# The Plasticity of the Bodily Self: Head Movements in Bodily Illusions and Their Relation to Gallagher's Body Image and Body Schema

Roel Lesur, Marte ; Gaebler, Michael ; Bertrand, Philippe ; Lenggenhager, Bigna

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## Head Movements in Bodily Illusions and Their Relation to Gallagher's Body Image and Body Schema

Marte Roel Lesur • University of Zurich, Switzerland • marteroel/at/gmail.com

Michael Gaebler • Max Planck Institute for Human Cognitive and Brain Sciences Leipzig, Germany michael.gaebler/at/gmail.com

Philippe Bertrand • Université Paris Descartes, France • digitalbertrand/at/gmail.com

Bigna Lenggenhager • University of Zurich, Switzerland • bigna.lenggenhager/at/uzh.ch

**> Context** • The integration of sensorimotor signals and prior beliefs contribute to our sense of body. An influential framework in the study of the bodily self is Gallagher's distinction between body image and body schema, which are roughly comparable to the perceived body and the lived body, respectively. Through systematic manipulations of sensorimotor signals, it is possible to induce the illusion of agency or ownership over foreign limbs or full bodies. Yet, there is diverging empirical evidence regarding the coherence of sensorimotor signals necessary to elicit such illusions. **> Problem** • The large amount of empirical evidence and its relation to the concepts of body image and schema is not well understood and requires more fine-graded distinctions of various aspects of sensorimotor coherences. **> Method** • We systematically discuss literature on sensorimotor coherence during bodily illusions and argue for the importance of distinguishing between head- and limb-related coherences. To support this discussion, we present new experimental findings where participants experienced a first-person perspective (1PP) full-body illusion over another human through the manipulation of hand-related visuotactile or visuomotor coherence. **> Results** • Participants showed no significant reduction in ownership after asynchronous visuotactile, but after asynchronous visuomotor stimulation. Based on these results and the literature, we propose that head-related temporal sensorimotor coherences are necessary to integrate limb-related incoherent signals during full-body illusions. Furthermore, we speculate that during full-body illusions, head-related coherences are a binding factor between the body image and the body schema; that is, only through the coherent manipulation of the visual field over a 1PP resulting from an immersive image (body image) is our body schema manipulated. **> Implications** • While yet to be experimentally tested, distinguishing head- and limb-related sensorimotor integration and their influences on body image and body schema could refine the study of the bodily self. **> Constructivist content** • The plasticity of the bodily self – as shown in bodily illusions – reflects the dynamism of the subject as observer and its binding to its environment.

**> Key words** • **Bodily self, sensorimotor integration, body schema, body image, bodily illusions.**

### The bodily self and its alteration through sensorimotor stimulation

«1» In both theoretical and empirical work, there is growing evidence that the brain actively constructs our sense of a bodily self from multisensory afferents (e.g., visual, vestibular, tactile or proprioceptive), motor efferents, and longer-term assumptions about the self (e.g., Blanke, Slater & Serino 2015). Over the last decades, an increasing number of empirical studies have developed experimental setups that systematically manipulate the coherences between different sensorimotor signals[1] to investigate various aspects of the bodily self. These studies typically induce illusory self-identification with an external body part to study the *feeling of ownership* (the experience of the body being one's own) and the *feeling of agency* (the experience of self-generating an action), which have been argued to be the most crucial aspects of the bodily self (see, e.g., Gallagher 2000; Longo et al. 2008). In this framework, it is broadly accepted that

1 | We use the term *sensorimotor* to refer to the integration either of multiple sensory or of sensory and motor signals.

both integrative and competitive dynamic relations of sensorimotor information about the body contribute to the unity of the bodily self and its stability over time. In other words, the sense of one's own body results from a probabilistic integration of information from sensorimotor signals and from beliefs based on previous experiences (Apps & Tsakiris 2014; Limanowski & Blankenburg 2013). Yet, so far, it has not been possible to integrate the large amount of – partially contradictory – empirical findings into a unified model of the bodily self. Moreover, the manner of interaction between the different sensory inputs and their potential to modulate prior beliefs with respect to bodily illusions remain largely unclear.

« 2 » We here intend to disentangle some of the lesser discussed characteristics of sensorimotor coherences during bodily illusions and attempt to integrate these properties into the influential framework of body image and body schema, as proposed by Shaun Gallagher (2005b). For Gallagher, the body image is related to how the body appears in one's perceptual field while the body schema is related to how the body shapes or constrains such a perceptual field. We will discuss how these two concepts, though dissociated, might interact during bodily illusions.[2] It is generally thought that for illusory embodiment to occur, temporal sensorimotor coherence is necessary, albeit not sufficient (Botvinick & Cohen 1998; Tsakiris & Haggard 2005); however, recent results show that in some cases illusory embodiment can be achieved despite temporal sensorimotor incoherence (Caola et al. 2018; Maselli et al. 2016; Maselli & Slater 2013; Slater et al. 2010). In light of this divergence, we suggest the need to refine particular aspects of sensorimotor coherences. Most importantly, visuoproprioceptive coherence is often referred to as a single process, but integration mechanisms might differ between effectors (e.g., movement of peripheral limbs as compared to movement of the head). We will discuss

- diverging evidence regarding the necessity of temporal sensorimotor coherence for inducing body ownership illusions;
- how head-related sensorimotor signals have been neglected in the literature (but we speculate that they may help explain this diverging evidence); and
- how such head-related signals may be an important factor for the interaction between body schema and body image during illusory ownership.

