s near my hand! Parietal and premotor coding of hand-centered space contributes to localization and self-attribution of the hand. *Journal of Neuroscience*, 32(42), 14573–14582. <http://dx.doi.org/10.1523/JNEUROSCI.2660-12.2012>.
- Crappe, T. B., & Sommer, M. A. (2008). Corollary discharge across the animal kingdom. *Nature Reviews Neuroscience*, 9(8), 587–600. <http://dx.doi.org/10.1038/nrn2457>.
- Daprati, E., Franck, N., Georgieff, N., Proust, J., Pacherie, E., Dalery, J., et al (1997). Looking for the agent: An investigation into consciousness of action and self-consciousness in schizophrenic patients. *Cognition*, 65(1), 71–86.
- David, N., Newen, A., & Vogeley, K. (2008). The “sense of agency” and its underlying cognitive and neural mechanisms. *Consciousness and Cognition*, 17(2), 523–534. <http://dx.doi.org/10.1016/j.concog.2008.03.004>.
- Dummer, T., Picot-Annand, A., Neal, T., & Moore, C. (2009). Movement and the rubber hand illusion. *Perception*, 38(2), 271–280.
- Edin, B. B., & Abbs, J. H. (1991). Finger movement responses of cutaneous mechanoreceptors in the dorsal skin of the human hand. *Journal of Neurophysiology*, 65(3), 657–670.
- Edin, B. B., & Johansson, N. (1995). Skin strain patterns provide kinaesthetic information to the human central nervous system. *The Journal of Physiology*, 487(Pt 1), 243–251.
- 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. <http://dx.doi.org/10.1523/JNEUROSCI.0800-05.2005>.
- 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. <http://dx.doi.org/10.1126/science.1097011>.
- Ehrsson, H. H. (2012). The concept of body ownership and its relation to multisensory integration. In B. E. Stein (Ed.), *The new handbook of multisensory processes* (pp. 775–792). Cambridge, MA: MIT Press.
- Farrer, C., Bouchereau, M., Jeannerod, M., & Franck, N. (2008). Effect of distorted visual feedback on the sense of agency. *Behavioural Neurology*, 19(1–2), 53–57.
- Farrer, C., Franck, N., Paillard, J., & Jeannerod, M. (2003). The role of proprioception in action recognition. *Consciousness and Cognition*, 12(4), 609–619.
- Gallagher, S. (2000). Philosophical conceptions of the self: Implications for cognitive science. *Trends in Cognitive Sciences*, 4(1), 14–21.
- Gandevia, S. C., Smith, J. L., Crawford, M., Proske, U., & Taylor, J. L. (2006). Motor commands contribute to human position sense. *The Journal of Physiology*, 571(3), 703–710. <http://dx.doi.org/10.1113/jphysiol.2005.103093>.
- Goodwin, G. M., McCloskey, D. L., & Matthews, P. (1972). The contribution of muscle afferents to kinaesthesia shown by vibration induced illusions of movement and by the effects of paralysing joint afferents. *Brain*, 95(4), 705–748.
- Guterstam, A., Petkova, V. I., & Ehrsson, H. H. (2011). The illusion of owning a third arm. *PLoS One*, 6(2), e17208. <http://dx.doi.org/10.1371/journal.pone.0017208.g008>.
- Haans, A., Kaiser, F. G., Bouwhuis, D. G., & IJsselstein, W. A. (2010). Individual differences in the rubber-hand illusion: Predicting self-reports of people’s personal experiences. *Actpsy*, 141(2), 169–177. <http://dx.doi.org/10.1016/j.actpsy.2012.07.016>.
- Hagura, N., Hirose, S., Matsumura, M., & Naito, E. (2012). Am I seeing my hand? Visual appearance and knowledge of controllability both contribute to the visual capture of a person’s own body. *Proceedings of the Royal Society B: Biological Sciences*, 279(1742), 3476–3481. <http://dx.doi.org/10.1038/415429a>.
- Heed, T., Gründler, M., Rinkleb, J., Rudzik, F. H., Collins, T., Cooke, E., et al (2011). Visual information and rubber hand embodiment differentially affect reach-to-grasp actions. *Actpsy*, 138(1), 263–271. <http://dx.doi.org/10.1016/j.actpsy.2011.07.003>.

