

University of Groningen

The rubber hand universe

Riemer, Martin; Trojan, Joerg; Beauchamp, Marta; Fuchs, Xaver

Published in:
Neuroscience and Biobehavioral Reviews

DOI:
[10.1016/j.neubiorev.2019.07.008](https://doi.org/10.1016/j.neubiorev.2019.07.008)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2019

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Riemer, M., Trojan, J., Beauchamp, M., & Fuchs, X. (2019). The rubber hand universe: On the impact of methodological differences in the rubber hand illusion. *Neuroscience and Biobehavioral Reviews*, *104*, 268-280. <https://doi.org/10.1016/j.neubiorev.2019.07.008>

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.



ELSEVIER

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

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

The rubber hand universe: On the impact of methodological differences in the rubber hand illusion

Martin Riemer^{a,b,c,*}, Jörg Trojan^d, Marta Beauchamp^e, Xaver Fuchs^{f,g}

^a Aging and Cognition Research Group, German Center for Neurodegenerative Diseases (DZNE), Magdeburg, Germany

^b Center for Behavioral Brain Sciences, Magdeburg, Germany

^c Department of Experimental Psychology, University of Groningen, Netherlands

^d Department of Psychology, University of Koblenz-Landau, Landau, Germany

^e Faculty of Design, Bielefeld University of Applied Sciences, Bielefeld, Germany

^f Biopsychology & Cognitive Neuroscience, Faculty of Psychology & Sports Science, Bielefeld University, Bielefeld, Germany

^g Excellence Cluster Cognitive Interaction Technology (Citec), Bielefeld University, Bielefeld, Germany

ARTICLE INFO

Keywords:

Rubber hand illusion
Body representation
Body ownership
Proprioceptive drift
Embodiment

ABSTRACT

The rubber hand illusion (RHI) is a widely applied paradigm to investigate changes in body representations. Extensive scientific interest has produced a great variability in the observed results and many contradictory findings have been reported. Taking into account the numerous variations in the experimental implementation of the RHI, many of these contradictory findings can be reconciled, but to date a thorough analysis of the methodological differences between RHI studies is lacking.

Here we summarize and analyse methodological differences between RHI studies. In distinction from other reviews focusing on the integration of findings from various studies, the present paper is devoted to the differences in (i) the experimental setup, (ii) the method used to induce the RHI, (iii) the quantification of its effects, and (iv) aspects of the experimental design and data analysis. This approach will provide a reference frame for the interpretation of previous studies as well as for the design of future studies.

1. Introduction

The rubber hand illusion (RHI) is an established and frequently used paradigm to investigate changes in body representations (Abdulkarim and Ehrsson, 2016; Botvinick and Cohen, 1998; Tsakiris and Haggard, 2005). Its core feature is the experimentally induced embodiment of an artificial hand, which is processed as belonging to the own body. This involves somatosensory (e.g., Kilteni and Ehrsson, 2017), affective (e.g., Armel and Ramachandran, 2003) and motor components (e.g., Heed et al., 2011). At a phenomenological level, the RHI often evokes the feeling that the artificial hand belongs to the own body, referred to as a sense of body ownership. This illusory experience is usually induced by synchronously touching the participant's own hand, which is hidden from view, and an artificial hand, which is placed visibly in front of the participant in an anatomically plausible position. The most common methods for quantifying the strength of the RHI include subjective self-reports assessed with questionnaires and measures of the perceived position of the own hand. In RHI questionnaires, subjective experiences relating to the sense of ownership over the artificial hand and/or the

sense of agency over movements of the artificial hand are typically rated on a Likert scale (section 4.1). Verbal or behavioural judgments about the own hand's location usually reveal a systematic mislocation of the unseen own hand towards the artificial hand, a phenomenon commonly referred to as *proprioceptive drift* (section 4.2).

In recent years, the RHI has been extensively studied and has advanced our understanding of human bodily awareness. A large number of studies on the RHI has been published since its seminal description by Botvinick and Cohen (1998), and during this period, the original paradigm has been developed and refined in many aspects, including the procedure of induction, the type of the used artificial hand and the method for assessing altered body representations. Not surprisingly, the wealth of studies on the RHI has also produced a great variability in the obtained results and many contradictory findings have been reported. Subjective reports about the perceived strength of the illusion exhibit a large variability between studies and even the arguably more objective measure of proprioceptive drift of the own hand towards the artificial hand ranges from 1 cm (e.g., Riemer et al., 2013) to more than 5 cm (e.g., Kammers et al., 2009a). Moreover, while Armel and

* Corresponding author.

E-mail address: martin.riemer@dzne.de (M. Riemer).

<https://doi.org/10.1016/j.neubiorev.2019.07.008>

Received 21 January 2019; Received in revised form 4 July 2019; Accepted 15 July 2019

Available online 20 July 2019

0149-7634/ © 2019 Elsevier Ltd. All rights reserved.

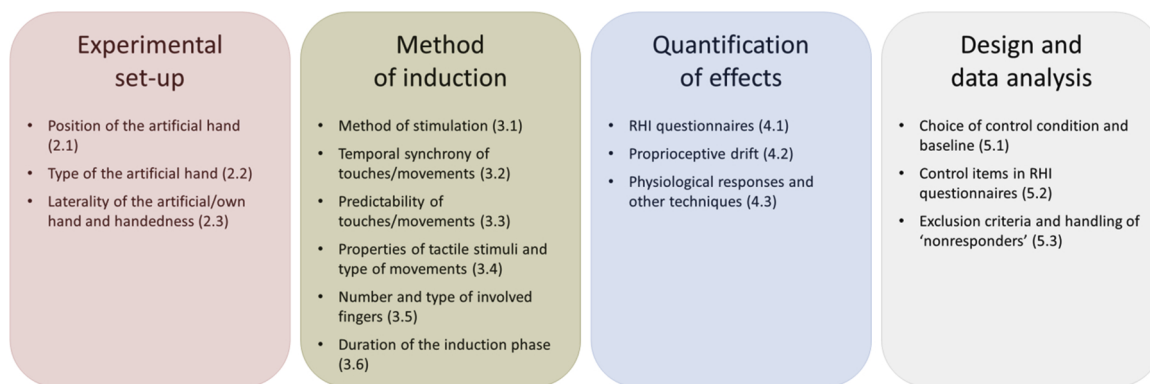


Fig. 1. Schematic depiction of discussed topics, related to the experimental set-up (section 2), the induction method (section 3), the quantification of RHI effects (section 4), and the experimental design and data analysis (section 5). Numbers in parentheses refer to the corresponding sections.

Ramachandran (2003) reported an embodiment of the table surface when it was stroked in synchrony with the hidden hand, other researchers did not find evidence for an embodiment of objects deviating from a basic bodily shape (e.g., Holmes et al., 2006; Tsakiris and Haggard, 2005), suggesting that a rudimentary resemblance of shape between own and artificial hands is a necessary prerequisite for the RHI (de Preester and Tsakiris, 2009; Riemer et al., 2014; Tsakiris, 2010). Reviewing the scientific literature, we argue that many of these discrepancies can be explained by variations in the RHI paradigm and that several conflicts between seemingly contradictory findings can be resolved by taking into account the experimental conditions under which they have been observed.

The aim of this article is therefore to compile the existing differences between implementations of the RHI paradigm and to discuss to which extent these differences can account for the diverging results in this field of research. We will focus on studies based on multisensory integration between tactile stimuli at (or movements of) the own hand and visual stimuli at (or movements of) an external object. Studies using different paradigms, for which a different methodology is considered a defining aspect rather than a theoretically negligible side detail (e.g., the somatic RHI, Ehrsson et al., 2005), are beyond the scope of this review. The article is subdivided into four main sections (see Fig. 1) focusing on differences related to (i) the experimental set-up, (ii) the method used to induce the illusion, (iii) the quantification of RHI effects, and (iv) aspects of the study design and data preprocessing.

2. Experimental set-up

Generally, many aspects of the experimental set-up differ between studies and research groups, depending on the specific research question, the laboratory setting, and the technical equipment. In this section we will only discuss the differences in the experimental set-up which are specifically related to RHI experiments, namely (i) the position of the artificial hand relative to the own hand, (ii) the type of the artificial hand, and (iii) the laterality of the hand, i.e., whether the RHI is induced at the right or the left hand.

2.1. Position of the artificial hand

An important difference between RHI studies relates to the spatial axis along which the artificial hand is displaced (relative to the participant's own hand), and therefore the axis, along which a proprioceptive drift is expected. Although in most studies the artificial hand is positioned next to the own hand along the horizontal axis (e.g., Kammers et al., 2009b; Lloyd, 2007; Riemer et al., 2014), a considerable number of studies also implemented a spatial discrepancy along the vertical axis, i.e., the artificial hand was placed *above* the participant's own hand (Azañón and Soto-Faraco, 2007; Bekrater-Bodmann

et al., 2012; Heed et al., 2011; Jenkinson and Preston, 2015; Kalckert and Ehrsson, 2012, 2014b, 2014a; Kammers et al., 2010; Ma and Hommel, 2015, 2018; Marotta et al., 2017; Pavani et al., 2000; Wen et al., 2016; Zeller et al., 2011). However, it has frequently been shown that distances in depth, i.e., along the participant's line of sight, are perceived as shorter than equivalent distances along the fronto-parallel axis (Loomis and Philbeck, 1999; Norman et al., 1996, 2015). With respect to the RHI, Snijders et al. (2007) found evidence for a different weighting of visual and proprioceptive postural information along the horizontal and the vertical axis, with the influence of vision being stronger along the horizontal axis. A vertically displaced artificial hand would therefore appear as being spatially closer to the own hand than a horizontally displaced artificial hand, and indeed, Bekrater-Bodmann et al. (2012) found higher subjective ratings of illusory hand ownership for a vertical than for a horizontal set-up. Also the measure of proprioceptive drift is influenced by the perceived distance between the seen artificial and the felt own hand (Kalckert and Ehrsson, 2014b; Preston, 2013), and it is of considerable importance to take the axis into account, along which this drift is induced and measured. Thus, assuming all other aspects discussed in the following sections as being equal, one should expect a smaller proprioceptive drift when the artificial hand is placed above rather than beside the participant's own hand, because the spatial displacement is perceived as smaller. Due to the considerably larger number of studies using a horizontal rather than a vertical displacement and due to the variety of other aspects in which they differ, a fair comparison is difficult to make, but we can note that the largest proprioceptive drift reported along the horizontal axis was about 6 cm (Kammers et al., 2009a) and only about 3 cm along the vertical axis (Wen et al., 2016). Furthermore, Riemer et al. (2019) reported age-related differences in the perception of arm length, which can influence the perceived mismatch for a vertical, but not for a horizontal displacement of the artificial hand.

One example for the importance of differentiating between vertical and horizontal RHI set-ups is given by Smit et al. (2018). In their study, they investigated the intriguing finding by Ferri et al. (2013), namely that the mere expectation of touch is sufficient to induce the RHI (i.e., in the absence of any actual touch) – a finding that challenges the generally held assumption that tactile perception is essential for the RHI to occur and which is under current debate (Ferri and Costantini, 2016; Guterstam et al., 2016, 2019). By directly comparing both set-ups, Smit et al. (2018) could show that the effect of tactile expectations occurred only in the vertical, but not the horizontal set-up, i.e., when the own and the artificial hand were aligned along the (vertical) trajectory of the approaching stimulus. However, it should be noted that, in the respective experiment of their study, Smit et al. (2018) only assessed subjective reports of perceived ownership, which were not supported by more implicit measures of the RHI. Assessing proprioceptive drift and threat-evoked skin conductance responses (cf. section 4.2 and 4.3),

Guterstam et al. (2019) found mere tactile expectations to be insufficient to induce the RHI.

Of special relevance in this regard are studies using virtual reality or mirror set-ups (cf. section 2.2), in which the spatial location of the own and the artificial hand are perfectly aligned (Bekrater-Bodmann et al., 2014; Longo et al., 2008a; Tieri et al., 2015). In these situations, experienced ownership over the artificial hand is expected to be much larger compared to a situation involving a spatial mismatch between own and artificial hands, but obviously these set-ups also prevent the quantification of the RHI via proprioceptive drift.