Of the many methods of manipulating the bodily self that have emerged over the past decades, we will focus on two classes of illusions that manipulate visual, tactile, proprioceptive, vestibular, and/or motor signals from a first-person perspective (1PP): illusory limb identification and the first-person perspective full-body illusion.[3]

## Types of experimentally induced illusions of the bodily self

### Illusory limb identification

« 3 » During *illusory limb identification* (ILI), a fake limb at a spatially different location is felt as one's own. This is the case, for example, in the well-known Rubber Hand Illusion (RHI; Botvinick & Cohen 1998): in this paradigm, participants see a rubber hand located in an anatomically plausible position, which is touched or stroked synchronously with their own hand (which is positioned out of view but next to the rubber hand). The temporally coherent visuotactile feedback in the RHI supersedes the visuoproprioceptive conflict, resulting in illusory ownership over the fake hand (in the majority of participants). Such illusory embodiment has also been demonstrated for other limbs, such as the foot (Flögel et al. 2016; Lenggenhager, Hilti & Brugger 2015), and with other sensory and motor temporal couplings, such as visual and proprioceptive (Rohde, Luca & Ernst 2011) or visual and motor (Kalckert & Ehrsson 2012, 2014; Ratcliffe & Newport 2017; Sanchez-Vives et al. 2010), with this latter case additionally resulting in illusory agency over the fake hand. It has been suggested that the fake limb must be anatomically credible both in shape (as no illusion occurs for anatomically implausible objects) and postural position (Tsakiris & Haggard 2005). What distinguishes ILI from sensorimotor manipulation of the full body is that participants perceive illusory ownership over an external/supernumerary dummy body part while maintaining a *natural* 1PP over their own bodies and environment.

### First-person perspective full-body illusion

« 4 » In the case of the *first-person perspective full-body illusion* (1PP FBI), the body of the participants, who are wearing head-mounted displays (HMDs), is substituted by the view of either a virtual (Maselli et al. 2016; Maselli & Slater 2013; Slater et al. 2010), a manikin's (Petkova & Ehrsson 2008), or another person's body (Bertrand et al. 2014; Petkova & Ehrsson 2008). Similar to the case of ILI, at least *some* correspondence of motor, tactile, vestibular, and/or proprioceptive signals between the participant's own body and the one they see seems necessary (see Maselli & Slater 2013). Such manipulations can result in illusory ownership and/or agency over the seen body. The particularity of the 1PP FBI is that both the whole body and the perceptual field of the participant are visually exchanged with that of the illusion. Yet, the 1PP over this foreign body remains natural; that is, the virtual visual field matches the participant's head position and orientation. It is worth noting, however, that in many 1PP FBI setups, the 1PP perspective is restricted by asking participants to avoid head movements, thus limiting head-related sensorimotor interactions (Petkova & Ehrsson 2008; Petkova, Khoshnevis & Ehrsson 2011).

2| While the literature regarding the body image and schema is extensive and has been discussed by several authors including Jacques Paillard, Marc Jeannerod and Jonathan Cole, we here focus on the distinction as discussed by Gallagher (2005a, 2005b).

3| Other experimental manipulations of the bodily self that require different or additional categorizations will not be covered in the current article; these include the manipulation of interoceptive (Aspell et al. 2013; Suzuki et al. 2013), auditory (Tajadura-Jiménez et al. 2012; Tajadura-Jiménez et al. 2016), or passive vestibular (Macauda et al. 2015) signals, as well as manipulations from different perspectives such as the enfacement paradigm (Sforza et al. 2010; Tsakiris 2008) or full-body illusions from a third-person perspective (Ehrsson 2007; Lenggenhager et al. 2007).

# Disentangling characteristics of sensorimotor integration during illusory embodiment

## The importance of temporal incoherence in illusory embodiment

« 5 » Temporally coherent sensorimotor stimulation has been considered a necessary component for ILI to occur. In contrast, temporally incoherent sensorimotor stimulation generally reduces the illusion and has been used as a control condition for sensorimotor stimulation without illusory embodiment (please refer to Table 1 for an overview of how sensorimotor coherences affect ownership in selected studies). Asynchronous visuotactile stimulation typically results in a significantly weaker feeling of ownership (Botvinick & Cohen 1998), while asynchronous visuo*motor* stimulation leads to lower scores in the sense of both ownership and agency (Kalckert & Ehrsson 2012, 2014). This has been assessed explicitly, using questionnaires, as well as implicitly, using measures like proprioceptive drift (i.e., people's perception of the location of their own limb is biased towards the fake limb) or physiological reaction (typically in response to a threat towards the illusorily embodied limb). It is important to distinguish between two types of sensorimotor incoherence: spatial shifts and temporal shifts. An example of a spatial shift is the visuoproprioceptive interaction during the RHI, where the seen (fake) hand is in a different position from the participant's own hand, yet the spatial difference remains constant. That is, even though there is a difference between the information from proprioception and vision, the spatial relation between the two signals remains the same throughout the stimulation procedure. In contrast, during temporal shifts, the relation between the different sensorimotor signals is dynamic. An example of the latter, in the case of visuoproprioceptive temporal incoherence, would be when the participant's own hand is moved while the rubber hand remains stationary.

« 6 » In the case of 1PP FBIs, diverging results concerning the necessity of temporal sensorimotor coherence have been reported by the few available studies (refer to Table 1 for an overview). While some studies found that asynchronous visuotactile stimulation significantly reduces the illusion as in ILI (Petkova & Ehrsson 2008; Petkova, Khoshnevis & Ehrsson 2011), others show that it does not (Maselli et al. 2016; Maselli & Slater 2013; and Slater et al. 2010, for some elements of their questionnaire). Antonella Maselli and Mel Slater's (2013) work is particularly illustrative in that they proposed a model integrating the *building blocks* of illusory full-body ownership. In their model, the crucial components are

- a natural view of the body from a 1PP with a clear resemblance to a human body and
- a high coherence of visuoproprioceptive cues.

If these conditions are met, then visuotactile temporal incoherence does not reduce the illusion – a phenomenon that is remarkably different from what has been found for ILI. If these conditions are not met, then visuotactile temporal coherence may still elicit the illusion (i.e., in ILI).

« 7 » Whereas Maselli, Slater, and colleagues (Maselli et al. 2016; Slater et al. 2010) used virtual characters, we confirmed their findings using live videos of another human being (cf. Section "Empirical study" for these previously unpublished data). It needs to be noted that we included a slight visuoproprioceptive shift in space (10 cm) between the seen and the participant's own hand, comparable to the classical RHI. Even in this condition, visuotactile temporal incoherence did not break the illusion, suggesting that under certain circumstances, the visuoproprioceptive correspondence needed to induce the illusion can be lower than previously thought (Maselli & Slater 2013). Importantly, these authors did not distinguish between proprioceptive spatial and temporal shifts when referring to incoherence, despite different effects of each type of visuoproprioceptive incoherence on the RHI (Tsakiris & Haggard 2005). However, if we assume some flexibility in visuoproprioceptive correspondence in space, why would temporally incoherent sensorimotor signals not result in illusory ownership in the case of ILI? This unexplained difference in the integration of incoherent signals between ILI and 1PP FBI points at a need for a more detailed model that accommodates such loose temporal integration of sensorimotor signals for embodiment during 1PP FBIs. To this end, we propose a differentiation of head-related and limb-related sensorimotor integration, which will be discussed in the following subsection.