- Holle, H., McLatchie, N., Maurer, S., & Ward, J. (2011). Proprioceptive drift without illusions of ownership for rotated hands in the “rubber hand illusion” paradigm. *Cognitive Neuroscience*, 2(3–4), 171–178. <http://dx.doi.org/10.1080/17588928.2011.603828>.
- Holmes, N. P., & Spence, C. (2005). Visual bias of unseen hand position with a mirror: Spatial and temporal factors. *Experimental Brain Research Experimentelle Hirnforschung Experimentation Cerebrale*, 166(3–4), 489–497. <http://dx.doi.org/10.1007/s00221-005-2389-4>.
- Holst, von E., & Mittelstaedt, H. (1950). Das Reafferenzprinzip – Wechselwirkungen zwischen Zentralnervensystem und Peripherie. *Die Naturwissenschaften*, 20, 464–476.
- Jeannerod, M. (2003). The mechanism of self-recognition in humans. *Behavioural Brain Research*, 142(1–2), 1–15.
- Kalckert, A., & Ehrsson, H. H. (2012). Moving a rubber hand that feels like your own: A dissociation of ownership and agency. *Frontiers in Human Neuroscience*, 6.
- Kammers, M. P. M., Longo, M. R., Tsakiris, M., Dijkerman, H. C., & Haggard, P. (2009). Specificity and coherence of body representations. *Perception*, 38(12), 1804–1820.
- 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. <http://dx.doi.org/10.1016/j.bandc.2006.09.013>.
- Longo, M. R., & Haggard, P. (2009). Sense of agency primes manual motor responses. *Perception*, 38(1), 69–78.
- Longo, M. R., Schüür, F., Kammers, M. P. M., Tsakiris, M., & Haggard, P. (2008). What is embodiment? A psychometric approach. *Cognition*, 107(3), 978–998. <http://dx.doi.org/10.1016/j.cognition.2007.12.004>.
- MacDonald, P. A., & Paus, T. (2003). The role of parietal cortex in awareness of self-generated movements: A transcranial magnetic stimulation study. *Cerebral Cortex*, 13(9), 962–967.
- Makin, T. R., Holmes, N. P., & Ehrsson, H. H. (2008). On the other hand: Dummy hands and peripersonal space. *Behavioural Brain Research*, 191(1), 1–10. <http://dx.doi.org/10.1016/j.bbr.2008.02.041>.
- Matthews, P. B. C. (1982). Where does Sherrington’s “muscular sense” originate? Muscles, joints, corollary discharge. *Annual Review of Neuroscience*, 5, 189–218.
- Nahab, F. B., Kundu, P., Gallea, C., Kakareka, J., Pursley, R., Pohida, T., et al (2011). The neural processes underlying self-agency. *Cerebral Cortex*, 21(1), 48–55. <http://dx.doi.org/10.1093/cercor/bhq059>.
- Nielsen, T. I. (1963). Volition: A new experimental approach. *Scandinavian Journal of Psychology*, 4, 225–230.
- Petkova, V. I., Björnsdotter, M., Gentile, G., Jonsson, T., Li, T.-Q., & Ehrsson, H. H. (2011). From part-to whole-body ownership in the multisensory brain. *Cortex*, 21(13), 1118–1122. <http://dx.doi.org/10.1016/j.cub.2011.05.022>.
- Petkova, V. I., & Ehrsson, H. H. (2008). If I were you: Perceptual illusion of body swapping. *PLoS One*, 3(12), e3832. <http://dx.doi.org/10.1371/journal.pone.0003832>.
- Petkova, V. I., & Ehrsson, H. H. (2009). When right feels left: Referral of touch and ownership between the hands. *PLoS One*, 4(9), e6933. <http://dx.doi.org/10.1371/journal.pone.0006933>.
- Petkova, V. I., Zetterberg, H., & Ehrsson, H. H. (2012). Rubber hands feel touch, but not in blind individuals. *PLoS One*, 7(4), e35912.
- Preston, C., & Newport, R. (2010). Self-denial and the role of intentions in the attribution of agency. *Consciousness and Cognition*, 19(4), 986–998. <http://dx.doi.org/10.1016/j.concog.2010.04.005>.
- Proske, U., & Gandevia, S. C. (2012). The proprioceptive senses: Their roles in signaling body shape, body position and movement, and muscle force. *Physiological Reviews*, 92(4), 1651–1697. <http://dx.doi.org/10.1152/physrev.00048.2011>.
