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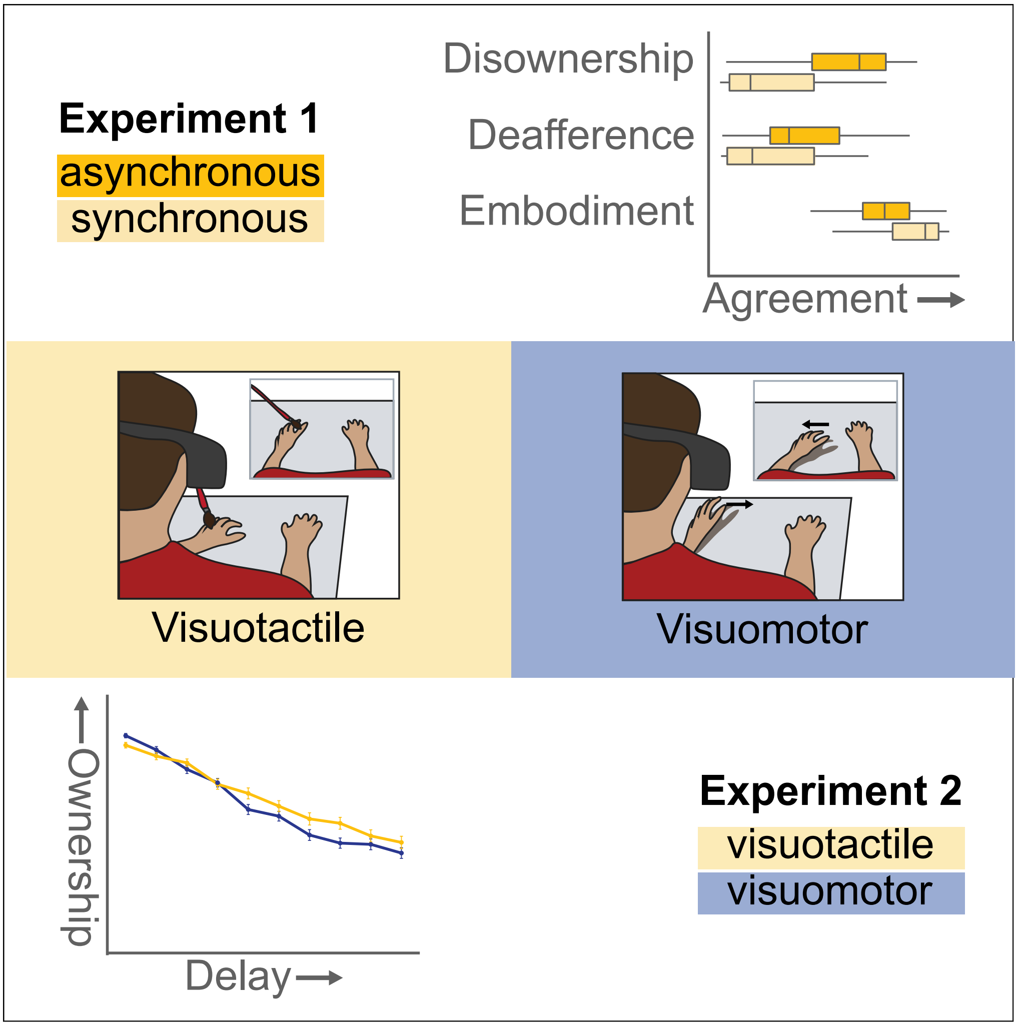

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HIGHLIGHTS

Temporal multimodal conflict from own body induces disembodiment

Main components of disembodiment are disownership, deafference, and reduced embodiment

Subjective reports are not reflected by implicit measures

Disembodiment increases faster with visuomotor than with visuotactile mismatch

Roel Lesur et al., iScience *23*, 100901
March 27, 2020
https://doi.org/10.1016/j.isci.2020.100901

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Psychometrics of Disembodiment and Its Differential Modulation by Visuomotor and Visuotactile Mismatches

Marte Roel Lesur,[1,4,5,*] Marieke Lieve Weijs,[1,4] Colin Simon,[1] Oliver Alan Kannape,[2,3] and Bigna Lenggenhager[1,*]