« 8 » Maselli et al. (2016) tested whether a humanoid computer-generated body during a 1PP FBI with active head movements results in a longer temporal binding window for visuotactile integration than an implausible body. In their experiment, the implausible body consisted of two virtual wooden sticks in a position corresponding to the body as seen from 1PP. They showed that when participants embodied the humanoid body, they were less sensitive to temporal sensorimotor incoherence. Such variation in the temporal binding window for sensorimotor integration can be considered evidence for how the particular properties of the 1PP FBI can affect sensorimotor integration. It suggests that an immersive representation of a realistic full body that corresponds to the head's orientation (within certain boundaries of spatial visuoproprioceptive correspondence) can widen the window of sensorimotor integration. Our own results confirm and extend this finding (cf. Section "Empirical study") by showing that the feeling of ownership occurred not only when embodying a *virtual* character, but also in an online video of a human body, regardless of temporal synchrony[4] during visuotactile stimulation. In contrast, to our knowledge, relaxed constraints for temporal sensorimotor coherence have not been reported for ILIs (Kalckert & Ehrsson 2012, 2014; Tsakiris & Haggard 2005; Botvinick & Cohen 1998).

« 9 » Along these lines, a recent study (Caola et al. 2018) used a 1PP FBI setup with

4| Our data further speak against the hypothesis that asynchronous visuotactile stimulation significantly reduces the illusion in video-based setups (Petkova & Ehrsson 2008; Petkova et al. 2011), while it does not in computer-generated setups (Maselli et al. 2016; Maselli & Slater 2013; Slater et al. 2010). It could be argued that the medium of stimulation changes expectations and thus affects how sensorimotor signals are integrated, yet our data show similar effects to the computer-generated setups (cf. Section "Empirical study"). This medium-based contrast was also questioned by Petkova et al. (2011) comparing HMD versus stimulation without digital devices.

| Type | Medium | Limb-related coherences | | Optic flow | Difference in ownership during mismatch | | Reference |
|---|---|---|---|---|---|---|---|
| | | Independent variable of interest and mismatch type | Initial mismatch and type | | Implicit measure | Explicit measure | |
| ILI | Physical | VT (temporal) | Proprioceptive (spatial) | matched | yes | yes | Botvinick & Cohen 1998 |
| ILI | Physical | VT (temporal) | Proprioceptive (spatial) | matched | no | yes | Flögel et al. 2016 |
| ILI | Physical | VT (temporal) | Proprioceptive (spatial) | matched | no | yes | Lenggenhager et al. 2015 |
| ILI | Physical | VT (temporal) and no touch | Proprioceptive (spatial) | matched | yes | no | Rohde et al. 2011 |
| ILI | Physical | VM (temporal) | Proprioceptive (spatial) | matched | yes | yes | Kalckert & Ehrsson 2012, 2014 |
| ILI | Physical | VM (temporal) | Proprioceptive (spatial) | matched | yes | yes | Ratcliffe & Newport 2017 |
| ILI | 3D screen | VM (temporal) | Proprioceptive (spatial) | matched | yes | yes | Sánchez-Vives et al. 2010 |
| ILI | Physical | VT (temporal), proprioceptive postural (spatial) | Proprioceptive (spatial) | matched | yes | n/a | Tsakiris & Haggard 2005 |
| 1PP FBI | HMD (VR) | VT (temporal and spatial), body shape | n/a | matched | n/a | yes (a) | Maselli et al. 2016 |
| 1PP FBI | HMD (VR) | VT & VM (temporal), body shape | n/a | matched/ fixed | no | no | Maselli and Slater 2013 |
| 1PP FBI | HMD (VR) | VT (temporal) | n/a | matched (b) | yes (VT only) | for some items | Slater et al. 2010 |
| 1PP FBI | HMD (video) | VT (temporal) | n/a | fixed | yes | yes | Petkova & Ehrsson 2008 |
| 1PP FBI | HMD (video), physical | VT (temporal) | n/a | fixed | yes | yes | Petkova, Khoshnevis & Ehrsson 2011 |
| 1PP FBI | HMD (VR) | VT and visuoproprioceptive (temporal) | n/a | matched | n/a | for some cases | Caola et al. 2018 |
| 1PP FBI | HMD (VR) | VM (spatial and temporal) | n/a | matched | yes | no | Kokkinara et al. 2015 |
| 1PP FBI | HMD (VR) | n/a | Proprioceptive & postural (temporal) | partial (c) | for perspective | for perspective | Kokkinara et al. 2016 |

**Table 1** • Systematic literature overview over the two experimentally induced illusions of the bodily self that are central to this target article: illusory limb identification (ILI) and first-person perspective full-body illusion (1PP FBI). The table shows the type of illusion, the manipulated parameters of interest (limb- and head-related), the sensorimotor coupling (visuotactile and visuomotor couplings are coded as VT and VM, respectively), the type of mismatch (temporal or spatial), whether the optic flow was coherent with head movements, and if there was a significant difference in the measures of ownership. HMD refers to head-mounted display. Please note that this is an oversimplified overview and each paper has many subtleties to be considered. The variables shown are the ones relevant to our discussion, not necessarily the only ones manipulated in the studies. *Notes:* (a) Not a measure of embodiment but of the temporal binding of visuotactile signals. (b) Head movements of the avatar were not matched, but optic flow (i.e., the apparent motion of the visual surroundings from a 1PP perspective) was. (c) A condition included head sway while participants were not swaying, yet orientation was coherent to head movements there, which affected the perceived agency.

active head movements to demonstrate that participants feel ownership for a moving virtual arm even when they are not physically moving (i.e., with large temporal incoherence). Similarly, Elena Kokkinara et al. (2016) showed that seated participants who were only allowed head movement in a 1PP FBI setup experienced illusory ownership over a walking body. Both studies are in line with the idea that there is a larger tolerance for sensorimotor incoherence in 1PP FBI setups,[5] which is not the case for ILI.