There are practical constraints in terms of where to place the artificial hand, and the range of locations to the side of the participant's own hand, which are still visible, is considerably larger than the range of possible locations above the own hand (Kalckert and Ehrsson, 2014b). Therefore, a smaller proprioceptive drift along the vertical axis might also be a natural consequence of an on average smaller discrepancy between the spatial locations of artificial and own hand. Along the horizontal axis, the spatial distance between artificial and own hand is usually about 15 cm (e.g., Durgin et al., 2007; Kammers et al., 2009a; Riemer et al., 2015), whereas along the vertical axis, distances of about 12 cm are most common (e.g., Heed et al., 2011; Kalckert and Ehrsson, 2012, 2014a)¹. One possibility to enhance the comparability between RHI studies and to overcome the difficulties in the interpretation of proprioceptive drift values consists in percentage values, i.e., in addition to the absolute drift (in cm), authors could provide a weighted drift value that relates the absolute drift to the actual distance between artificial and own hand (Cowie et al., 2013; Kalckert and Ehrsson, 2014b; Preston, 2013).

There seem to be spatial limits for the RHI, as the strength of the illusion decreases with increasing distance between artificial and real hand. This has been found both for displacements along the horizontal axis (Lloyd, 2007; Preston, 2013; but see Zopf et al., 2010) and the vertical axis (Kalckert and Ehrsson, 2014b). Importantly, the spatial distance rule seems to apply only for measures of proprioceptive drift and the sense of ownership over the artificial hand, whereas the sense of agency (in case of the RHI being induced by active movements) is relatively resistant to increases in spatial distance (Kalckert and Ehrsson, 2014b). This observation will be further discussed in section 4.1.

Finally, Preston (2013) suggested that the strength of the RHI depends not so much on the distance between artificial and own hand, but rather on the distance between the artificial hand and the trunk of the participant's body. Assuming a disembodiment of the own hand during the RHI, it makes sense that the distance between those parts which are experienced as belonging to the own body (i.e., artificial hand and trunk) is of greater importance than the distance between the embodied artificial hand and the disembodied own hand. According to Preston (2013), given a fixed distance between artificial and own hand, the strength of the illusion could be increased by placing the artificial hand closer to the participant's trunk. However, it should be noted that the anatomical plausibility of hand/arm posture decreases with an increasing distance between the artificial hand and the body, and that anatomical plausibility seems to be an important factor for the RHI (Ehrsson et al., 2004; Pavani et al., 2000; Tsakiris and Haggard, 2005). Nevertheless, if the assumption by Preston (2013) is to be confirmed within the limits of anatomical constraints (e.g., within reaching distance), it imposes a further important aspect of experimental RHI set-ups, which varies between studies and might be of value to explain deviating or even conflictive findings.

¹ In case of video-recorded and virtual hands displayed on a screen surface (see section 2.2), the actual height difference between artificial and own hand cannot be clearly determined. However, the perceived elevation of the seen hand has to be lower than the screen surface on which it is presented (e.g., Ma and Hommel, 2015, 2018; Wen et al., 2016).

2.2. Type of the artificial hand

The term *rubber hand illusion* already alludes to the type of the artificial hand used in the seminal study by Botvinick and Cohen (1998), but of course, the RHI does not depend on the artificial hand being made of rubber, and a variety of other types of artificial hands have been used as well (Kalckert and Ehrsson, 2012; Senna et al., 2014). Because participants do not need to touch the artificial hand during the experiment, the different materials of which the artificial hand can consist of (rubber, wood, plastic, etc.) is rather irrelevant for the illusion itself, as long as the artificial hand is unequivocally recognized as an external object that does *not* belong to the own body (Fig. 2A). However, in many studies the artificial hand was not an external object at all, but instead the mirror reflection of the participant's own contralateral hand (Fig. 2B; Holmes et al., 2006, 2004; Holmes and Spence, 2005; Longo et al., 2008a; Ro et al., 2004; Snijders et al., 2007; Tajima et al., 2015) or the video-recorded image of the ipsilateral hand (Fig. 2C; Abdulkarim and Ehrsson, 2018; Gentile et al., 2013; Kammers et al., 2009b; Longo and Haggard, 2009; Newport et al., 2010; Newport and Preston, 2010; Pavani and Zampini, 2007; Tsakiris et al., 2010a, 2006). Both the application of mirror and video images in the RHI have some important advantages compared to the use of prosthetic hands. For example, real-time video images allow the implementation of active movements, i.e., self-executed movements of the own hand can be observed at the spatially displaced video image of the hand (Kammers et al., 2009b; Tsakiris et al., 2006). Also regarding the visual similarity between artificial and own hand, both video and mirror images have clear advantages, as they capture the individual appearance of the participants' own hand, which is especially relevant for comparisons between groups of differing hand size and/or structure (e.g., young vs. old adults, Riemer et al., 2019).

However, the advantages of video and mirror images are accompanied by a larger influence of top-down processes about body ownership, potentially resulting in higher ownership ratings, because it can be assumed that most participants are very familiar with mirrors and videos and therefore are well aware that they are indeed looking at their own hand, even if it is spatially displaced (Bertamini et al., 2011; Jenkinson and Preston, 2015). As the RHI paradigm is a method to investigate the perceptual incorporation of body-extraneous objects into a representation of the own body, this difference is of fundamental importance. Mirror and video-based versions of the RHI are useful tools to investigate the bottom-up influences of visuo-tactile integration under a synchronous stroking condition, but it has to be taken into account that they trigger additional top-down influences that might boost the measured effects compared to studies using unequivocally body-extraneous, prosthetic hands (e.g., Jenkinson and Preston, 2015; Kalckert and Ehrsson, 2014a; Riemer et al., 2013). Special caution is warranted regarding some items from standard RHI questionnaires, such as "it felt like the hand I was looking at was my own hand" (e.g., Longo and Haggard, 2009) or "it felt as if the hand in the mirror was part of my body" (e.g., Tajima et al., 2015). These *it-felt-as-if*-statements are referring to something objectively true in the case of mirror reflections and video images of the own hand (participants actually *are* looking at their own hand), while they are referring to something objectively false in the case of prosthetic hands. Presumably, this difference is reflected in an elevated level of agreement reported by participants. For example, it might explain why, with respect to video-recorded hands, sometimes even the asynchronous condition results in a tendency for affirmative responses (e.g., Longo and Haggard, 2009; Tsakiris et al., 2010a), while, with respect to prosthetic hands, asynchronous touches almost always results in negative responses (e.g., Kalckert and Ehrsson, 2012, 2014a, 2014b, 2017; Kammers et al., 2009a; Riemer et al., 2013, 2014, 2015). This example highlights the importance to relate RHI scores to an adequate control condition, e.g., asynchronous stroking, rather than interpreting the absolute scores (cf. section 5.2). Nevertheless, it cannot be ruled out that the effect of

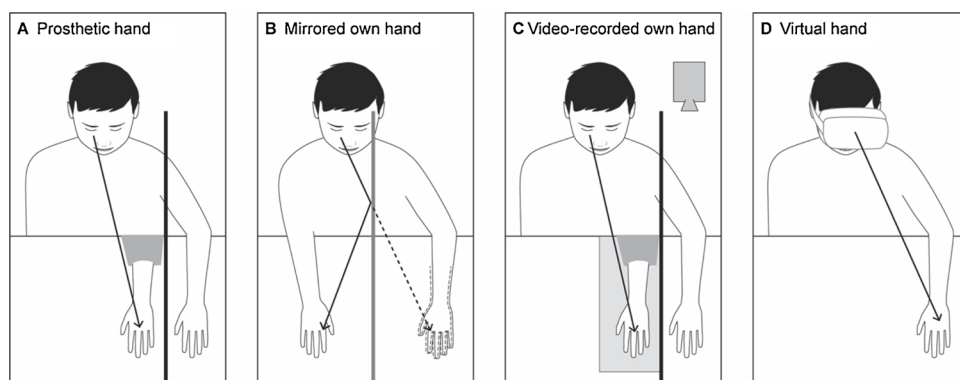


Fig. 2. Four different ways to present an artificial hand in the RHI, discussed in section 2.2. (A) The classical RHI set-up using a prosthetic hand, an unambiguously body-external object, (B) a mirror image of the own contralateral hand reflected in a parasagittally-placed mirror, (C) a video-recorded image of the own ipsilateral hand projected in front of the participant, and (D) a virtual hand displayed in virtual or augmented reality.

synchrony on subjectively reported ownership and other measures is modulated by the type of the artificial hand. To give one example, the knowledge that it actually is my own hand that I am looking at might increase my attention towards temporal asynchronies between felt and observed touches, or between executed and observed movements, respectively.

These considerations do not apply to another possibility of presenting artificial hands, provided by the development of virtual reality techniques. Virtual hands can be presented on a monitor (Farrer et al., 2003; IJsselstein et al., 2006; Ma and Hommel, 2013, 2015, 2018; Ma et al., 2017; Wen et al., 2016), as 3D projection on a screen in an augmented reality set-up (Choi et al., 2016; Perez-Marcos et al., 2009; Sanchez-Vives et al., 2010; Slater et al., 2009), or within fully immersed VR environments using a head-mounted display (Fig. 2D; Bach et al., 2012; Bekrater-Bodmann et al., 2014; Nierula et al., 2017; Tieri et al., 2015). Another advantage of virtual hands is that their appearance can be systematically varied in size, shape and skin texture, and they easily allow for the implementation of active hand movements. Top-down influences due to the knowledge about the identity of the artificial hand, as they were outlined for mirror- and video-based RHI set-ups, are therefore unlikely in VR studies. However, the use of VR in everyday life is on the rise and the familiarity with VR set-ups increases steadily, so that in future applications a similar issue has to be taken into account: In VR experiments, the participants know that their own hand *can* be in exactly the same location in which the virtual hand is seen (and most participants might even hold this assumption per default), while in studies using body-extraneous prosthetic hands, it is obviously impossible that the own hand occupies the same space as the prosthetic hand. Consequently, a comparatively larger proprioceptive drift in VR studies might partially be driven by the perceived likelihood of a location near the artificial hand, rather than on visuo-tactile or visuo-motor integration mechanisms.

It should be noted that the considerations about the type of the artificial hand do not necessarily hinder interpretations within one study (or between studies using the same set-up), but they reveal important limitations regarding the comparability between studies using different experimental set-ups.

2.3. Laterality of the artificial/own hand² and handedness

As the strength of the RHI seems to correlate with reduced attention towards sensory signals from the own hand (Zeller and Hullin, 2018), it can be speculated that the induction of the RHI might be facilitated at the non-dominant hand. In addition, bodily self-awareness has been predominantly associated with the right cortical hemisphere (for a

recent review see Blanke et al., 2015), and therefore, in right-handers, the non-dominant left hand might be more directly linked to processes affecting body ownership.

Some studies did not find substantial differences between hands (Mussap and Salton, 2006; Niebauer et al., 2002; Smit et al., 2017; Zeller and Hullin, 2018) or only side effects such as a higher relationship between proprioceptive drift and subjective ratings for the left compared to the right hand (Bertamini and O'Sullivan, 2014). However, other studies reported higher subjective ratings (Ocklenburg et al., 2011; Reinersmann et al., 2013), larger proprioceptive drifts (Dempsey-Jones and Kritikos, 2019) and increased skin conductance responses after a threat (Ocklenburg et al., 2011) for the left compared to the right hand. Niebauer et al. (2002) observed a negative relationship between the strength of hand dominance and the intensity of the illusion.

In the few studies directly addressing the role of handedness³, one found clear differences between left- and right-handers concerning the proprioceptive drift (Dempsey-Jones and Kritikos, 2019), while two did not (Ocklenburg et al., 2011; Smit et al., 2017). In line with the latter, no interaction between handedness and RHI scores were found when both left- and right-handed participants were included and the RHI was induced only at the right hand (Haans et al., 2008).

These findings suggest that there might be a small advantage for inducing the RHI in the non-dominant hand, at least in right-handed participants. For left-handers, the results are not conclusive, probably due to the fact that they form a more heterogeneous group than right-handers.

However, it should also be noted that to date no study investigated the influence of handedness on the RHI induced by active movements rather than passive touch (cf. section 3.1 on different induction methods). In contrast to the right-hemispheric dominance for bodily self-awareness, a left-hemispheric dominance has frequently been reported for motor control (Barber et al., 2012; Janssen et al., 2011; Mutha et al., 2012). Therefore, handedness might still be an important factor for the RHI induced by active movements. Interestingly, in nearly all studies implementing an active RHI induction, the illusion was induced at the right hand (one exception is Wen et al., 2016). To our knowledge, only Longo and Haggard (2009) induced the active RHI at both hands, but they did not analyse differences in the subjective report of illusion strength. Instead they found shorter reaction times (for key presses in response to visual stimuli) with the left hand, when the RHI was induced on the right hand, than vice versa. However, as pointed out by the authors, this effect might not be driven by changes in the sense of body ownership but rather by the right-hemispheric dominance for self-related stimuli (Keenan et al., 2005). Thus, the influence of handedness on the active RHI has not been explored yet.