SUMMARY

Altered states of embodiment are fundamental to the scientific understanding of bodily self consciousness. The feeling of disembodiment during everyday activities is common to clinical conditions; however, the direct study of disembodiment in experimental setups is rare compared to the extensive investigation of illusory embodiment of an external object. Using mixed reality to modulate embodiment through temporally mismatching sensory signals from the own body, we assessed how such mismatches affect phenomenal and physiological aspects of embodiment and measured perceptual thresholds for these across multimodal signals. The results of a principal component analysis suggest that multimodal mismatches generally induce disembodiment by increasing the sense of disownership and deafference and decreasing embodiment; however, this was not generally reflected in physiological changes. Although visual delay decreased embodiment both during active movement and passive touch, the effect was stronger for the former. We discuss the relevance of these findings for understanding bodily self plasticity.

INTRODUCTION

Over the past two decades, experimental evidence has shown that the sense of body of healthy subjects is remarkably plastic and built upon a constant prediction, weighting, and integration of multimodal signals (e.g. Blanke, 2012; Ehrsson, 2012; Kilteni et al., 2015). Protocols involving multimodal stimulation suggest that a majority of healthy individuals embody foreign or virtual limbs or full bodies when bodily sensations (e.g. body movements or touch) are visually displayed in synchrony to matching sensations on the hidden body (e.g. Botvinick and Cohen, 1998; Tsakiris et al., 2006; Lenggenhager et al., 2007; Slater et al., 2010). Such illusory embodiment is usually manifested by the senses of body ownership and agency (Kalckert and Ehrsson, 2012; Tsakiris et al., 2006) as well as self location (Longo et al., 2008) and has been evidenced using a variety of experimental setups using both explicit (e.g. questionnaire) and implicit (e.g. proprioceptive drift or physiological response) measures (Blanke et al., 2015).

This line of research predominately investigated the influence of multimodal coherence on illusory embodiment of an external or supernumerary bodily object; far more elusive, however, is how breaking multimodal information about the own body might reduce embodiment or even induce a feeling of disembodiment (Gentile et al., 2013; Graham et al., 2015; Hoover and Harris, 2012; Kannape et al., 2019; Newport and Preston, 2011; Otsuru et al., 2014; Newport and Gilpin, 2011; Longo and Haggard, 2009; Osumi et al., 2018). This is surprising, as disorders of bodily self awareness in clinical populations predominantly manifest in a loss of embodiment, as a break of (own) body ownership and one's sense of agency (Aglioti et al., 1996; Brugger and Lenggenhager, 2014; Otsuru et al., 2014; Vallar and Ronchi, 2009). For example, in the case of somatoparaphrenia, resulting from a brain lesion, patients lack the feeling of ownership for the contralesional arm, often attributing that arm to someone else (Aglioti et al., 1996; Brugger and Lenggenhager, 2014; Vallar and Ronchi, 2009) or even showing aggression toward it (Loetscher et al., 2006). Similarly, individuals suffering from body integrity dysphoria feel strong alienation from one or several body parts often combined with a desire for amputation (Blom et al., 2012; Brugger and Lenggenhager, 2014; Lenggenhager et al., 2015). Such a feeling of disembodiment might also extend to the full body, both in neurological (Smit et al., 2018) as well as in psychiatric disorders, as during depersonalization (Davidson, 1966; Sierra et al., 2005) or borderline personality disorder (Löffler et al., 2019).

Important theoretical differences between ownership of an external body, reduced ownership for one's own body, and body disownership have been proposed (de Vignemont, 2011), and the degree of alteration