« 10 » That temporal constraints for sensorimotor integration are relaxed during 1PP FBIs is also consistent with the model of Maselli et al. (2016), which includes the point that mismatching sensorimotor cues are more loosely integrated when there is a strong feeling of ownership over a complete foreign body. The authors argue that body ownership illusions function as a causal binding factor for sensorimotor integration. They refer to a Bayesian inference model when they write that

> “the illusion arises when the brain associates a higher than chance probability to the existence of a single cause (the own-body) for all the incoming sensory input: the visual from the fake body and the somatosensory/motor from the physical body.” (ibid: 6)

This approach is highly explanatory and corresponds to our own evidence of relaxed temporal constraints for sensorimotor integration under 1PP FBIs. However, we propose that specifically head-related sensorimotor signals allow for such binding of sensorimotor integration during body ownership illusions.

## The importance of head- versus limb-related coherences in illusory embodiment

« 11 » The (probabilistic) integration of proprioception, vision, and touch has been considered an important aspect of (illusory) embodiment since the seminal RHI (Botvinick & Cohen 1998). We argue, however, that for both ILI and 1PP FBI, the full complexity of such integration has often been neglected. As illustrated above, visuoproprioceptive mismatch can be spatial or temporal, and both have been shown to differentially influence illusory embodiment. Furthermore, while sensorimotor coherence is usually just manipulated for peripheral limbs, head-related visuoproprioceptive coherence is much less discussed or manipulated in this literature (see Table 1).[6] There are, however, important fundamental differences between limb- and head-related sensorimotor signals[7]:

- head-related changes not only modify the visual inputs of the limb but of the whole scene; and
- head-related changes not only affect visuoproprioceptive but also visuovestibular coherence (see also Lenggenhager & Lopez 2014, for a more extensive debate).

« 12 » While the vestibular system has been claimed to be crucial for various aspects of the bodily self, it has hardly been discussed in current models of illusory embodiment (see Blanke, Slater & Serino 2015; Pfeiffer, Serino & Blanke 2014; Lenggenhager & Lopez 2014 for exceptions) or specifically manipulated experimentally (see Macauda et al. 2015 for an exception). One way in which visuovestibular interaction has been accounted for during 1PP FBIs is the so-called “redirected walking” technique (see Nilsson et al. 2018, for a review). By mapping the virtual to the physical space in a ratio other than 1:1, locomotion in the physical world is slightly (to the level that it is not consciously perceived) mismatched with locomotion in the virtual world. For example, if a person wants to see herself (from a 1PP) walking in a straight line in the virtual world, there may be a slight mismatch so that in the physical world, she has to move in a curved way to achieve such motion. The effect can be pronounced, particularly when visual input is combined with other sensory modalities, to the point that participants feel that they are walking in an infinite straight line while actually walking in circles (Nilsson et al. 2018). Similar to the precedence of vision in illusory ownership over peripheral limbs, vision seems to also dominate proprioceptive and vestibular cues in the presence of sensorimotor mismatches in FBIs. Furthermore, a small visuovestibular mismatch in head movements, such as during walking in a virtual body with or without head sway, has resulted in illusory ownership in a 1PP FBI setup with active head tracking (Kokkinara, et al. 2015). But this does not yet answer our question: do head-related versus limb-related visuoproprioceptive and motor cues differentially affect bodily illusions?

« 13 » While some authors limited head movement during 1PP FBIs (Maselli & Slater 2013; Petkova & Ehrsson 2008; Petkova, Khoshnevis & Ehrsson 2011), only a few have systematically investigated the effects of head-related sensorimotor coherences on illusory embodiment (see Table 1 for an overview of the literature). Notably, this manipulation of head-related signals is not easy to achieve in ILI. In Maselli and Slater’s (2013) study, participants were either able to freely move their heads or had to keep them static, which did not have a significant effect on the embodiment results. Although there was no visual-field movement in the control group in this study, the perspective over the body and the proprioceptive coherence remained matched. However, limiting head movements does not allow us to dissociate visuoproprioceptive correspondence of the peripheral body and visuoproprioceptive correspondence of head movements. Interestingly, their results showed that when asynchronous touch was used during active, rather than limited, head movements, participants attributed the origin of the tactile sensations to the visual (virtual) source. These findings suggest that head movements influence the integration of sensorimotor signals related to embodiment.

5 | These temporal mismatches, however, were passive: participants were not moving their bodies (apart from the head) while they saw moving bodies; this is in contrast to the (active) visuomotor task presented in the Section “Empirical study.”

6 | While our argument focuses on the relationship between vision and other sensory modalities, the special status of head-related movements extends to audition. During head movements, the sensorimotor rules that govern our visual field change as much for audition. When acoustic waves reach the middle ear, they change as a function of their angular incidence with our heads and pinnae (see Cheng & Wakefield 2001). Even more so, auditory cues are almost always manipulated by our head but rarely by our limb movements.

7 | Please note that even different properties might be found for eye-movement-related visuoproprioceptive integration.

« 14 » An earlier study by the same group manipulated the synchrony of head movements (Slater et al. 2010). However, asynchrony affected only the movements of the virtual avatar's head (as seen in a virtual mirror) but not the field of view of the participants, which always matched the participant's head movements, even if the avatar's head did not. The experiment included asking participants whether they recognized themselves in the mirror as the avatar, which was more likely for synchronous than for asynchronous head movements. Yet, the feeling that the avatar's body was their own body was not influenced by the synchrony of head movements. These results point to a difference between how head-related optic-flow coherence (the apparent motion of the visual surroundings from an egocentric perspective) and peripheral visuoproprioceptive coherence are processed.