² The studies discussed in this section should not be confused with studies investigating the anatomical congruency between the laterality of artificial and own hand, e.g., when stimulating the participant's right hand in synchrony with an artificial left hand (e.g., Holle et al., 2011; Tsakiris and Haggard, 2005).

³ Related to the question of handedness, it seems relevant which method is used to quantify proprioceptive drift (discussed in section 4.2), because it can be assumed that pointing with the non-dominant hand is less reliable than with the dominant hand.

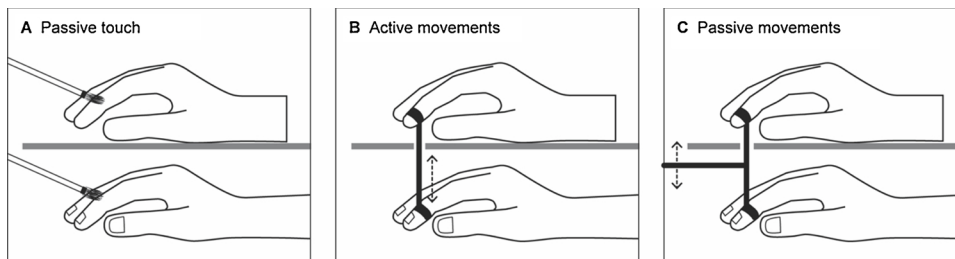


Fig. 3. Induction methods for the RHI, discussed in section 3.1. (A) Induction via tactile stimuli applied synchronously to the own and the artificial hand. (B) Induction via active movements, executed by the participant. Moving the finger of the own hand causes the same movement of the artificial hand. (C) Induction via passive movements, executed by the experimenter.

3. Induction of the RHI

Typically, RHI experiments consist in two phases. An induction phase, in which the artificial and the participant's own hand are stimulated in a synchronous vs. an asynchronous manner, and a response phase, in which the strength of the illusion is assessed (e.g., by measures of proprioceptive drift or subjective reports of ownership and/or agency). The induction phase is therefore of crucial importance, because it sets the fundament for all subsequent quantifications of RHI effects. Across studies, the induction phase differs in many ways, which might well have explanatory value for different results between studies. In the present section, we discuss differences regarding (i) the induction method, e.g., whether the RHI is induced by tactile stimulation or movements, (ii) the realization of temporal synchrony between touches at, or movements of, the artificial and the own hand, (iii) the predictability of touches/movements, (iv) properties of touches/movements, (v) the number and type of involved fingers, and (vi) the duration of the induction phase.

3.1. Method of induction

Three induction methods for the RHI can be distinguished (Fig. 3): tactile stimulation⁴ (e.g., Botvinick and Cohen, 1998), active movements⁵ (e.g., Kalckert and Ehrsson, 2012) and passive movements (e.g., Tsakiris et al., 2006). Some studies have directly compared the effects of these induction methods, revealing the quite consistent picture that proprioceptive drift and subjective reports of perceived ownership are equally affected, while a sense of agency is significantly more induced via active movements compared to passive movements and tactile stimulation (Kalckert and Ehrsson, 2012, 2014a, 2014b; Kammers et al., 2009b; Longo and Haggard, 2009; Riemer et al., 2013, 2014; Tsakiris et al., 2010a; Wen et al., 2016; but see Dummer et al., 2009). Thus, the sense of agency depends more on efferent motor signals than the sense of ownership. Tsakiris et al. (2006) suggested that induction via active movements is rather special in the sense that the resulting proprioceptive drift spreads over the entire hand, i.e., even though only one finger moved during the induction phase, other fingers are mislocalized as well. This stands in contrast to what the authors found after an induction via tactile stimulation and passive movements, where a

⁴ Recently, a new induction method based on the integration of visual and thermal stimuli has been introduced by Trojan et al. (2018), showing the same effects on perceived ownership over the artificial hand.

⁵ It should be noted that the induction method of active movements often coincides with mirrored contralateral own hands (e.g., Holmes and Spence, 2005), video-recorded ipsilateral own hands (e.g., Kammers et al., 2009b), or virtual hands (e.g., Sanchez-Vives et al., 2010) being presented as the artificial hand, the potential caveats of which have been discussed in section 2.2. This is probably due to technical issues, as the implementation of self-controlled movements of prosthetic hands imposes obvious technical obstacles. Nevertheless, in some studies active movements over prosthetic hands have been realized (Azañón and Soto-Faraco, 2007; Dummer et al., 2009; Kalckert and Ehrsson, 2012, 2014a, 2014b, 2017; Marotta et al., 2017; Riemer et al., 2013, 2014; see also Walsh et al., 2011 for presenting only an actively controlled artificial finger).

proprioceptive drift was exclusively found for the touched/moved finger (Tsakiris et al., 2006). However, this is a rather extraordinary finding which should not be taken for granted on the basis of a single study, particularly as other studies using tactile stimulation successfully measured proprioceptive drift of fingers that were not stimulated (e.g., Durgin et al., 2007; Fuchs et al., 2016). Furthermore, it should be noted that this spreading effect was associated with comparatively low drift values after induction via active movements (cf. their Fig. 2), so it seems that the comparatively larger spread (which the authors refer to as “inverse transfer” value, cf. their Fig. 3) was due to the involved finger showing a decreased rather than to the non-involved finger showing an increased drift (relative to other induction methods).

Induction via tactile stimulation and via active movements are often considered to trigger two fundamental aspects of the body, namely the body as the source of sensation, and the body as the source of action, respectively (Kalckert and Ehrsson, 2012; Kammers et al., 2009b; Riemer et al., 2013; Synofzik et al., 2008). Given that a primary and evolutionary deeply rooted function of the acting body relates to flight reflexes, it would be interesting to compare the induction methods of tactile stimulation and active movements with respect to their effects on physiological responses to bodily threats. However, though many studies included the assessment of skin conductance responses (e.g., Armel and Ramachandran, 2003; Ocklenburg et al., 2011; Riemer et al., 2015), to date no study has compared the effects of different induction methods in this regard.

When discussing the capability of different induction methods, it is important to consider some studies, in which the RHI was induced by mere visual exposure of the artificial hand (Holmes et al., 2006; Pavani et al., 2000; Schaefer et al., 2007, 2009). In these studies neither synchronous touches nor movements were presented, and yet participants reported a sense of ownership for the artificial hand (Pavani et al., 2000; Schaefer et al., 2007, 2009) or were influenced in reaching movements with their own hand (Holmes et al., 2006, 2004; Snijders et al., 2007). Although the effects of mere visual exposure are smaller than those of tactile stimulation or active movements (Azañón and Soto-Faraco, 2007; Guterstam et al., 2019; Holmes and Spence, 2005; Samad et al., 2015), these studies suggest that changes in body representations may not exclusively depend on the experience of visuo-tactile and/or visuo-motor synchrony (Ferri et al., 2013; Samad et al., 2015). As mere visual exposure has also been used as an additional control condition for RHI effects (Rohde et al., 2011), these considerations are also important for the discussion of the appropriate reference against which RHI effects should be measured (see section 5.1).

3.2. Temporal synchrony of touches/movements

Arguably the most important factor in the RHI is the synchrony between tactile stimuli at (or movements of) the artificial and the own hand (Collins et al., 2017; Costantini et al., 2016). The comparison between synchronous and asynchronous conditions is central to many studies on the RHI. However, while synchrony is clearly defined, the implementation of asynchronous or out-of-phase stimuli is open to interpretation and varies between studies. The temporal delay between stimuli in asynchronous conditions ranges from 300 ms (e.g., Bekrater-Bodmann et al., 2014) up to 2 s (e.g., Riemer et al., 2015). Furthermore,

the relation between visuo-tactile asynchrony and RHI strength seems to follow a continuous rather than a dichotomic pattern (Bekrater-Bodmann et al., 2014; Shimada et al., 2009). Franck et al. (2001) have demonstrated that visuo-motor asynchronies below 150 ms cannot be reliably detected by healthy participants, suggesting that small asynchronies in brush strokes are still perceived as synchronous. However, in the same study it was also shown that schizophrenic patients often fail to detect visuo-motor asynchronies of up to 500 ms (larger delays were not tested). As delays around this magnitude are commonly used in the asynchronous condition (e.g., Graham et al., 2014; Tsakiris, Longo, et al., 2010), this highlights the importance of using sufficiently large asynchronies when testing patient groups for which the perception of temporal asynchronies might be impaired, because generally increased RHI scores could theoretically be explained by a deficit in detecting the intended delay in asynchronous conditions as well as occasionally unintended delays in synchronous conditions. Even in healthy participants, individual differences in the temporal binding window of visuo-tactile stimuli can explain differences in the susceptibility to the RHI (Costantini et al., 2016). Maselli et al. (2016) showed that the RHI itself can influence the perception of visuo-tactile asynchronies. In their study, participants showed a dilated temporal binding window for visuo-tactile stimuli that were presented in contact with a virtual hand compared to stimuli away from the virtual hand. This dilation of the temporal binding window correlated with perceived ownership over the virtual hand. This suggests that there is a bidirectional relationship between perceived ownership and the detection of asynchronies in visuo-tactile stimulation.

3.3. Predictability of touches/movements

Studies not only vary with respect to the magnitude of the temporal delay between stimuli, but also with respect to the regularity of this delay. For example, some studies used a fixed delay (e.g., Tsakiris et al., 2006), whereas others used jittered, less predictable delays (e.g., Fuchs et al., 2016; Rohde et al., 2011). In light of current theories of predictive coding, postulating a strong link between perception and a continuous prediction of upcoming sensations (Adams et al., 2013; Clark, 2013), the predictability of tactile sensations and motor effects should have a strong influence on body representations. It should make a difference whether observed stimuli at the artificial hand are followed by a tactile sensation constantly after a fixed delay (so that the onset of each sensation can be reliably predicted), or whether the sensation follows after a random, unpredictable delay. To date, no study specifically investigated the regularity of out-of-phase touches (or movements) in the RHI. Such studies would provide important information about the asynchronous conditions, against which RHI effects are usually measured.

In contrast to the temporal domain, the role of predictability has been investigated in the spatial domain. Kammers et al. (2009b) included a mismatch condition, in which touches at the artificial index finger were always coupled with touches at the own little finger, and vice versa, and showed that this anatomical mismatch reduced the RHI. This finding highlights the importance of anatomical congruent touches. To test for an additional role of predictability of tactile and/or motor events independent from their anatomical plausibility, Riemer et al. (2014) directly compared a consistent mismatch condition with a random condition, in which the coupling between artificial and own fingers varied randomly (i.e., unpredictably alternating between congruent and incongruent mapping), and found that the RHI was affected only by the anatomical plausibility and not by the predictability of touches/movements. This observation demonstrates that the plasticity of body representations is limited and that an anatomically congruent mapping between real and artificial fingers (as opposed to a just predictable mapping) constitutes a necessary condition for the RHI, both in the passive and the active version (Riemer et al., 2014).

3.4. Properties of the tactile stimuli and type of movements

With respect to the tactile induction method, it has been shown that RHI effects are modulated by the speed of stroking. A stroking velocity of 3 cm/s, which targets a subset of somatosensory “affective touch” fibers and is usually rated as more pleasant (Essick et al., 2010), induces greater changes in subjective self-reports of ownership (Crucianelli et al., 2013; Lloyd et al., 2013; van Stralen et al., 2014) and proprioceptive drift (van Stralen et al., 2014; but see Lloyd et al., 2013) than a stroking velocity of 30 cm/s. The same effect was found for soft compared to rough stroking materials (van Stralen et al., 2014). Thus, the pleasantness of touch seems to be a critical variable that might very well differ between studies. This is especially relevant when the affective components of the RHI are in the focus of the study (e.g., Engelen et al., 2017; Riemer et al., 2015), because an experimental condition imposing a threatening or aversive situation can change the perceived pleasantness of stroking, and ultimately the RHI effects that are to be expected. A possibility to control for the effects of pleasant touch would be to include specific questionnaire items targeting the affective experience during the illusion, e.g., the affect-related items specified in Longo et al. (2008). In addition to the influence of pleasant touch, Ward et al. (2015) and Filippetti et al. (2019) reported an effect of congruency between the felt touch and the visual features of the stroking tool: Feeling the touch of a paintbrush while seeing the artificial hand being touched with a pencil reduces the illusion compared to a congruent condition (but see White et al., 2010).