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https://doi.org/10.1016/j.isci.2020.100901

in embodiment of the own body in illusory limb or full-body ownership paradigms remains elusive. Although some authors suggest decreased ownership for the real body based on questionnaire (Longo et al., 2008; Moseley et al., 2008; Lane et al., 2017) or even immunological data (Barnsley et al., 2011), others found disownership of one's own body to be rare and rather weak in rubber-hand-illusion-like setups (Folegatti et al., 2009). Data from individuals with clinically caused alterations leading to loss of own-body ownership generally suggest enhanced illusory ownership for an external body, pointing to different mechanisms between embodiment and disembodiment in patients suffering from schizophrenia (Thakkar et al., 2011; see Shaqiri et al., 2018 for alternative findings during full body illusions), body integrity dysphoria (Lenggenhager et al., 2015), or somatoparaphrenia (Smit et al., 2018; van Stralen et al., 2013; White and Aimola Davies, 2017). This is further evidenced by a voxel-based lesion symptom mapping study that found a partial dissociation between brain areas involved in own-limb disembodiment as compared with supernumerary embodiment (Martinaud et al., 2017).

Here we directly manipulated embodiment of one's biological hand using a controlled multisensory conflict, without the use of a proxy/rubber hand. Previous studies suggest a feeling of disownership and numbness during delayed and therefore conflicting visual feedback of a tactile or motor event in a mixed reality setup using an infrared camera feed (Kannape et al., 2019), a mixed reality setup using a prerecorded video (Gentile et al., 2013), or in the MIRAGE setup where participants enter their hand in a box where visual aspects (spatial or temporal) of the hand are altered (e.g. Newport and Preston, 2010; Newport and Preston, 2011). We adapted such setups to be more realistic and ecologically valid using a wide field of view webcam mounted on a head-mounted display (HMD), providing an online, naturally colored, view of the video feed. This setup provides a direct view on the own full body in its current environment as seen from a first-person perspective, roughly corresponding to the direct view of the own body. Our setup was created to induce a strong prior assumption of actually viewing one's own body and surroundings. We then manipulated the delay of the video feed digitally, thus controlling the latency of visual as compared to other bodily signals (i.e. tactile, motor, or potentially others). We used this setup in two different experiments to evaluate the relative influence of multimodal mismatches about one's own body on the sense of embodiment and its physiological correlates. Importantly, although previous studies investigated the effect of either visuotactile incongruency or visuomotor incongruency on the sense of embodiment (e.g. Tsakiris et al., 2010; Kalckert and Ehrsson, 2012, 2014), the systematic comparison of these and their contribution to disembodiment remains scarce. Yet, differential roles of motor and somatosensory signals in the sense of body have been suggested (Asai, 2015; Tsakiris et al., 2006, 2010), and the role of actively (moving) in comparison to passively perceiving bodily signals to the bodily self has been extensively discussed (Grechuta et al., 2019; Pia et al., 2019). We thus compared the relative contribution of breaking visuomotor versus breaking visuotactile signals to disembodiment.

In Experiment 1 (Figure 1A), we manipulated visuotactile coherence, which is classically used to induce altered embodiment in rubber-hand-illusion-like paradigms. For two stimulation durations (1 and 3 min) the participant's hand was stroked with a paintbrush while the visual feedback, was either delayed (~disembodiment illusion condition) or not (~control condition). Alterations in embodiment, ownership, sensations of deafferentation, and related phenomenal sensations were measured using questionnaires adapted from Botvinick and Cohen (1998), Kannape et al. (2019), Lenggenhager et al. (2007), and Longo et al. (2008). To further understand the phenomenal qualities, we used a psychometric approach by performing a principal component analysis (PCA) on the questionnaire data of a larger sample. Furthermore, previously suggested implicit correlates of embodiment, namely skin temperature (see Moseley et al., 2008, but see also de Haan et al., 2017 for a critical view) and skin conductance responses (SCR) to threat (see Armel and Ramachandran, 2003) were assessed. Heart rate variability (HRV) measures were added, as homeostatic processes have suggested to be altered in conditions of alteration in body ownership (Barnsley et al., 2011). A measure of interoceptive accuracy has been included, as poor accuracy has previously shown to be related to higher susceptibility to illusory ownership and thus a more plastic bodily self (Monti et al., 2019; Tsakiris et al., 2011; but for exceptions see Crucianelli et al., 2018 and David et al., 2014). We hypothesized that the sensory conflict between tactile and delayed visual feedback would result in a reduced sense of embodiment and enhanced sense of disembodiment, which would be reflected in both explicit (subjective) and implicit (physiological) measures, especially in participants with a weak interoceptive accuracy.