« 15 » The direct comparison between a head-related and a limb-related system of visuoproprioceptive integration is something that, to our knowledge, has not been experimentally tested. From a technical perspective, this can easily be implemented with the use of HMDs and head tracking. In this sense, 1PP FBI, in contrast to ILI, offers a unique possibility to disentangle both systems of proprioceptive integration. It needs to be noted that a visuovestibular mismatch between the visual field and head movements may result in acute nausea; nevertheless, apart from the problems that this may entail, current technology allows for the manipulation of head-related coherences, as demonstrated by redirected walking (see above). Alternatively, head movements with a static field of view could be tested. Furthermore, eye movements could be tracked during the task, which may have an additional influence on 1PP FBI (see Footnote 4). So far, we know that if we maintain visuomotor (and proprioceptive) correspondence of head movements, illusory ownership may be maintained even if we break temporal sensorimotor coherence for peripheral limbs. However, we do not know what happens when such temporal coherence for head movements is broken. Would we still be able to elicit illusory ownership over the seen body? If we were to find that head-related temporal incoherence would suffice to significantly reduce the illusion even during temporally coherent sensorimotor stimulation for peripheral limbs, we should integrate this into current models.[8]

« 16 » In our 1PP-FBI scenario, dissociating head- from limb-related coherences would result in a special case of visuoproprioceptive integration. Special not only due to its seemingly distinct mechanisms, but also for being of fundamental importance for the bodily self. Yet, this has to be empirically tested. While it has been suggested that third-person-perspective sensorimotor manipulations may elicit out-of-body-like illusions (Ehrsson 2007; Lenggenhager et al. 2007), we have provided arguments for the importance of 1PP visuoproprioceptive coherence for illusory identification with a full humanoid body, which maintains bodily illusions even with asynchronous sensorimotor signals to peripheral limbs (Caola et al. 2018; Maselli et al. 2016; Maselli & Slater 2013; Slater et al. 2010). A 1PP over a humanoid body can serve as a "causal binding factor" (Maselli et al. 2016): an integrator between implausible sensorimotor signals and the feeling of self-identification with a fake body. However, could a 1PP also represent an integrator of body image and body schema?

## Empirical study: Synchronous and asynchronous visuotactile and visuomotor hand stimulation while full-body swapping with another human

### Aim and hypotheses

« 17 » Our study tested whether taking the perspective of a another human (i.e., not computer-generated but video-based) with matching head movements would confirm that illusory ownership during 1PP FBI is robust to certain sensorimotor mismatches (Maselli et al. 2016; Maselli & Slater 2013; Slater et al. 2010). In particular, we hypothesized that asynchronous visuotactile stimulation would not significantly reduce ownership as measured using proprioceptive drift and questionnaires (even with an initial visuoproprioceptive mismatch; see below). Regarding visuomotor synchrony, we did not have a clear hypothesis since previously reported methods and results varied widely.

### Methods and procedure

« 18 » 18 young healthy participants (8 men and 10 women; mean age = 29.7 years) adopted the visual perspective of another (female) person (the "performer") using "The Machine to Be Another" system (Bertrand et al. 2018; Oliveira et al. 2016; Bertrand et al. 2014; cf. Figure 1). The system uses a motorized video camera feeding the visual perspective of the performer into a head-mounted display (HMD) used by the participants. Head-related visuomotor coherences over the performer were always synchronous, active, and not restricted (unlike other video-based setups such as Petkova & Ehrsson 2008; Petkova, Khoshnevis & Ehrsson 2011), enabling a completely natural perspective on the other person's body. The manipulation of limb-related sensorimotor coherence was limited to the right hand and, in contrast to previous studies, we induced a slight initial visuoproprioceptive mismatch (i.e., the participant's hand was located at 10 cm from the seen hand) similar to the classical rubber hand illusion (RHI) paradigm. A repeated-measures experiment with four (counterbalanced) conditions based on the domain of the sensorimotor manipulation (visuotactile and visuomotor) and synchrony (synchronous and asynchronous) was conducted. For the visuotactile domain, an assistant stroked the index finger of both the performer and the participant either synchronously or asynchronously (opposing the direction of the touch) at a rate of approximately 1 Hz, as in the classical RHI. For the visuomotor domain, participants moved their right hand slowly while maintaining the forearm on top of a platform. The performer observed the participant's hand and either followed its movements with her own hand (synchronous) or moved it randomly (asynchronous). As mentioned, the participant's hand was shifted 10 cm to the right of the seen hand to enable the proprio-

8| It is interesting to note that experimentally induced dizziness, or dizziness induced by clinical conditions can increase disorders of the bodily self, such as symptoms of depersonalization (Lopez & Elzière 2017).