Similarly, the RHI as induced by active movements might depend on the type of executed movements. In most studies, participants were instructed to perform only small movements, e.g., lifting the index finger (Kammers et al., 2009a; Riemer et al., 2013), and often are trained to move at a specific pace and/or in a specific manner (Holmes and Spence, 2005; Tsakiris et al., 2006). These imposed restrictions might well reduce the RHI effects compared to study designs allowing for a wider range of self-determined movements that involve more than one finger or even the whole hand (Dummer et al., 2009; Wen et al., 2016). Another important aspect consists in the goal-directedness of movements. For example, Wen et al. (2016) could show that the extent of proprioceptive drift, induced by self-controlled movements, further increases when the movements are directed to a specific goal. In some studies, goal-directed movements are performed during the RHI induction, without the goal-directedness being the explicit focus of investigation (e.g., Azañón and Soto-Faraco, 2007; Choi et al., 2016). This is a sound strategy, as it supposedly enhances the illusion, but nevertheless, it has to be taken into account when comparing the results with other studies in which the RHI was induced by self-controlled, yet not goal-directed movements (e.g., Holmes and Spence, 2005; Kalckert and Ehrsson, 2012; Riemer et al., 2014).

Another aspect of tactile stimuli and/or movements within the RHI paradigm consists in concurring auditory cues (e.g., tapping sounds of a moving finger). From a methodological point of view, this is an important – though often overlooked – detail, because it has recently been shown that synchronous auditory cues (i.e., in addition to synchronous visuotactile stimulation) can enhance proprioceptive drift in the RHI (Darnai et al., 2017; Radziun and Ehrsson, 2018). As in most studies it is not reported whether auditory cues were eliminated (e.g., by earplugs) or not, it is difficult to exclude this potential source of inconsistencies between studies.

3.5. Number and type of touched/moved fingers

It seems reasonable to ask how many and which fingers were involved during the RHI induction across different studies. In most studies, stimulation was restricted to one finger, most frequently the index finger (e.g., Bekrater-Bodmann et al., 2014; Kammers et al., 2009a; Riemer et al., 2013). Only few studies included three or more finger types (Bekrater-Bodmann et al., 2012; Guterstam et al., 2016; Heed

et al., 2011; Rohde et al., 2011, 2013; Samad et al., 2015; Zeller et al., 2011) and/or applied the stimulation at the back of the hand (Abdulkarim and Ehrsson, 2016; Bekrater-Bodmann et al., 2012; Durgin et al., 2007; Guterstam et al., 2018; Rohde et al., 2011, 2013). This is surprising, as the stimulation of a wider part of the skin should enhance the vividness of the illusion. Heed et al. (2011) reported the observation in preliminary tests that a combination of stroking, pressing and pinching the hands was more successful in inducing the RHI than just stroking with brushes. In another study, it was reported that the supporting effect of pleasant touch (discussed in section 3.4) is more pronounced on hairy than on glabrous skin (van Stralen et al., 2014).

3.6. Duration of the induction phase

The duration of the induction phase varies substantially between studies, ranging from only a few seconds (e.g., Holmes and Spence, 2005) up to ten minutes (e.g., Botvinick and Cohen, 1998). In light of this variety, the impression arises that the duration of the induction phase is only of minor importance, because also in studies using a very short induction phase, significant effects were reported. Nevertheless, an influence of this factor cannot be ruled out. Rohde et al. (2011) repeatedly assessed proprioceptive drift during continued tactile stimulation and observed a plateau of proprioceptive drift after about 40 s. However, in this experiment no ownership was assessed. In another study (Fuchs et al., 2016), an increase in both ownership and proprioceptive drift was observed over the course of seven RHI induction phases, suggesting that the strength of the illusion increases over time. Despite this preliminary evidence, no study directly investigated the impact of different induction durations, a gap that needs to be filled by future research. One assumption is that it requires a minimum duration of the induction phase, after which the illusion is present according to an all-or-nothing principle. However, it is also possible that the strength and the measurable effects of the illusion increase with longer induction phases.

In several studies, RHI onset times were assessed, i.e., participants were asked to indicate themselves when they first perceived a feeling of ownership over the artificial hand (e.g., Ehrsson et al., 2004; Kalckert and Ehrsson, 2017; Lane et al., 2017; Lev-Ari et al., 2015; Lira et al., 2017; Lloyd, 2007; Niebauer et al., 2002; Wold et al., 2014). The reported average onset times for the illusion, relative to the start of the induction phase, vary from 10 (Ehrsson et al., 2004) to about 110 s (Lane et al., 2017). This wide range of reported illusion onset times between studies might well be caused by the exclusion/inclusion of non-responders (i.e., participants who do not perceive the RHI at all; see section 5.3). Studies reporting onset times of around 10 s usually preselected participants and excluded non-responders (e.g., Ehrsson et al., 2004; Kalckert and Ehrsson, 2017; Lloyd, 2007). When non-responders are included in the calculation of mean onset times, the resulting value clearly depends on the maximal duration of the induction phase (e.g., Lane et al., 2017). Moreover, naïve participants, experiencing the RHI for the first time, might be more reluctant with their response and wait longer (i.e., until they are sure that the illusion will not get stronger) than participants who are familiar with the RHI.

Although the approach to assess the time to experience the illusion reveals important information regarding the subjective experience of the RHI, the latter does not necessarily coincide with more implicit measures as proprioceptive drift and skin conductance responses. Especially for proprioceptive drift, considerably shorter durations of induction have been shown to be effective (Holmes and Spence, 2005, 2006).

4. Quantification of RHI effects

In order to quantify the RHI effects, various techniques have been developed and studies differ in the extent to which they make use of

these techniques. Amongst these assessment techniques are (i) retrospective self-reports regarding the phenomenal experience during the induction phase, (ii) proprioceptive drift of the own hand towards the artificial hand, (iii) physiological responses and other techniques. In this section we will discuss how the results in RHI studies can depend on the chosen measure to assess the effects.

4.1. RHI questionnaires

A widely used strategy to quantify the strength of the RHI is to assess retrospective judgments regarding the participants' experience during the induction phase. RHI questionnaires usually consist of target items, targeting the perceived sense of embodiment and/or agency over the artificial hand, and control items, which are related to other experiences (see Longo et al., 2008b, for an extensive analysis of RHI questionnaire items). Agreement to RHI statements is usually given on Likert scale consisting of 7 or 10 levels. While the number of levels might be less relevant, it is an important difference whether the scale range covers only positive numbers (e.g., from 1 to 7; Heed et al., 2011; Riemer et al., 2013; Slater et al., 2008) or extends to negative numbers (e.g., from -3 to 3; Holmes et al., 2006; Kammers et al., 2011; Rohde et al., 2011). The zero level can easily be interpreted as the "neutral" response and function as an anchor for the participants' judgments. This does not interfere with the conclusions drawn within a given study, but it complicates the comparison between studies using different scales. Even if identical labels are attached to the scale (e.g., "strongly agree", "neither agree nor disagree" and "strongly disagree"), a value of 4 judged on a 1 to 7 scale might not be the same as a value of 0 judged on a -3 to 3 scale.

Another often neglected issue with RHI questionnaires relates to the comparability between items targeting the sense of ownership vs. the sense of agency. Ideally, they should be analogous, but often there is a very fundamental difference between ownership items (e.g., "it felt as if the artificial hand was my hand") and agency items (e.g., "it felt as if I caused the movements I saw at the artificial hand"), namely that the ownership statement refers to an obviously illusory experience, i.e., participants know that the artificial hand does not really belong to their body and that it just *feels as if*, while the agency statement refers to an objectively true fact: Participants indeed *did* cause the movements of the artificial hand. This might, for example, explain why the sense of agency was sometimes found to be independent from an anatomically plausible posture, while the sense of ownership vanishes for unplausible hand postures (Kalckert and Ehrsson, 2012, 2014b; Marotta et al., 2017): It simply is true, for the unplausible as well as for the plausible posture, that the participants are controlling the movements of the artificial hand.

It also explains differences in agency ratings between studies using statements referring to something objectively true (e.g., "I felt as if I was controlling the movements of the artificial hand" in Kalckert and Ehrsson, 2012) vs. statements referring to something objectively false (e.g., "it seemed like I could grab something with the artificial hand" in Riemer et al., 2014).

4.2. Proprioceptive drift

Proprioceptive drift, i.e., an illusory shift of the felt location of the own hand towards the artificial hand, can be assessed via perceptual and motor responses. The distinction between perceptual and motor responses are closely related to the distinction between the concepts of body image and body schema (Gallagher, 2005; Head and Holmes, 1911; Kammers et al., 2009a, b; Paillard, 1999; Riemer et al., 2013). According to Gallagher (2005), the body image consists in a set of conscious perceptions and attitudes towards the own body, while the body schema is defined as an implicit reference for the execution and guidance of spontaneous movements. This dissociation is based on and

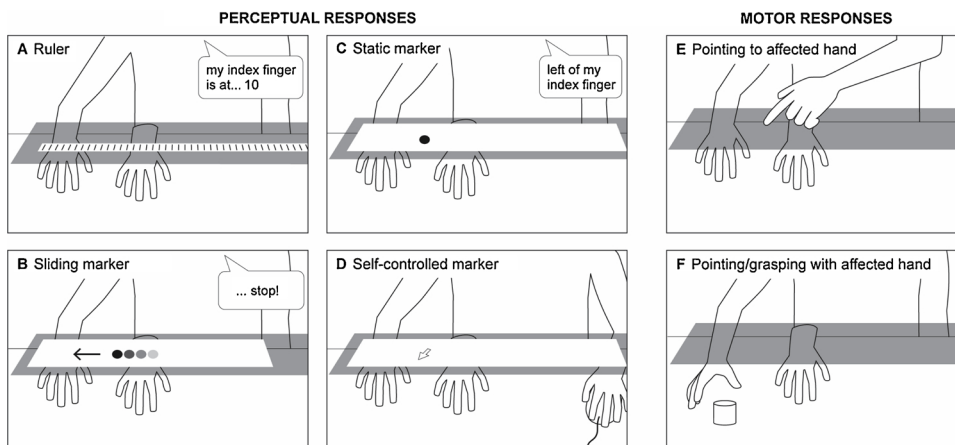


Fig. 4. Assessment methods for proprioceptive drift, discussed in section 4.2. (A) The participant names the number on a ruler that is perceived as directly above the own index finger, hidden under an occluding board. (B) A visual marker moves along the horizontal axis and the participant indicates when it has reached the position above the own index finger. (C) Visual markers are presented in randomized locations above the own hand and the participant indicates whether each marker is presented to the right or to the left of the own index finger. (D) The participant moves a projected mouse cursor to the position above the own index finger. (E) The participant points with the non-affected hand to the perceived position of the index finger of the affected hand (pointing movements can also be performed from under the table, e.g., Botvinick and Cohen, 1998), or (F) uses the affected hand to grasp or point towards a visible external object.

supported by clinical case reports (Buxbaum and Coslett, 2001; Head and Holmes, 1911; Paillard, 1999) and observations in healthy participants (Cardinali et al., 2011; Kammers et al., 2009a, 2006; Riemer et al., 2013). Within the scope of the RHI, effects on body image and body schema have been differentiated by the implementation of perceptual vs. motor tasks to determine the perceived location of the own hand (Kammers et al., 2009a, b; Kammers et al., 2006; Riemer et al., 2013).

With respect to perceptual responses, four main techniques can be differentiated (Fig. 4A–D)⁶. First, the ruler technique, where a ruler is placed above the participants' unseen own hand. Participants are asked to verbally indicate the number which is directly above their own index finger (e.g., Riemer et al., 2015; Tsakiris and Haggard, 2005; Zopf et al., 2010). Second, the sliding marker technique, where a visual marker slowly moves along a straight line, perpendicular to the participants' unseen own hand. Participants are asked to verbally indicate, when the marker is directly in front of their own index finger (e.g., Kammers et al., 2009a; Smit et al., 2017). Third, the static marker technique, where a series of single marker points are presented in slightly varying locations above the participants' unseen own hand. Participants are asked to indicate for each single marker point, whether it is left or right of their own index finger (e.g., Riemer et al., 2013, 2014; Rohde et al., 2011). In a fourth technique, participants navigate the cursor of a computer mouse (projected onto a nontransparent surface above their own hand) to indicate the location of their own hand (e.g., Riemer et al., 2019; Samad et al., 2015). In addition to proprioceptive drift along the lateral axis, this procedure also enables the assessment of proprioceptive drift along the in-depth axis (Riemer et al., 2019).

Motor responses usually consist in ballistic pointing or grasping movements either with the contralateral towards the felt location of the ipsilateral hand (Fig. 4E; e.g., Abdulkarim and Ehrsson, 2016; Fuchs et al., 2016; Kalckert and Ehrsson, 2014b; Kammers et al., 2009a; Riemer et al., 2013), or with the ipsilateral hand towards an external target (Fig. 4F; e.g., Heed et al., 2011; Holmes et al., 2006; Kammers et al., 2009b; Newport et al., 2010; Zopf et al., 2011). In the first case, the perceived position of the unseen own hand is directly reflected in the indicated position, and in the second case, it can be inferred on the basis of systematic reaching errors.