In Experiment 2 (Figure 1B), we investigated the temporal thresholds for detecting synchrony for visuomotor as compared to visuotactile delays and how different delays relate to the feeling of *dis*embodiment.

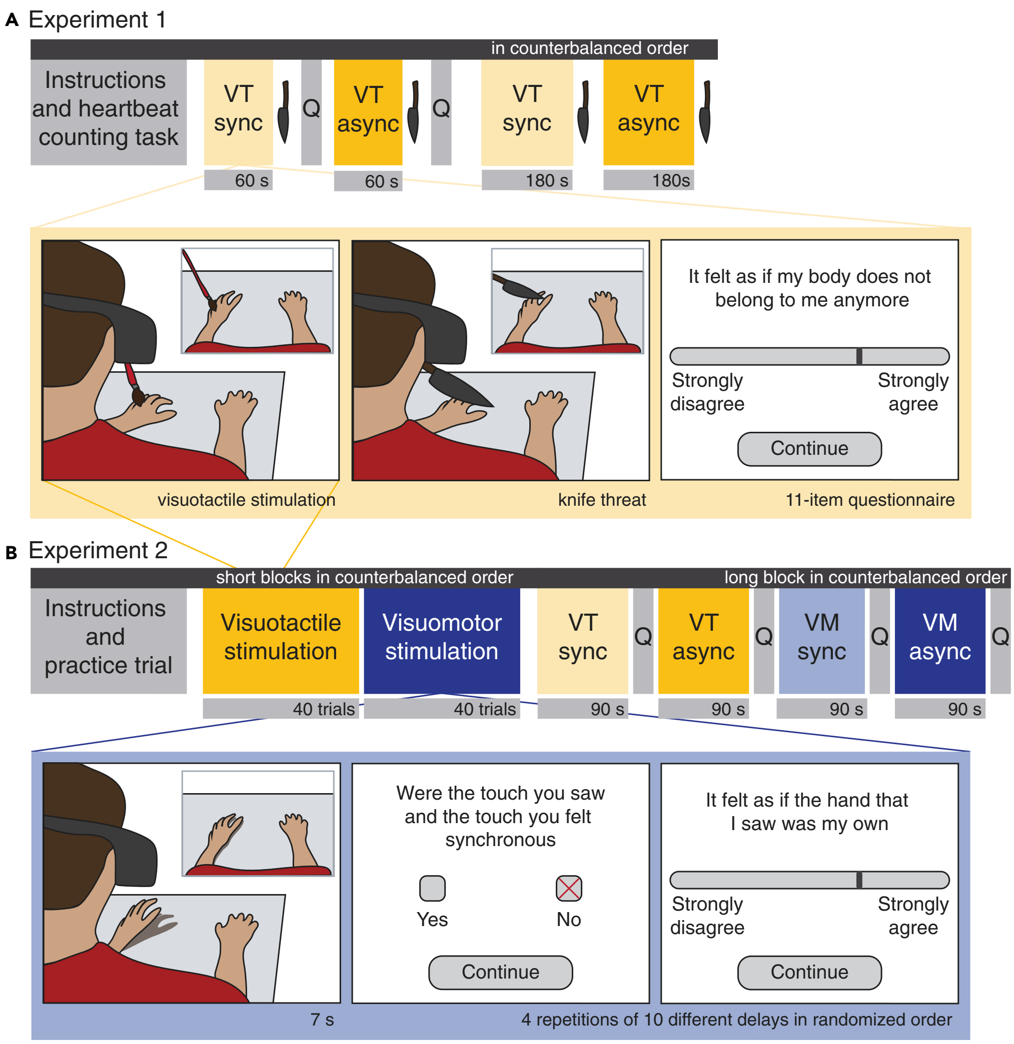

Figure 1. Experimental Procedure

Experimental setup in (A) Experiment 1 and (B) Experiment 2. In both experiments participants were sitting down with both hands placed on a table. In Experiment 1, the visuotactile stimulation was either synchronous (VT sync) or asynchronous (VT async). Each stimulation was followed by a knife threat and in the 60 s blocks also by the embodiment questionnaire (Q). The 60 s blocks were always presented first, followed by the 180 s blocks. The order of VT sync and VT async was counterbalanced across participants. In Experiment 2 the visuotactile stimulation was similar to that of Experiment 1. Here, visuomotor or visuotactile stimulation were presented for 7 s during which the participant's hand was stroked two times. After each 7 s trial two questions appeared on the HMD. This was repeated 40 times for each modality, with four repetitions of 10 possible delay steps. Then, a long block followed with synchronous visuotactile (VT sync) and visuomotor (VM sync) as well as asynchronous visuotactile (VT async) and visuomotor (VM async) stimulation presented in counterbalanced order.

Participants were exposed to 40 trials in each condition with differing delays across a range of 139–733 ms, and after each trial synchrony perception and the feeling of ownership were assessed. These were followed by a block of longer stimulation of 90 s in both a visuomotor and visuotactile condition where the visual feedback was either delayed (~disembodiment illusion condition) or not (~control condition). Systematic empirical comparisons of these multimodal couplings remain rather scarce, with some studies suggesting similarly strong bodily illusions for visuomotor and visuotactile synchrony (Kalckert and Ehrsson, 2012, 2014), others suggesting that visuomotor synchrony may be more important for illusory embodiment than visuotactile synchrony (Kokkinara and Slater, 2014; Roel Lesur et al., 2018), and some suggesting the relative importance of active movements versus passive touch for an integrated and global sense of body (Burin et al., 2015; Tsakiris et al., 2010, 2006). Moreover, there is evidence suggesting that the

		Varimax Rotated Factor Loadings			Commonalities
	Sometimes I Felt …	Component 1 *Disownership*	Component 2 *Deafference*	Component 3 *Embodiment*	
q4	Alienation from my body	**.81**	.21	.05	.70