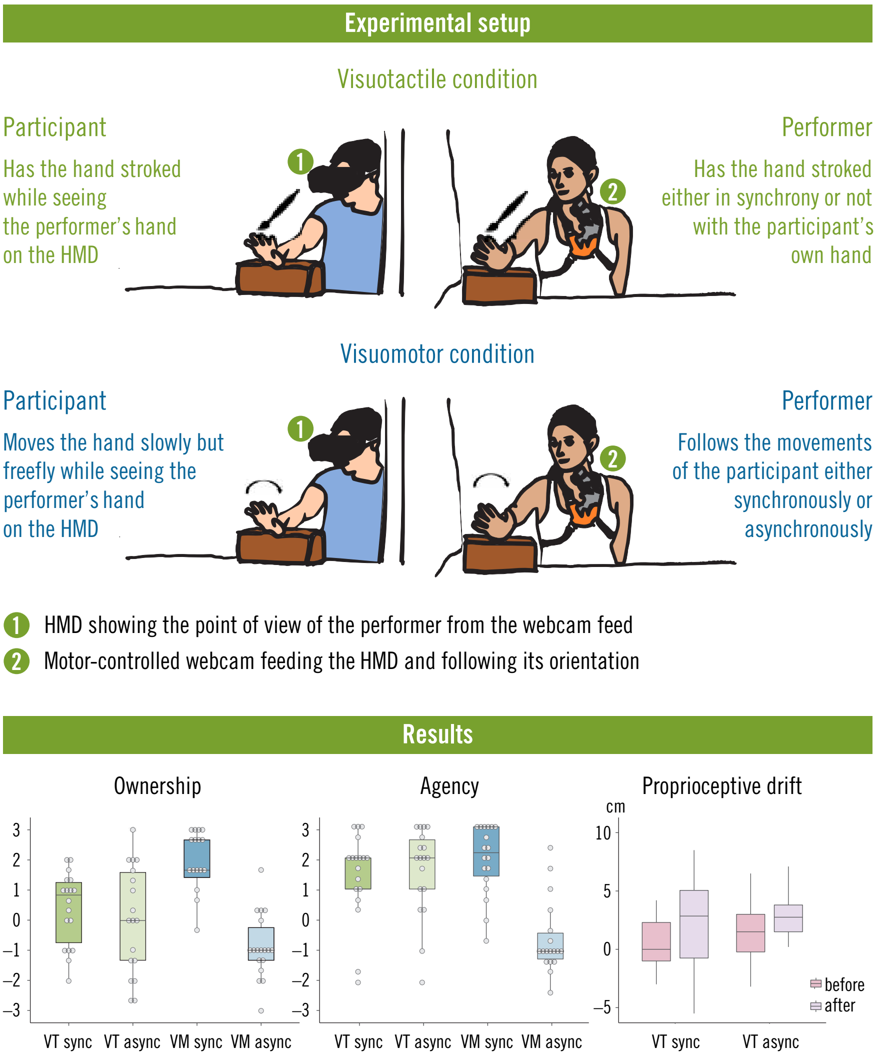


**Figure 1** • First-person perspective full-body illusion in a task of synchronous (sync) and asynchronous (async) visuotactile (VT) and visuomotor (VM) hand stimulation during full-body swapping with another human. The boxplots (in the bottom row) show the results of the questionnaire scores for body ownership (left) and the agency subscale (middle) as well as for the degree of proprioceptive drift (negative values represent distance away from the seen hand) for the visuotactile conditions before and after stimulation (right).

ceptive drift measure. After each condition, participants were asked to fill in a questionnaire consisting of 12 questions that could be answered on a 7-point Likert scale ranging from "strongly disagree" to "strongly agree" (adapted from Longo et al. 2008, and Kalckert & Ehrsson 2012). For conceptual reasons, we focused on the subscales "body ownership" (3 items: "I felt as if the hand that I was seeing was part of my body," "I felt as if I was seeing my own hand," and "I felt as if the hand that I was seeing was my hand") and agency (3 items: "I felt as if I could cause movements of the hand that I was seeing," "The hand that I was seeing was obeying my will" and "I can make it move just like I want it to"), which were compared for each condition. For the visuotactile conditions, we additionally measured proprioceptive drift: before and after stimulation (with the HMD turned off) participants would have to point (with the non-stimulated hand) to the position of the stimulated hand under the table. In our setup, a null drift value corresponds to the perceived location of the stimulated hand being where it is located, while positive drift values refer to the stimulated hand being perceived as closer to the seen hand, and negative values refer to the perceived location of the stimulated hand being away from the seen hand (however the interpretation of negative drift values in terms of illusory ownership have, to our knowledge, not been thoroughly discussed in the literature).

## Data analysis

« 19 » Since the questionnaire data were not normally distributed, Wilcoxon signed rank tests with Bonferroni correction were used to compare how the four experimental conditions affected ownership and agency. Drift measures were normally distributed and analyzed in a 2×2 analysis of variance (ANOVA) with the within-subject factors "time" (pre and post) and "synchrony" (synchronous and asynchronous) for the visuotactile domain. *Results of questionnaire data: Ownership* in the visuomotor condition was significantly higher for synchronous than for asynchronous stimulation ($Z=3.63$, $p_{(corr)}<0.001$) while there was no significant difference between synchronous and asynchronous stimulation in the visuotactile condition ($Z=0.70$, $p_{(corr)}=1$). Ownership between the two conditions (visuotactile versus visuomotor) did not significantly differ for synchronous ($Z=1.5$, $p_{(corr)}=0.42$) but did significantly differ for asynchronous stimulation ($Z=3.34$, $p_{(corr)}=0.002$; with higher scores for the visuotactile than for the visuomotor condition). *Agency* in the visuomotor condition was significantly higher for synchronous than for asynchronous stimulation ($Z=3.63$, $p_{(corr)}<0.001$) while in the visuotactile condition, there was no significant difference between synchronous and asynchronous stimulation ($Z=0.90$, $p_{(corr)}=1$). Agency between the two conditions significantly differed for synchronous stimulation ($Z=3.45$, $p_{(corr)}=0.002$; with higher scores for the visuomotor than for the visuotactile stimulation) but not for asynchronous stimulation ($Z=1.6$, $p_{(corr)}=0.32$). *Results of proprioceptive drift data:* There was a significant main effect of time ($F_{(1,17)}=12$, $p=0.003$) but not of synchrony and no interaction between the two (F values $<2.8$, $p>0.11$).

## Discussion

« 20 » Illusory ownership was found in all conditions except in the asynchronous visuomotor condition. Notably, illusory ownership was induced even during asynchronous visuotactile stimulation. This is confirmed by the proprioceptive drift towards the virtual hand both in the synchronous and asynchronous visuotactile conditions. For the subjective feeling of agency, the scores were significantly higher during synchronous visuomotor stimulation when compared to all the other conditions. In contrast to the model proposed by Maselli and Slater (2013), our data show that even with visuoproprioceptive spatial mismatches, asynchronous visuotactile stimulation during 1PP FBI results in illusory ownership. Our results also show that even with a head-matched video-based (not computer-generated) setup visuotactile asynchrony is not enough to reduce body ownership.