In addition to the acknowledged differences between the basic categories of perceptual and motor responses (Kammers et al., 2009a, b;

⁶ Detailed descriptions of the single techniques are beyond the scope of this paper. We therefore refer to the mentioned exemplary studies.

Riemer et al., 2013), there might also be differences between the various techniques within each of these categories. For example, there currently is an inconsistency in the scientific literature as to whether proprioceptive drift is correlated with ownership ratings (Rohde et al., 2011). However, taking into account the different techniques to assess proprioceptive drift reveals that studies reporting a correlation between proprioceptive drift and ownership ratings used pointing movements with the contralateral towards the ipsilateral hand (Bertamini and O'Sullivan, 2014; Botvinick and Cohen, 1998; Kalckert and Ehrsson, 2012, 2014a; static condition of experiment 2 in Abdulkarim and Ehrsson, 2016⁷), while studies employing different techniques did not find such a correlation (Holle et al., 2011; Holmes et al., 2006; Riemer et al., 2015, 2019; Rohde et al., 2011)⁸. Thus, the body representation underlying subjective ownership ratings seems to be similar to that which is accessed when the ipsilateral hand is the target of a ballistic pointing movement, while other behaviours seem to be based on different representations.

It is also important to consider the phrasing of task instructions. Tamè et al. (2018) pointed out that, while RHI questionnaire items almost always use an *it-feels-as-if* phrasing (cf. section 4.1), the instructions regarding proprioceptive drift are more variable between studies. In some studies, participants were asked to indicate *where their index finger was* (e.g., Tsakiris and Haggard, 2005), while in other studies they were asked *where they felt it to be* (e.g., Longo et al., 2008a). By directly comparing these different phrasings, Tamè et al. (2018) could show that the difference of proprioceptive drift between synchronous and asynchronous stroking conditions was not affected, but that the overall measured drift was considerably larger when participants indicated their feeling rather than their belief. However, it should be noted that Tamè et al. (2019) used a within-subjects design, and the explicit announcement of both task settings (subjective experience vs. objective beliefs) might well have led their participants to conclude that they should respond differently to the different phrasing types.

⁷ In other experimental conditions, Abdulkarim and Ehrsson (2016) systematically implemented movements of the own hand, resulting in a reduction of synchrony-induced proprioceptive drift, which makes it difficult to interpret the (non-significant) correlations with ownership ratings.

⁸ Asai et al. (2011) reported a correlation between RHI ratings and proprioceptive drift assessed with the ruler technique, but they averaged over all questionnaire items, including mainly items targeting perceived movement instead of perceived ownership (cf. Longo et al., 2008b). For the problem of differentiating between “illusion” and “control” items see section 5.2.

4.3. Physiological responses and other techniques

Various other methods to quantify RHI effects have been employed. In several studies, increased skin conductance responses were measured after a threat directed towards the artificial hand⁹, e.g., by forcibly bending back a finger (Armell and Ramachandran, 2003), by making brisk stabbing movements with a sharp object (Ehrsson et al., 2007; Ocklenburg et al., 2011; Reinersmann et al., 2013), or by actually stabbing the artificial hand (Ehrsson et al., 2008; Ma and Hommel, 2013; Trieri et al., 2015). In other studies, the skin temperature (Hohwy and Paton, 2010; Kammers et al., 2011; Moseley et al., 2008; Rohde et al., 2013; van Stralen et al., 2014) or histamine reactivity (Barnsley et al., 2011) of the own hand was measured as an indicator of an illusory disembodiment of the own hand during the RHI. However, while Moseley et al. (2008), who were the first to report a temperature drop in the RHI, replicated this effect within their series of experiments, most other studies reported less consistent results (Hohwy and Paton, 2010; van Stralen et al., 2014) and suggested that the temperature drop depends on factors such as the exact type of stroking (van Stralen et al., 2014) or even on factors previously considered as irrelevant for the RHI itself, e.g., the presence of another person and/or the pressure of tactile stimuli (Rohde et al., 2013). A recent study reports a lack of reproducibility and sheds serious doubt on the validity of the cooling-effect (de Haan et al., 2017). Finally, della Gatta et al. (2016) showed that the embodiment of an artificial hand coincides with a reduced excitability of the corresponding hand area in the primary motor cortex (M1). However, also in this case, another study failed to replicate this finding (Karabanov et al., 2017), and Isayama et al. (2019) did not find a difference in afferent inhibitory responses between synchronous and asynchronous stroking conditions.

Another approach consists in the analysis of the kinematic characteristics of goal-directed movements performed after the RHI is induced. For example, Kammers et al. (2010) used artificial hands with different grip apertures (distance between thumb and index finger) and measured whether their participants adapted their own unseen grip aperture accordingly when grasping an object (see also Heed et al., 2011). In another study, Kammers et al., 2009a analysed the duration and the velocity of pointing movements. Other methods comprise the analysis of crossmodal congruency effects (Pavani et al., 2000; Zopf et al., 2010) and temporal order judgments (Azañón and Soto-Faraco, 2007). However, due to the small number of studies using these techniques, it remains difficult to judge to which extent they reflect effects also found with more common measurement methods or actually highlight additional facets of the RHI.

5. Experimental design and data analysis

Even assuming a similar experimental set-up, a comparable induction method and an equivalent quantification technique for the same dependent variable, RHI studies often differ in their employed baseline measures and control conditions against which the effects are referenced. Furthermore, different exclusion/inclusion criteria are applied to define the investigated sample. These differences are considered in the present section. We will discuss (i) the choice of an appropriate control condition, (ii) the choice of appropriate control items in RHI questionnaires, and (iii) the application of exclusion criteria and handling of “nonresponders”.

⁹ It should be noted that increased skin conductance responses have also been reported for non-aversive stimuli (Ferri et al., 2013) and for aversive stimuli not specifically directed towards the artificial hand (Riemer et al., 2015), suggesting that the RHI generally induces a state of increased physiological arousal.

5.1. Choice of control conditions

The choice of an adequate control condition is elementary to the experimental design (Fig. 5). Generally, the goal is to keep all factors between experimental and control conditions constant apart from one experimental factor. In the case of the RHI the aim is to manipulate the factor embodiment such that the artificial hand is embodied in the experimental condition but not in the control condition. Botvinick and Cohen (1998) introduced the commonly used control condition of asynchronous tactile stimulation. The asynchronous condition is elegant as it keeps the visual and the tactile stimulation applied to the artificial hand identical to the synchronous condition and only varies the timing of the tactile input to the hidden real hand. However, it should be noted that the asynchronous condition might be doing more than merely *not* leading to embodiment, because it generates incongruency of visuotactile input (Valenzuela Moguillansky et al., 2013), which can induce different illusory sensations and feelings of discomfort. In some studies, incongruency between felt and seen movements has been reported as unpleasant or associated with illusory sensations on the skin or distortions in body perception (Foell et al., 2013; McCabe et al., 2005).

Some studies have also shown systematic effects of the asynchronous condition compared to alternative control conditions. Rohde et al. (2011) observed weaker proprioceptive drift in the asynchronous condition compared to a condition using just a visual presentation of a hand without tactile stimuli and argued that the asynchronous condition actively *prevents* embodiment. Fuchs et al. (2016) compared both the synchronous and the asynchronous condition to a condition without an artificial hand and observed that in the asynchronous condition both ownership ratings and proprioceptive drift increased over time. Effects of the asynchronous condition on proprioceptive drift (compared to a pretest baseline assessment) have also been reported (e.g., Riemer et al., 2014). Notably, some studies also found a negative drift after asynchronous stimulation, i.e., away from the artificial hand compared to a pretest (Kalckert and Ehrsson, 2014b, 2014a; Riemer et al., 2013).

In addition, it can be pointed out that there is a high variability in the participants' reactions to the asynchronous condition. In some RHI studies, the asynchronous condition has led to relatively high ratings of perceived ownership as well, at least for some participants (e.g., Costantini et al., 2016; Fuchs et al., 2016; Valenzuela Moguillansky et al., 2013). Recently, Costantini et al. (2016) showed that responding to the asynchronous condition is associated with a wider temporal binding window for visuotactile stimuli, giving a partial explanation for embodiment despite asynchronous stimulation (see section 3.2).

Furthermore, other control conditions have been used that prevent or reduce perceived ownership, for example substituting the artificial hand with non-corporeal objects such as wooden blocks (e.g., Tsakiris et al., 2010b) or cardboard boxes (Hohwy and Paton, 2010). Other studies have used hands in anatomically implausible or impossible postures, for example rotated by 180° (e.g., Ehrsson et al., 2004). Hand similarity and anatomical plausibility has often been considered as a prerequisite for embodiment according to the idea that a hand or non-hand object is compared to an internal body model and multisensory integration only occurs with objects matching the body model (Tsakiris, 2010). It should be noted, however, that this idea is under debate and that it is possible that mere bottom-up sensory correlation can be sufficient to induce embodiment of non-corporeal objects at least under certain conditions (for a discussion see Kilteni et al., 2015; Litwin, 2018). For example, Guterstam et al. (2013) reported that the artificial hand (whether anatomically plausible or not) does not have to be visible at all to induce a feeling of ownership (in this special case over a discrete volume of empty space).

Taken together, the asynchronous control condition, although elegantly keeping visuotactile stimulation constant and reliably leading to lower levels of ownership, might at least in some participants cause effects that are not yet sufficiently understood. Other control conditions

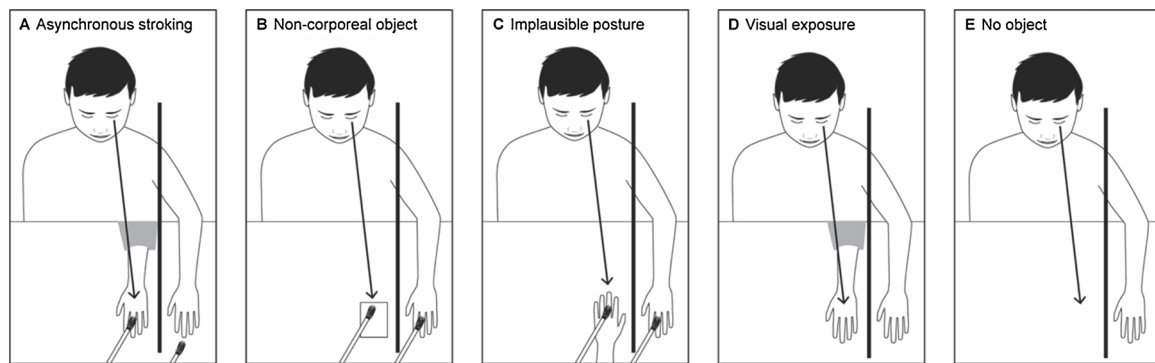


Fig. 5. Control conditions in the RHI, discussed in section 5.1. (A) Tactile stimuli at the own and the artificial hand are applied in temporal asynchrony. (B) Tactile stimuli are applied synchronously to the own hand and to a non-corporeal object. (C) The artificial hand is positioned in an anatomically implausible posture. (D) The artificial hand is presented in the absence of any stimulation. (E) Neither artificial hand nor object is presented, and no stimuli are delivered.

that present synchronous stimulation to non-hand objects or hands in unplausible postures are alternatives but are also under debate because it is not warranted that they do not lead to embodiment of the object. Hence, there does not seem to be a perfect control condition in the RHI. Some studies have included several additional control conditions, for example, presentation of a hand without applying tactile stimuli (Rohde et al., 2011) or not presenting a hand at all (Fuchs et al., 2016). The use of several control conditions allows quantifying effects of both the synchronous and the asynchronous condition separately which can increase our understanding of the effects of synchrony in the RHI.

5.2. Control items in RHI questionnaires

Botvinick and Cohen (1998) introduced a set of nine questionnaire items, assessing various phenomenological aspects of the RHI (see section 4.1) but they stated that only three of them capture the phenomena they had predicted, i.e., referral of felt touch to the artificial hand, and body ownership. Many studies have adapted (and extended) this original questionnaire, but whether and how the single items were grouped and analysed is extremely inconsistent. In some studies, items were divided into target and control items, the latter of which are argued to be unspecific or even to assess suggestibility (e.g., Bekrater-Bodmann et al., 2014; Ehrsson et al., 2005), while in other studies an average score was computed over all items irrespective of whether they are usually classified as target or control items (e.g., Asai et al., 2011). Most studies, however, computed RHI scores (the average of target items) and control item scores both for the synchronous and the asynchronous condition (Ehrsson et al., 2004, 2008; Preston, 2013; Suzuki et al., 2013). The classification into target and control items slightly varies between studies. For example, Botvinick and Cohen (1998) defined three items as relevant, Preston (2013) used four items to calculate an illusion score, and Ehrsson et al. (2004) used two. Other studies have created subsets of items and aggregated them to reflect certain categories, for example, body ownership, agency, and control (e.g., Kalckert and Ehrsson, 2012; Riemer et al., 2014) or ownership, location and control/compliance (Walsh et al., 2015).