- Riemer, M., Kleinböhl, D., Hölzl, R., & Trojan, J. (2013). Action and perception in the rubber hand illusion. *Experimental Brain Research*, 1–11. <http://dx.doi.org/10.1007/s00221-012-3374-3>.
- Rohde, M., Di Luca, M., & Ernst, M. O. (2011). The rubber hand illusion: Feeling of ownership and proprioceptive drift do not go hand in hand. *PLoS One*, 6(6), e21659. <http://dx.doi.org/10.1371/journal.pone.0021659.g004>.
- Sanchez-Vives, M. V., Spanlang, B., Frisoli, A., Bergamasco, M., & Slater, M. (2010). Virtual hand illusion induced by visuomotor correlations. *PLoS One*, 5(4), e10381. <http://dx.doi.org/10.1371/journal.pone.0010381>.
- Sato, A., & Yasuda, A. (2005). Illusion of sense of self-agency: Discrepancy between the predicted and actual sensory consequences of actions modulates the sense of self-agency, but not the sense of self-ownership. *Cognition*, 94(3), 241–255. <http://dx.doi.org/10.1016/j.cognition.2004.04.003>.
- Shimada, S., Qi, Y., & Hiraki, K. (2009). Detection of visual feedback delay in active and passive self-body movements. *Experimental Brain Research*, 201(2), 359–364. <http://dx.doi.org/10.1007/s00221-009-2028-6>.
- Slater, M., Perez-Marcos, D., Ehrsson, H. H., & Sanchez-Vives, M. V. (2008). Towards a digital body: The virtual arm illusion. *Frontiers in Human Neuroscience*, 2, 6. <http://dx.doi.org/10.3389/neuro.09.006.2008>.
- Synofzik, M., Vosgerau, G., & Newen, A. (2008). Beyond the comparator model: A multifactorial two-step account of agency. *Consciousness and Cognition*, 17(1), 219–239. <http://dx.doi.org/10.1016/j.concog.2007.03.010>.
- Tsakiris, M. (2009). My body in the brain: A neurocognitive model of body-ownership. *Neuropsychologia*. <http://dx.doi.org/10.1016/j.neuropsychologia.2009.09.034>.
- Tsakiris, M., Carpenter, L., James, D., & Fotopoulou, A. (2010). Hands only illusion: Multisensory integration elicits sense of ownership for body parts but not for non-corporeal objects. *Experimental Brain Research*, 204(3), 343–352.
- 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. <http://dx.doi.org/10.1037/0096-1523.31.1.80>.
- Tsakiris, M., Haggard, P., Franck, N., Mainy, N., & Sirigu, A. (2005). A specific role for efferent information in self-recognition. *Cognition*, 96(3), 215–231. <http://dx.doi.org/10.1016/j.cognition.2004.08.002>.
- Tsakiris, M., Prabhu, G., & Haggard, P. (2006). Having a body versus moving your body: How agency structures body-ownership. *Consciousness and Cognition*, 15(2), 423–432. <http://dx.doi.org/10.1016/j.concog.2005.09.004>.
- Tsakiris, M., Schütz-Bosbach, S., & Gallagher, S. (2007). On agency and body-ownership: Phenomenological and neurocognitive reflections. *Consciousness and Cognition*, 16(3), 645–660. <http://dx.doi.org/10.1016/j.concog.2007.05.012>.
- 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.
- Walsh, L. D., Moseley, G. L., Taylor, J. L., & Gandevia, S. C. (2011). Proprioceptive signals contribute to the sense of body ownership. *The Journal of Physiology*, 589(12), 3009–3021. <http://dx.doi.org/10.1113/jphysiol.2011.204941>.
- Wolpert, D. M., & Ghahramani, Z. (2000). Computational principles of movement neuroscience. *Nature Neuroscience*, 3(Suppl), 1212–1217. <http://dx.doi.org/10.1038/81497>.
- Zopf, R., Savage, G., & Williams, M. (2009). Crossmodal congruency measures of lateral distance effects on the rubber hand illusion. *Neuropsychologia*. <http://dx.doi.org/10.1016/j.neuropsychologia.2009.10.028>.
- Zopf, R., Savage, G., & Williams, M. A. (2013). The crossmodal congruency task as a means to obtain an objective behavioral measure in the rubber hand illusion paradigm. *Journal of Visualized Experiments* (77). <http://dx.doi.org/10.3791/50530>.