## Integration with Gallagher's paradigm: Implications for the body image and schema

« 21 » We discussed how FBIs alter the way in which sensorimotor signals are integrated and provided arguments for a dissociation between head-related and limb-related sensorimotor coherence. We now attempt to fit our discussion to the concepts of body image and body schema as discussed by Gallagher (2005b). The demarcation between the mentioned concepts has many important subtleties to consider, but we would like to begin the discussion by addressing two questions proposed by Gallagher: "to what extent, and in what precise way, does one's body appear as part of one's perceptual field?" and "to what extent, and in what precise way, does one's body constrain or shape the perceptual field?" (Gallagher 2005b: 17). In Gallagher's opinion, the concept of body image is useful to address the first question, while that of body schema is useful for the second. For further clarification of the difference between body image and body schema, we quote Gallagher's *provisional* definition:[9]

> "A *body image* consists of a system of perceptions, attitudes, and beliefs pertaining to one's own body. In contrast, a *body schema* is a system of sensory-motor capacities that function without awareness of the necessity of perceptual monitoring. This conceptual distinction between body image and body schema is related respectively to the difference between having a perception of (or belief about) something and having a capacity to move (or an ability to do something)." (Gallagher 2005b: 24)

« 22 » Regarding the body image, Gallagher (2005b) further explores three conceptual distinctions emanating from the literature. These are

- *body percept:* the subject's perceptual experience of his/her own body;
- *body concept:* the subject's conceptual understanding (including folk and/or scientific knowledge) of the body in general; and
- *body affect:* the subject's emotional attitude towards his/her own body.[10]

During both ILI and 1PP FBIs, it is the *body percept* that is initially manipulated when participants look at their new bodies or limbs; their perceptual experience becomes determined by another limb/body. However, it seems that the seen body has to fit within certain boundaries of a *body concept* for the illusion to occur. Such a *body concept* is not necessarily conscious (Gallagher 2005b). As mentioned in the previous sections, the literature shows that not just any fake body or object can elicit illusory ownership (e.g., Lenggenhager et al. 2007; Maselli et al. 2016; Maselli & Slater 2013; Tsakiris & Haggard 2005). Yet, in the presence of sensorimotor coherence, there are some examples of illusory ownership over implausible virtual bodies (Maseli and Slater 2013; Ahn et al. 2016). More remarkably, and following our previous discussion, during 1PP FBI only bodies resembling human bodies *very* closely, that is, adhering to a plausible *body concept* (cf. Section "Empirical study" and Maselli & Slater 2013), result in illusory self-identification even during asynchronous feedback.[11]

« 23 » As for the body schema, Gallagher (2005b) defines it as "a system of sensory-motor capacities that function without awareness of the necessity of perceptual monitoring" (Gallagher 2005b: 24). While the relationship between these sensorimotor capacities and the body schema is quite general (Maravita, Spence & Driver 2003), Frédérique de Vignemont (2010) argues that apart from conceptual differences between several authors, there is some agreement that the body schema is distinguished by its role in guiding action. In this context, de Vignemont discusses various experimental results regarding the dissociation of body schema and body image during ILI. For example, one study shows an effect of altering body image during ILI on body schema, as manifested by grasping (Kammers et al. 2010). In the study, participants' motor programs were manipulated after visuotactile stimulation in an RHI-like protocol. However, another study reported different results for proprioceptive drift (Kammers et al. 2009). In that study, participants exhibited a drift towards the RH when carefully pointing at or when referring verbally to the position of their finger, but not when pointing at it through ballistic motor action.[12] It seems that action commands were thus not affected by the illusion. However, pointing may not be ideal for measuring modified motor commands (see de Vignemont 2010). While de Vignemont (2010) has integrated divergent findings from ILI studies in an attempt to disentangle body image and body schema,

9| Since our purpose is to match our empirically informed hypothesis with the author's distinction rather than to thoroughly discuss the two concepts, we will use Gallagher's provisional definition as a working definition.

10| While body affect certainly plays a role in FBIs, it is not strictly relevant to our argument and is – unfortunately – outside the scope of the current article.

11| During 1PP FBI, implausible bodies may also result in illusory ownership (see Ahn et al. 2016, for an example) but only through synchronous sensorimotor stimulation.

12| A ballistic motor action, or ballistic movement, is a rapid motor action requiring fast muscular activation. In this context, we contrast this type of action with that of carefully moving and adjusting movement based on other sensory input. According to de Vignemont, a ballistic motor action "should be entirely accounted for by commands existing before its initiation executed without visual feedback" (de Vignemont 2010: 674).

we propose that 1PP FBIs may be more applicable in demonstrating how body image and body schema interact during bodily illusions.

« 24 » Manipulations of body image could be considered the most important aspect of 1PP FBIs. Using immersive HMDs, the perspective of a humanoid body can induce illusory ownership by replacing one's perceptual field with that of another body. In contrast to ILI, 1PP FBIs occupy the entire visual field over a full body, with the possibility of additionally mapping new visual perceptual fields according to our head movements (i.e., our optic flow). In some cases, this even results in illusory ownership over the fake body despite asynchronous sensorimotor stimulation (see above). Moreover, the time window of sensorimotor integration has been reported to widen during illusory ownership in 1PP FBIs (Maselli et al. 2016). If we refer to these changes in sensorimotor integration as modifications of the sensorimotor capacities (to stick to the definition in Gallagher 2005b), we can address them as manipulations of the body schema. Thus, if the body image is manipulated to a certain degree in terms of the body percept and body concept, then the body schema changes. Fittingly, visually manipulating the angular mismatch of arm movements between the seen and the participant's own bodies during 1PP FBIs has been shown to affect the size estimation of surrounding space (Kokkinara et al. 2015).

« 25 » Remarkably, Maselli and Slater (2013) demonstrated that only when head motion was permitted did participants attribute the felt touch to the virtual (seen) object during asynchronous visuotactile stimulation. Hence, there seems to be a link between head-related visuoproprioceptive coherence during 1PP FBIs and the integration of sensorimotor signals (see above). Head movements, coupled with the strength with which the visual field is manipulated during 1PP FBIs, seem to be enough for the *image-schema* interaction to occur. While not enough empirical studies have systematically manipulated the sensorimotor coherences related to head movements, we argue that there is something unique about such head-related coherences. According to Gallagher,

> “Neurologically, the body schema depends on proprioceptive/kinesthetic/vestibular (and other sensory afferent) processes, registering in centrally organized neural matrixes, and issuing in (efferent) motor control commands.” (Gallagher 2005a: 239)

all of which are involved in head movements. In addition, head movements alter perspectival visual information in a way that peripheral-limb movements do not. If it is clear that head movements are a special sensorimotor process, and there is evidence of this process having an influence on the integration of sensorimotor signals during 1PP FBI, what would happen if we break the temporal match of head-related sensorimotor signals? Would the *image* still integrate with the *schema*?