It is remarkable that the use of control items has become common practice although empirical support justifying this practice is lacking. There is neither a psychometric examination of whether the “control items” are adequate to assess suggestibility nor of whether they are indeed unspecific. To the contrary, Longo et al. (2008b) qualitatively analysed free reports in five pilot participants and generated an item pool of 27 items that were applied in a large sample ($N = 130$) and subsequently fed into a principal component analysis to detect the dimensionality of the questionnaire data. This analysis showed that even allegedly unspecific items (e.g., “the rubber hand began to resemble my own hand”; Botvinick and Cohen, 1998) were actually strongly

correlated with the factor “embodiment” and are therefore not unspecific (Longo et al., 2008b). Hence, subtracting these items from “embodiment” items might also subtract meaningful variance (e.g., Radziun and Ehrsson, 2018).

Since the study by Longo et al. (2008b), many “hybrid” questionnaires have been used that combine items from this study and Botvinick and Cohen (1998). Some studies choose a large selection from Longo et al. (2008) in order to represent their principal components (e.g., Ferri et al., 2013), while others choose specific items to represent certain categories of interest, for example, embodiment and dis-embodiment (Lane et al., 2017).

In conclusion, there is great variation in terms of the chosen questionnaire items to assess the subjective experience of the RHI. One study hardly resembles the other. On the other hand, certain items clearly targeting body ownership (e.g., “it seemed like the rubber hand was my hand”) have been used in almost every study. When comparing results from RHI studies, the choice of questionnaire items and aggregation level needs to be carefully considered.

5.3. Sampling biases and exclusion of “nonresponders”

Not every person is susceptible to the RHI and almost every study includes “nonresponders”, i.e., participants whose judgments (verbally and/or indirect via proprioceptive drift) are not influenced by the synchrony of stimulation. For example, Ehrsson et al. (2004) reported a rate of 28% (7 out of 25) nonresponders among their healthy participants and Kalckert and Ehrsson (2014a) a rate of 23% (9 of 40). It has not been clarified why some people respond to the RHI whereas others do not. Some studies have tried to explain this variance using personality traits, such as empathy and schizotypy (Asai et al., 2011), sensory suggestibility (Marotta et al., 2016; Walsh et al., 2015), bodily awareness (David et al., 2014) and differences in multisensory integration mechanisms (Costantini et al., 2016), but found only weak correlations with phenomenological self-reports in the RHI.

Despite this being an interesting question in itself, the rate of non-responders between studies and the method to deal with this issue impacts their comparability. In most studies, nonresponders were not excluded and analyses have to be carried out with caution to the skewedness of the distributions, as low rating values tend to be over-represented. In several studies, however, nonresponders were removed based on questionnaire cut-off criteria (Durgin et al., 2007; Wold et al., 2014). Ehrsson et al. (2004) conducted a pre-test to select participants before their testing session and did not invite participants that have been found to be unsusceptible to the RHI. A similar strategy was used by Trojan et al. (2018) who selected participants based on a criterion of sufficient difference in ownership ratings between synchronous and asynchronous stroking. In spite of the importance of these selection

procedures, most often these crucial exclusion criteria are only briefly mentioned without further consideration when the results are compared to other studies.

To conclude, although the exclusion of nonresponders can be – depending on the research question – a valid approach, it highly influences the results and impairs their comparability to studies applying no such exclusion criteria. It should also be noted that a classification of participants into responders and nonresponders is usually based on phenomenological self-reports and not on behavioural measures as proprioceptive drift. Given the relatively low correlation between these measures (see section 4.2) it is possible that participants classified as nonresponders based on questionnaire data nonetheless react to the RHI on a different measure.

6. Conclusions

In the present article, we discussed differences between studies on the RHI, which are related to the experimental set-up, the method used to induce the illusion, the quantification of effects, the design of the study and approaches for data preprocessing. Many of these differences impede a direct comparison between studies and are crucial to understand apparent inconsistencies in the scientific literature. Of course, a comparison between different studies using the RHI paradigm is necessary, and therefore it is important to be aware of the various aspects which might differ between studies and about the potential impact these differences might bear on the observed results. Based on the reviewed literature, we summarize a few recommendations for the implementation of future studies as well as for the interpretation of past studies.

First, it is important to take into account the spatial arrangement and the type of the artificial hand (i.e., prosthetic, mirrored, video-recorded or virtual), because these factors can differ in the degree to which top-down processes are evoked. Especially for the research on body representations and the sense of ownership over body-extraneous objects, it is essential to consider our prior knowledge about bodies, mirrors and video images. Video-recorded and mirrored own hands are conceptually different from prosthetic hands or other unequivocally body-extraneous objects, and it should be expected that they result in much higher embodiment scores.

Second, various factors during the induction phase can influence the magnitude of the observed effects. While some of them are quite prominent and are widely acknowledged as leading to different effects (e.g., whether the RHI is induced via passive tactile stimulation or via active movements), others are more subtle and their impact on the results is less clear (e.g., the duration of the induction phase, the type and number of involved fingers, and the implementation of temporal synchrony/asynchrony).

Third, the common measure of proprioceptive drift can be quantified by means of very different techniques, some of which are more and some less prone to reflect specific aspects of the RHI. Even within the category of motor responses, pointing towards the own hand (on which the illusion is induced) and pointing with it seems to have different effects regarding the correlation between proprioceptive drift and perceived ownership.

Fourth, it is rather the rule than an exception that RHI data are analysed very differently between studies. Questionnaire ratings sometimes refer to an average of all items without differentiation between control and target items (e.g., Asai et al., 2011), and sometimes they refer only to items loading on the factor body ownership (Longo et al., 2008b), which in turn are sometimes referenced against control items (e.g., Ehrsson et al., 2005) and sometimes stand for themselves (e.g., Palomo et al., 2018). Furthermore, in some studies nonresponders were removed before the data were analysed (e.g., Wold et al., 2014), whereas in others the complete set of participants entered the analysis.

All these differences explain the great variability in the results found between RHI studies. For a thorough integration of the knowledge

gathered in the scientific literature, an important basis is to be aware of the various differences between studies and of the impact they might have on the results.

Declaration of Competing Interest

None

References

- Abdulkarim, Z., Ehrsson, H.H., 2016. No causal link between changes in hand position sense and feeling of limb ownership in the rubber hand illusion. *Atten. Percept. Psychophys.* 78 (2), 707–720.
- Abdulkarim, Z., Ehrsson, H.H., 2018. Recalibration of hand position sense during unconscious active and passive movements. *Exp. Brain Res.* 236, 551–561.
- Adams, R.A., Shipp, S., Friston, K.J., 2013. Predictions not commands: active inference in the motor system. *Brain Struct. Funct.* 218 (3), 611–643.
- Armell, K.C., Ramachandran, V.S., 2003. Projecting sensations to external objects: evidence from skin conductance response. *Proceedings of the Royal Society B: Biological Sciences* 270, 1499–1506.
- Asai, T., Mao, Z., Sugimori, E., Tanno, Y., 2011. Rubber hand illusion, empathy, and schizotypal experiences in terms of self-other representations. *Conscious. Cogn.* 20 (4), 1744–1750.
- Azañón, E., Soto-Faraco, S., 2007. Alleviating the “crossed-hands” deficit by seeing uncrossed rubber hands. *Exp. Brain Res.* 182 (4), 537–548.
- Bach, F., Çakmak, H., Maaß, H., Bekrater-Bodmann, R., Foell, J., Diers, M., et al., 2012. Illusory hand ownership induced by an MRI compatible immersive virtual reality device. *Biomedizinische Technik* 57 (SUPPL. 1 TRACK-L), 718–720.
- Barber, A.D., Srinivasan, P., Joel, S.E., Caffo, B.S., Pekar, J.J., Mostofsky, S.H., 2012. Motor “dexterity”: evidence that left hemisphere lateralization of motor circuit connectivity is associated with better motor performance in children. *Cereb. Cortex* 22 (1), 51–59.
- Barnsley, N., McAuley, J.H., Mohan, R., Dey, A., Thomas, P., Moseley, G.L., 2011. The rubber hand illusion increases histamine reactivity in the real arm. *Curr. Biol.* 21 (23), R945–R946.
- 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 Res.* 1452, 130–139.
- Bekrater-Bodmann, R., Foell, J., Diers, M., Kamping, S., Rance, M., Kirsch, P., et al., 2014. The importance of synchrony and temporal order of visual and tactile input for illusory limb ownership experiences - an fMRI study applying virtual reality. *PLoS One* 9 (1), e87013.
- Bertamini, M., Berselli, N., Bode, C., Lawson, R., Wong, L.T., 2011. The rubber hand illusion in a mirror. *Conscious. Cogn.* 20 (4), 1108–1119.
- Bertamini, M., O’Sullivan, N., 2014. The use of realistic and mechanical hands in the rubber hand illusion, and the relationship to hemispheric differences. *Conscious. Cogn.* 27 (1), 89–99.
- Blanke, O., Slater, M., Serino, A., 2015. Behavioral, neural, and computational principles of bodily self-consciousness. *Neuron* 88 (1), 145–166.
- Botvinick, M., Cohen, J., 1998. Rubber hands “feel” touch that eyes see. *Nature* 391, 756.
- Buxbaum, L.J., Coslett, H.B., 2001. Specialised structural descriptions for human body parts: evidence from autotopagnosia. *Cogn. Neuropsychol.* 18 (4), 289–306.
- Cardinali, L., Brozzoli, C., Urquizar, C., Saleme, R., Roy, A.C., Farnè, A., 2011. When action is not enough: tool-use reveals tactile-dependent access to Body Schema. *Neuropsychologia* 49 (13), 3750–3757.
- Choi, W., Li, L., Satoh, S., Hachimura, K., 2016. Multisensory integration in the virtual hand illusion with active movement. *Biomed Res. Int.* 2016.
- Clark, A., 2013. Whatever next? Predictive brains, situated agents, and the future of cognitive science. *Behav. Brain Sci.* 36 (3), 181–204.
- Collins, K.L., Guterstam, A., Cronin, J., Olson, J.D., Ehrsson, H.H., Ojemann, J.G., 2017. Ownership of an artificial limb induced by electrical brain stimulation. *Proc. Natl. Acad. Sci.* 114 (1), 166–171.
- Costantini, M., Robinson, J., Migliorati, D., Donno, B., Ferri, F., Northoff, G., 2016. Temporal limits on rubber hand illusion reflect individuals’ temporal resolution in multisensory perception. *Cognition* 157, 39–48.
- Cowie, D., Makin, T.R., Bremner, A.J., 2013. Children’s responses to the rubber-hand illusion reveal dissociable pathways in body representation. *Psychol. Sci.* 24 (5), 762–769.
- Crucianelli, L., Metcalf, N.K., Fotopoulou, A., Jenkinson, P.M., 2013. Bodily pleasure matters: velocity of touch modulates body ownership during the rubber hand illusion. *Front. Psychol.* 4, 703.
- Darnai, G., Szolcsányi, T., Hegedüs, G., Kincses, P., Kállai, J., Kovács, M., Simon, E., Nagy, Z., Janszky, J., 2017. Hearing visuo-tactile synchrony - Sound-induced proprioceptive drift in the invisible hand illusion. *Br. J. Psychol.* 108, 91–106.
- David, N., Fiori, F., Aglioti, S.M., 2014. Susceptibility to the rubber hand illusion does not tell the whole body-awareness story. *Cogn. Affect. Behav. Neurosci.* 14 (1), 297–306.
- de Haan, A.M., Van Stralen, H.E., Smit, M., Keizer, A., Van der Stigchel, S., Dijkerman, H.C., 2017. No consistent cooling of the real hand in the rubber hand illusion. *Acta Psychol. (Amst)* 179, 68–77.
- de Preester, H., Tsakiris, M., 2009. Body-extension versus body-incorporation: Is there a need for a body-model? *Phenomenol. Cogn. Sci.* 8 (3), 307–319.
- della Gatta, F., Garbarini, F., Puglisi, G., Leonetti, A., Berti, A., Borroni, P., 2016. Decreased motor cortex excitability mirrors own hand disembodiment during the

- rubber hand illusion. *eLife* 5, 1–14.
- Dempsey-Jones, H., Kritikos, A., 2019. Handedness modulates proprioceptive drift in the rubber hand illusion. *Exp. Brain Res.* 237, 351–361.
- Dummer, T., Picot-Annand, A., Neal, T., Moore, C., 2009. Movement and the rubber hand illusion. *Perception* 38 (2), 271–280.
- Durgin, F.H., Evans, L., Dunphy, N., Klostermann, S., Simmons, K., 2007. Rubber hands feel the touch of light. *Psychol. Sci.* 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. *J. Neurosci.* 25 (45), 10564–10573.
- Ehrsson, H.H., Rosén, B., Stockselius, A., Ragnö, C., Köhler, P., Lundborg, G., 2008. Upper limb amputees can be induced to experience a rubber hand as their own. *Brain* 131 (12), 3443–3452.
- Ehrsson, H.H., Spence, C., Passingham, R., 2004. That's my hand! Activity in premotor cortex reflects feelings of ownership of a limb. *Science* 305 (6), 875–877.
- Ehrsson, H.H., Wiech, K., Weiskopf, N., Dolan, R.J., Passingham, R.E., 2007. Threatening a rubber hand that you feel is yours elicits a cortical anxiety response. *Proc. Natl. Acad. Sci.* 104 (23), 9828–9833.
- Engelen, T., Watson, R., Pavani, F., de Gelder, B., 2017. Affective vocalizations influence body ownership as measured in the rubber hand illusion. *PLoS One* 12 (10), e0186009.
- Essick, G.K., McGlone, F., Dancer, C., Fabricant, D., Ragin, Y., Phillips, N., et al., 2010. Quantitative assessment of pleasant touch. *Neurosci. Biobehav. Rev.* 34 (2), 192–203.
- Farrer, C., Franck, N., Georgieff, N., Frith, C.D., Decety, J., Jeannerod, M., 2003. Modulating the experience of agency: a positron emission tomography study. *NeuroImage* 18 (2), 324–333.
- Ferri, F., Chiarelli, A.M., Merla, A., Gallese, V., Costantini, M., 2013. The body beyond the body: expectation of a sensory event is enough to induce ownership over a fake hand. *Proceedings of the Royal Society B: Biological Sciences* 280 20131140.
- Ferri, F., Costantini, M., 2016. Commentary: the magnetic touch illusion: a perceptual correlate of visuo-tactile integration in peripersonal space. *Front. Hum. Neurosci.* 10, 492.
- Filippetti, M.L., Kirsch, L.P., Crucianelli, L., Fotopoulou, A., 2019. Affective certainty and congruency of touch modulate the experience of the rubber hand illusion. *Sci. Rep.* 9, 2635.
- Foell, J., Bekrater-Bodmann, R., McCabe, C.S., Flor, H., 2013. Sensorimotor incongruence and body perception: an experimental investigation. *Front. Hum. Neurosci.* 7, 310.
- Franck, N., Farrer, C., Georgieff, N., Marie-Cardine, M., Daléry, J., D'Amato, T., Jeannerod, M., 2001. Defective recognition of one's own actions in patients with schizophrenia. *Am. J. Psychiatry* 158 (3), 454–459.
- Fuchs, X., Riemer, M., Diers, M., Flor, H., Trojan, J., 2016. Perceptual drifts of real and artificial limbs in the rubber hand illusion. *Sci. Rep.* 6, 24362.
- Gallagher, S., 2005. *How the Body Shapes the Mind*. Oxford University Press Inc., New York.
- Gentile, G., Guterstam, A., Brozzoli, C., Ehrsson, H.H., 2013. Disintegration of multisensory signals from the real hand reduces default limb self-attribution: an fMRI study. *J. Neurosci.* 33 (33), 13350–13366.
- Graham, K.T., Martin-Iverson, M.T., Holmes, N.P., Jablensky, A., Waters, F., 2014. Deficits in agency in schizophrenia, and additional deficits in body image, body schema, and internal timing, in passivity symptoms. *Front. Psychiatry* 5, 126.
- Guterstam, A., Gentile, G., Ehrsson, H.H., 2013. The invisible hand illusion: multisensory integration leads to the embodiment of a discrete volume of empty space. *J. Cogn. Neurosci.* 25 (7), 1078–1099.
- Guterstam, A., Larsson, D.E.O., Zeberg, H., Ehrsson, H.H., 2019. Multisensory correlations - not tactile expectations - determine the sense of body ownership. *PLoS One* 14 (2), e0213265.
- Guterstam, A., Szczotka, J., Zeberg, H., Ehrsson, H.H., 2018. Tool use changes the spatial extension of the magnetic touch illusion. *J. Exp. Psychol. Gen.* 147 (2), 298–303.
- Guterstam, A., Zeberg, H., Özçiftci, V.M., Ehrsson, H.H., 2016. The magnetic touch illusion: a perceptual correlate of visuo-tactile integration in peripersonal space. *Cognition* 155, 44–56.
- Haans, A., IJsselstein, W.A., de Kort, Y.A.W., 2008. The effect of similarities in skin texture and hand shape on perceived ownership of a fake limb. *Body Image* 5 (4), 389–394.
- Head, H., Holmes, G., 1911. Sensory disturbances from cerebellar lesions. *Brain* 34, 102–254.
- Heed, T., Gründler, M., Rinkleib, J., Rudzik, F.H., Collins, T., Cooke, E., O'Regan, J.K., 2011. Visual information and rubber hand embodiment differentially affect reach-to-grasp actions. *Acta Psychol. (Amst)* 138 (1), 263–271.
- Hohwy, J., Paton, B., 2010. Explaining away the body: experiences of supernaturally caused touch and touch on non-hand objects within the rubber hand illusion. *PLoS One* 5 (2), e9416.
- Holle, H., McLatchie, N., Maurer, S., Ward, J., 2011. Proprioceptive drift without illusions of ownership for rotated hands in the “rubber hand illusion” paradigm. *Cogn. Neurosci.* 2 (3–4), 171–178.
- Holmes, N.P., Crozier, G., Spence, C., 2004. When mirrors lie: ‘Visual capture’ of arm position impairs reaching performance. *Cogn. Affect. Behav. Neurosci.* 4 (2), 193–200.
- Holmes, N.P., Snijders, H.J., Spence, C., 2006. Reaching with alien limbs: visual exposure to prosthetic hands in a mirror biases proprioception without accompanying illusions of ownership. *Percept. Psychophys.* 68 (4), 685–701.
- Holmes, N.P., Spence, C., 2005. Visual bias of unseen hand position with a mirror: spatial and temporal factors. *Exp. Brain Res.* 166, 489–497.
- IJsselstein, W.A., de Kort, Y.A.W., Haans, A., 2006. Is this my hand I see before me? The rubber hand illusion in reality, virtual reality, and mixed reality. *Presence* 15 (4), 455–464.
- Isayama, R., Vesia, M., Jegatheeswaran, G., Elahi, B., Gunraj, C.A., Cardinali, L., Farnè, A., Chen, R., 2019. *J. Neurophysiol.* 121, 563–573.
- Janssen, L., Meulenbroek, R.G.J., Steenbergen, B., 2011. Behavioral evidence for left-hemisphere specialization of motor planning. *Exp. Brain Res.* 209 (1), 65–72.
- Jenkinson, P.M., Preston, C., 2015. New reflections on agency and body ownership: the moving rubber hand illusion in the mirror. *Conscious. Cogn.* 33, 432–442.
- Kalckert, A., Ehrsson, H.H., 2012. Moving a rubber hand that feels like your own: a dissociation of ownership and agency. *Front. Hum. Neurosci.* 6, 40.
- Kalckert, A., Ehrsson, H.H., 2014a. The moving rubber hand illusion revisited: comparing movements and visuotactile stimulation to induce illusory ownership. *Conscious. Cogn.* 26 (1), 117–132.
- Kalckert, A., Ehrsson, H.H., 2014b. The spatial distance rule in the moving and classical rubber hand illusions. *Conscious. Cogn.* 30, 118–132.
- Kalckert, A., Ehrsson, H.H., 2017. The onset time of the ownership sensation in the moving rubber hand illusion. *Front. Psychol.* 8, 344.
- Kammers, M.P.M., de Vignemont, F., Verhagen, L., Dijkerman, H.C., 2009a. The rubber hand illusion in action. *Neuropsychologia* 47 (1), 204–211.
- Kammers, M.P.M., Kootker, J.A., Hogendoorn, H., Dijkerman, H.C., 2010. How many motoric body representations can we grasp? *Exp. Brain Res.* 202 (1), 203–212.
- Kammers, M.P.M., Longo, M.R., Tsakiris, M., Dijkerman, H.C., Haggard, P., 2009b. Specificity and coherence of body representations. *Perception* 38 (12), 1804–1820.
- Kammers, M.P.M., Rose, K., Haggard, P., 2011. Feeling numb: temperature, but not thermal pain, modulates feeling of body ownership. *Neuropsychologia* 49 (5), 1316–1321.
- Kammers, M.P.M., van der Ham, I.J.M., Dijkerman, H.C., 2006. Dissociating body representations in healthy individuals: differential effects of a kinesthetic illusion on perception and action. *Neuropsychologia* 44 (12), 2430–2436.
- Karabanov, A.N., Ritterband-Rosenbaum, A., Christensen, M.S., Siebner, H.R., Nielsen, J.B., 2017. *Eur. J. Neurosci.* 45, 964–974.
- Keenan, J., Rubio, J., Racioppi, C., Johnson, A., Barnacz, A., 2005. The right hemisphere and the dark side of consciousness. *Cortex* 41, 695–704.
- Kilteni, K., Ehrsson, H.H., 2017. Body ownership determines the attenuation of self-generated tactile sensations. *Proc. Natl. Acad. Sci.* 114 (31), 8426–8431.
- Kilteni, K., Maselli, A., Kording, K.P., Slater, M., 2015. Over my fake body: body ownership illusions for studying the multisensory basis of own-body perception. *Front. Hum. Neurosci.* 9, 141.
- Lane, T., Yeh, S.-L., Tseng, P., Chang, A.-Y., 2017. Timing disownership experiences in the rubber hand illusion. *Cogn. Res. Princ. Implic.* 2 (1), 4.
- Lev-Ari, L., Hirschmann, S., Dyskin, O., Goldman, O., Hirschmann, I., 2015. The rubber hand illusion paradigm as a sensory learning process in patients with schizophrenia. *Eur. Psychiatry* 30 (7), 868–873.
- Lira, M., Egitto, J.H., Dall'Agnol, P.A., Amodio, D.M., Gonçalves, Ó.F., Boggio, P.S., 2017. The influence of skin colour on the experience of ownership in the rubber hand illusion. *Sci. Rep.* 7, 15745.
- Litwin, P., 2018. Rubber hand illusion does not arise from comparisons with internal body models: a new multisensory integration account of the sense of ownership. *PeerJ Preprints*.
- 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 Cogn.* 64 (1), 104–109.
- Lloyd, D.M., Gillis, V., Lewis, E., Farrell, M.J., Morrison, I., 2013. Pleasant touch moderates the subjective but not objective aspects of body perception. *Front. Behav. Neurosci.* 7, 207.
- Longo, M.R., Cardozo, S., Haggard, P., 2008a. Visual enhancement of touch and the bodily self. *Conscious. Cogn.* 17 (4), 1181–1191.
- 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., 2008b. What is embodiment? A psychometric approach. *Cognition* 107 (3), 978–998.
- Loomis, J.M., Philbeck, J.W., 1999. Is the anisotropy of perceived 3D shape invariant across scale? *Percept. Psychophys.* 61 (3), 397–402.
- Ma, K., Hommel, B., 2013. The virtual-hand illusion: effects of impact and threat on perceived ownership and affective resonance. *Front. Psychol.* 4, 604.
- Ma, K., Hommel, B., 2015. The role of agency for perceived ownership in the virtual hand illusion. *Conscious. Cogn.* 36, 277–288.
- Ma, K., Hommel, B., 2018. Metacontrol and body ownership: divergent thinking increases the virtual hand illusion. *Psychol. Res.*
- Ma, K., Lippelt, D.P., Hommel, B., 2017. Creating virtual-hand and virtual-face illusions to investigate self-representation. *J. Vis. Exp.* 121, 1–14.
- Marotta, A., Bombieri, F., Zampini, M., Schena, F., Dallocchio, C., Fiorio, M., Tinazzi, M., 2017. The moving rubber hand illusion reveals that explicit sense of agency for tapping movements is preserved in functional movement disorders. *Front. Hum. Neurosci.* 11, 1–15.
- Marotta, A., Tinazzi, M., Cavedini, C., Zampini, M., Fiorio, M., 2016. Individual differences in the rubber hand illusion are related to sensory suggestibility. *PLoS One* 11 (12), e0168489.
- Maselli, A., Kilteni, K., López-Moliner, J., Slater, M., 2016. The sense of body ownership relaxes temporal constraints for multisensory integration. *Sci. Rep.* 6, 30628.
- McCabe, C.S., Haigh, R.C., Halligan, P.W., Blake, D.R., 2005. Simulating sensory-motor incongruence in healthy volunteers: implications for a cortical model of pain. *Rheumatology* 44 (4), 509–516.
- Moseley, G.L., Olthoff, N., Venema, A., Don, S., Wijers, M., Gallace, A., Spence, C., 2008. Psychologically induced cooling of a specific body part caused by the illusory ownership of an artificial counterpart. *PNAS* 105 (35), 13169–13173.
- Mussap, A.J., Salton, N., 2006. A “rubber-hand” illusion reveals a relationship between perceptual body image and unhealthy body change. *J. Health Psychol.* 11 (4),