« 26 » While this is currently purely speculative, our hypothesis is that breaking the temporal matching of sensorimotor integration related to head movements would prevent the manipulation of body schema by body image during 1PP FBIs. However, this should and could be experimentally tested. In our view, coherence between head movement and the visual field embodying a full humanoid body works as an integrating element between the two concepts proposed by Gallagher. An experimentally induced temporal mismatch in head-related sensorimotor signals could alter the body schema in such a way that participants may struggle with their motor commands. Yet, following our argument we believe that such changes in the body schema will not be consistent or bound to the body image presented on the HMDs. While it seems that temporal mismatches related to the peripheral body do not necessarily break the *image-schema* interaction, we hypothesize that temporal mismatches related to head movements would.

« 27 » If the *schema* and the *image* were not integrated during mismatched head-related sensorimotor stimulation, the question remains whether the seen body (from 1PP) would still be considered one's own body (image). We believe this to be the case, since

- our (primarily visual) perceptual field (or visual body percept) over our body has changed, and
- the foreign body may still fit the parameters of body percept and body concept.

« 28 » In the most radical simile to our own body image, we could imagine an experiment using an HMD and live video where participants see their own bodies from a 1PP, yet the visuomotor responses related to their head movements are not matched. In this hypothetical experiment, the body image would remain that of our own bodies, but the integration with our body schema would be broken by mismatching head-related visuomotor responses.

## Conclusion

« 29 » We have attempted to integrate recent experimental literature on illusions of the bodily self and our own data (cf. Section “Empirical study”) – showing conflicting results in terms of the temporal constraints for sensorimotor integration during bodily illusions – with Gallagher's distinction between body image and body schema. In our argument, we distinguished the integration of sensorimotor signals during two types of bodily illusions, illusory limb identification and first-person perspective full-body illusions, and proposed a dissociation between head- and limb-related sensorimotor integration. We emphasized head-related sensorimotor signals as a possible binding factor between body image and body schema in the context of 1PP FBIs.

« 30 » While purely speculative at the moment, this distinction could be important for the scientific study of the bodily self and might motivate future experiments, for which we have outlined experimental designs and hypotheses. To date, sensorimotor signals related to the body have been ascribed to a single category (conflating the head and the peripheral body). A distinction between head- and limb-related signals could refine experimental procedures aimed to further our understanding of the plasticity of the bodily self and sensorimotor integration. New ways to modify the bodily self and the integration of body image and body schema could also be applied in the clinical context (e.g., for motor-/neuro-rehabilitation).

« 31 » To summarize, given that the seen image fits a *body concept* of the body image during 1PP FBIs, our body image

**MARTE ROEL LESUR**
is a doctoral researcher in Cognitive Neuropsychology at the University of Zurich; his work lies in the intersection of art and science. Marte is a member of the art/research collective BeAnotherLab, who develop multisensory collaborative platforms for generating the illusion of embodying another person.

**MICHAEL GAEBLER**
is a postdoctoral cognitive neuroscientist at the Max Planck Institute for Human Cognitive and Brain Sciences and the MindBrainBody Institute at the Berlin School of Mind and Brain. Michael studies how mental processes like thoughts or feelings relate to brain-body interactions in pathology and health. He conducts behavioral and neurophysiological experiments in classical lab environments but also uses virtual reality, which may allow a more "holistic" investigation of mental phenomena.

**PHILIPPE BERTRAND**
is a doctoral researcher in Psychology at the Université Paris Descartes and the Centre de Recherches Interdisciplinaires in Paris. Co-creator of the system The Machine to Be Another, he works in the intersection of art, science, technology and education to develop, implement and analyze the use of embodied VR as a learning tool of empathy-related abilities.

**BIGNA LENGGENHAGER**
is professor at the University of Zurich and head of the research group Cognitive Neuropsychology with focus Body, Self and Plasticity; her work focuses on the empirical investigation of multisensory integration mechanisms, the bodily self, and embodied cognition in both pathology and health.



(i.e., the perceptual field showing a foreign body) may modify our body schema (i.e., how we integrate sensorimotor signals). We hypothesize that if we were to break head-related body schematic coherence, the interaction between body image and body schema would not occur. This conveys a seemingly paradoxical idea regarding bodily illusions: while these illusions are a result of the experimental procedure, they are also a cause of their own resistance to sensorimotor incoherence. In other words, the resistance to the illusion partly depends on parameters of the illusion itself. Our hypothesis is that the perception of immersive 1PP optic-flow coherence to head movements is a parameter with enough strength to alter the illusion itself. By attempting to synthesize recent results (from others and from us) and integrate them with philosophical considerations, we aim to further our understanding of what constitutes the bodily self, and what accounts for its remarkable plasticity.

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# Open Peer Commentaries

## on Marte Roel Lesur et al.'s "The Plasticity of the Bodily Self"

### Sense of Ownership and Sense of Agency in First-Person-Perspective Full-Body Illusions

Felipe León
University of Copenhagen, Denmark
felipe.leon/at/hum.ku.dk

**> Abstract** • In my commentary, I raise some questions about the applicability of Gallagher's distinction between body image and body schema to the experimental research reported and discussed in the target article. I suggest that the distinction between body image and body schema is of limited help in this context, and that Gallagher's distinction between sense of ownership and sense of agency provides a more natural and fruitful theoretical framework to discuss that research.

«1» The possibility of inducing illusions of bodily ownership and bodily agency over foreign limbs and full foreign bodies has given rise to a thought-provoking literature about the constituents and malleability of the human sense of bodily self. Marte Roel Lesur et al.'s target article illustrates nicely how the experimental manipulation of sensorimotor signals, in tandem with technological advances, enables an increasingly fine-grained investigation of the bodily self, and in particular of the role that different sensorimotor factors play in bodily illusions. The authors focus on two types of illusions: the illusory limb identification (ILI) (§3) – a paradigm of which is the rubber hand illusion – and first-person perspective full-body illusions (1PP FBI) (§4), in which a subject wearing a head-mounted display gains virtual access to the perceptual and embodied perspective of someone else. While I agree with the authors that investigating different types of bodily signals during bodily illusions can shed light on the sense of bodily self, I have reservations about the way in which they link their discussion with Shaun Gallagher's distinction between body image and body schema. I will briefly suggest that Gallagher's distinction between sense of ownership and sense of agency could be more