- 627–639.
- Mutha, P.K., Haaland, K.Y., Sainburg, R.L., 2012. The effects of brain lateralization on motor control and adaptation. *J. Mot. Behav.* 44 (6), 455–469.
- Newport, R., Pearce, R., Preston, C., 2010. Fake hands in action: embodiment and control of supernumerary limbs. *Exp. Brain Res.* 204 (3), 385–395.
- Newport, R., Preston, C., 2010. Pulling the finger off disrupts agency, embodiment and peripersonal space. *Perception* 39 (9), 1296–1298.
- Niebauer, C.L., Aselage, J., Schutte, C., 2002. Hemispheric interaction and consciousness: degree of handedness predicts the intensity of a sensory illusion. *Laterality* 7 (1), 85–96.
- Nierula, B., Martini, M., Matamala-Gomez, M., Slater, M., Sanchez-Vives, M.V., 2017. Seeing an embodied virtual hand is analgesic contingent on collocation. *J. Pain* 18 (6), 645–655.
- Norman, J.F., Adkins, O.C., Pedersen, L.E., Reyes, C.M., Wulff, R.A., Tungate, A., 2015. The visual perception of exocentric distance in outdoor settings. *Vision Res.* 117, 100–104.
- Norman, J.F., Todd, J.T., Perotti, V.J., Tittle, J.S., 1996. The visual perception of three-dimensional length. *J. Exp. Psychol. Hum. Percept. Perform.* 22 (1), 173–186.
- Ocklenburg, S., Rüter, N., Peterburs, J., Pinnow, M., Güntürkün, O., 2011. Laterality in the rubber hand illusion. *Laterality* 16 (2), 174–187.
- Paillard, J., 1999. Body Schema and Body Image - a Double Dissociation in Deafferented Patients. *Motor Control, Today and Tomorrow* (Sofia: Bulgarian Academy of Sciences, Academic Publishing House), pp. 197–214.
- Palomo, P., Borrego, A., Cebolla, A., Llorens, R., Demarzo, M., Baños, R.M., 2018. Subjective, behavioral, and physiological responses to the rubber hand illusion do not vary with age in the adult phase. *Conscious. Cogn.* 58, 90–96.
- Pavani, F., Spence, C., Driver, J., 2000. Visual capture of touch: out-of-the-body experiences with rubber gloves. *Psychol. Sci.* 11 (5), 353–359.
- Pavani, F., Zampini, M., 2007. The role of hand size in the fake-hand illusion paradigm. *Perception* 36 (10), 1547–1554.
- Perez-Marcos, D., Slater, M., Sanchez-Vives, M.V., 2009. Inducing a virtual hand ownership illusion through a brain-computer interface. *NeuroReport* 20 (6), 589–594.
- Preston, C., 2013. The role of distance from the body and distance from the real hand in ownership and disownership during the rubber hand illusion. *Acta Psychol. (Amst)* 142 (2), 177–183.
- Radziun, D., Ehrsson, H.H., 2018. Auditory cues influence the rubber-hand illusion. *J. Exp. Psychol. Hum. Percept. Perform.* 44 (7), 1012–1021.
- Reinersmann, A., Landwehr, J., Krumova, E.K., Peterburs, J., Ocklenburg, S., Güntürkün, O., Maier, C., 2013. The rubber hand illusion in complex regional pain syndrome: preserved ability to integrate a rubber hand indicates intact multisensory integration. *Pain* 154 (9), 1519–1527.
- Riemer, M., Bublatzky, F., Trojan, J., Alpers, G.W., 2015. Defensive activation during the rubber hand illusion: ownership versus proprioceptive drift. *Biol. Psychol.* 109, 86–92.
- Riemer, M., Fuchs, X., Bublatzky, F., Kleinböhl, D., Hölzl, R., Trojan, J., 2014. The rubber hand illusion depends on a congruent mapping between real and artificial fingers. *Acta Psychol. (Amst)* 152, 34–41.
- Riemer, M., Kleinböhl, D., Hölzl, R., Trojan, J., 2013. Action and perception in the rubber hand illusion. *Exp. Brain Res.* 229 (3), 383–393.
- Riemer, M., Wolbers, T., Kuehn, E., 2019. Preserved multisensory body representations in advanced age. *Sci. Rep.* 9, 2663.
- Ro, T., Wallace, R., Hagedorn, J., Farnè, A., Pienkos, E., 2004. Visual enhancing of tactile perception in the posterior parietal cortex. *J. Cogn. Neurosci.* 16 (1), 24–30.
- 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.
- Rohde, M., Wold, A., Karnath, H.O., Ernst, M.O., 2013. The human touch: skin temperature during the rubber hand illusion in manual and automated stroking procedures. *PLoS One* 8 (11), e80688.
- Samad, M., Chung, A.J., Shams, L., 2015. Perception of body ownership is driven by Bayesian sensory inference. *PLoS One* 10 (2), e0117178.
- 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.
- Schaefer, M., Flor, H., Heinze, H.J., Rotte, M., 2007. Morphing the body: illusory feeling of an elongated arm affects somatosensory homunculus. *NeuroImage* 36 (3), 700–705.
- Schaefer, M., Heinze, H.J., Rotte, M., 2009. My third arm: Shifts in topography of the somatosensory homunculus predict feeling of an artificial supernumerary arm. *Hum. Brain Mapp.* 30 (5), 1413–1420.
- Senna, I., Maravita, A., Bolognini, N., Parise, C.V., 2014. The marble-hand illusion. *PLoS One* 9 (3), e91688.
- Shimada, S., Fukuda, K., Hiraki, K., 2009. Rubber hand illusion under delayed visual feedback. *PLoS One* 4 (7), e6185.
- Slater, M., Perez-Marcos, D., Ehrsson, H.H., Sanchez-Vives, M.V., 2008. Towards a digital body: the virtual arm illusion. *Front. Hum. Neurosci.* 2, 6.
- Slater, M., Perez-Marcos, D., Ehrsson, H.H., Sanchez-Vives, M.V., 2009. Inducing illusory ownership of a virtual body. *Front. Neurosci.* 3 (2), 214–220.
- Smit, M., Brummelman, J.T.H., Keizer, A., van der Smagt, M.J., Dijkerman, H.C., van der Ham, I.J.M., 2018. Body ownership and the absence of touch: approaching the rubber hand inside and outside peri-hand space. *Exp. Brain Res.* 3251–3265.
- Smit, M., Kooistra, D.I., van der Ham, I.J.M., Dijkerman, H.C., 2017. Laterality and body ownership: effect of handedness on experience of the rubber hand illusion. *Laterality* 22 (6), 703–724.
- Snijders, H.J., Holmes, N.P., Spence, C., 2007. Direction-dependent integration of vision and proprioception in reaching under the influence of the mirror illusion. *Neuropsychologia* 45 (3), 496–505.
- Suzuki, K., Garfinkel, S.N., Critchley, H.D., Seth, A.K., 2013. Multisensory integration across exteroceptive and interoceptive domains modulates self-experience in the rubber-hand illusion. *Neuropsychologia* 51 (13), 2909–2917.
- Synofzik, M., Vosgerau, G., Newen, A., 2008. Beyond the comparator model: a multifactorial two-step account of agency. *Conscious. Cogn.* 17, 219–239.
- Tajima, D., Mizuno, T., Kume, Y., Yoshida, T., 2015. The mirror illusion: Does proprioceptive drift go hand in hand with sense of agency? *Front. Psychol.* 6, 200.
- Tamè, L., Linkenauger, S.A., Longo, M.R., 2018. Dissociation of feeling and belief in the rubber hand illusion. *PLoS One* 13 (10), e0206367.
- Tieri, G., Tidoni, E., Pavone, E.F., Aglioti, S.M., 2015. Body visual discontinuity affects feeling of ownership and skin conductance responses. *Sci. Rep.* 5, 17139.
- Trojan, J., Fuchs, X., Speth, S.-L., Diers, M., 2018. The rubber hand illusion induced by visual-thermal stimulation. *Sci. Rep.* 8, 12417.
- Tsakiris, M., 2010. My body in the brain: a neurocognitive model of body-ownership. *Neuropsychologia* 48 (3), 703–712.
- Tsakiris, M., Carpenter, L., James, D., Fotopoulou, A., 2010a. Hands only illusion: multisensory integration elicits sense of ownership for body parts but not for non-core objects. *Exp. Brain Res.* 204 (3), 343–352.
- Tsakiris, M., Haggard, P., 2005. The rubber hand illusion revisited: visuotactile integration and self-attribution. *J. Exp. Psychol. Hum. Percept. Perform.* 31 (1), 80–91.
- Tsakiris, M., Longo, M.R., Haggard, P., 2010b. Having a body versus moving your body: neural signatures of agency and body-ownership. *Neuropsychologia* 48 (9), 2740–2749.
- Tsakiris, M., Prabhu, G., Haggard, P., 2006. Having a body versus moving your body: how agency structures body-ownership. *Conscious. Cogn.* 15 (2), 423–432.
- Valenzuela Moguillansky, C., O'Regan, J.K., Petitengien, C., 2013. Exploring the subjective experience of the “rubber hand” illusion. *Front. Hum. Neurosci.* 7, 659.
- van Stralen, H.E., van Zandvoort, M.J.E., Hoppenbrouwers, S.S., Vissers, L.M.G., Kappelle, L.J., Dijkerman, H.C., 2014. Affective touch modulates the rubber hand illusion. *Cognition* 131, 147–158.
- Walsh, E., Guilmette, D.N., Longo, M.R., Moore, J.W., Oakley, D.A., Halligan, P.W., et al., 2015. Are you suggesting that's my hand? The relation between hypnotic suggestibility and the rubber hand illusion. *Perception* 44 (6), 709–723.
- Walsh, L.D., Moseley, G.L., Taylor, J.L., Gandevia, S.C., 2011. Proprioceptive signals contribute to the sense of body ownership. *J. Physiol. (Lond.)* 589 (12), 3009–3021.
- Ward, J., Mensah, A., Jünemann, K., 2015. The rubber hand illusion depends on the tactile congruency of the observed and felt touch. *J. Exp. Psychol. Hum. Percept. Perform.* 41 (5), 1203–1208.
- Wen, W., Muramatsu, K., Hamasaki, S., An, Q., Yamakawa, H., Tamura, Y., et al., 2016. Goal-directed movement enhances body representation updating. *Front. Hum. Neurosci.* 10, 329.
- White, R.C., Davies, A.M.A., Hallett, T.J., Davies, M., 2010. Tactile expectations and the perception of self-touch: an investigation using the rubber hand paradigm. *Conscious. Cogn.* 19 (2), 505–519.
- Wold, A., Limanowski, J., Walter, H., Blankenburg, F., 2014. Proprioceptive drift in the rubber hand illusion is intensified following 1 Hz TMS of the left EBA. *Front. Hum. Neurosci.* 8, 390.
- Zeller, D., Gross, C., Bartsch, A., Johansen-Berg, H., Classen, J., 2011. Ventral premotor cortex may be required for dynamic changes in the feeling of limb ownership: a lesion study. *J. Neurosci.* 31 (13), 4852–4857.
- Zeller, D., Hullin, M., 2018. Spatial attention and the malleability of bodily self in the elderly. *Conscious. Cogn.* 59, 32–39.
- Zopf, R., Savage, G., Williams, M.A., 2010. Crossmodal congruency measures of lateral distance effects on the rubber hand illusion. *Neuropsychologia* 48 (3), 713–725.
- Zopf, R., Truong, S., Finkbeiner, M., Friedman, J., Williams, M.A., 2011. Viewing and feeling touch modulates hand position for reaching. *Neuropsychologia* 49 (5), 1287–1293.