q6	As if my body does not belong to me anymore	**.78**	.18	.29	.73
q9	The seen body as an image rather than as my actual body	**.65**	.24	-.04	.50
q10	As if my body was numb	.12	**.81**	-.03	.68
q8	As though the experience of my hand was less vivid than normal	.23	**.81**	-.14	.73
q7	As though my body had disappeared	.25	**.78**	.30	.75
q1	As if the body I saw was my own	.02	.00	**.89**	.79
q11	As if I could move the seen body	.10	.05	**.81**	.67
q5	As if I was looking at another person's body	**.53**	-.05	**.57**	.61
Eigenvalues		2.11	2.06	1.98	
% Of variance		23	23	22	

Table 1. Factor Loadings from the PCA on Nine Items of the Questionnaire in the Asynchronous Visuotactile Condition

Note. Factor loadings >.50 are in boldface.

temporal window of multisensory integration of peripheral signals is narrowed when followed by efferent signals as compared to only afferent signals (Zierul et al., 2019); however, these findings have not explicitly been linked to the sense of body.

RESULTS

Results of Experiment 1

Principal Component Analysis Reveals Three Main Components of Disembodiment

A PCA was used to investigate the structure of participants' experience and to quantify the complex experience during this illusion. The PCA was conducted on the questionnaire data after synchronous or asynchronous visuotactile stimulation. Data from Experiment 1 (n = 30), Experiment 2 (n = 32), and additional data from an unpublished experiment of 15 participants were used for the PCA. After running a primary PCA to determine the number of components, a secondary PCA with three components was used for the analysis. The three components together explained 68% of the variance in the questionnaire data (see Table 1 for component loadings after varimax rotation and explained variance of each component). The first component was termed disownership and comprised items that refer to the experience of not belonging of the body, alienation, and perceiving the body as an image rather than an actual body (q4, q6, and q9). The second component was termed deafference (Longo et al., 2008) and included items related to the feeling of numbness, vividness, and disappearing of the body (q10, q8, and q7). The final component, embodiment, consisted of items related to the experience of own body ownership, agency, and looking at one's own body (q1, q11, and q5).

Responses to questionnaire items are in line with our hypotheses (Figure 2, see Table S2 for descriptive statistics and results of the comparisons for all individual items). Participants reported a relative increase

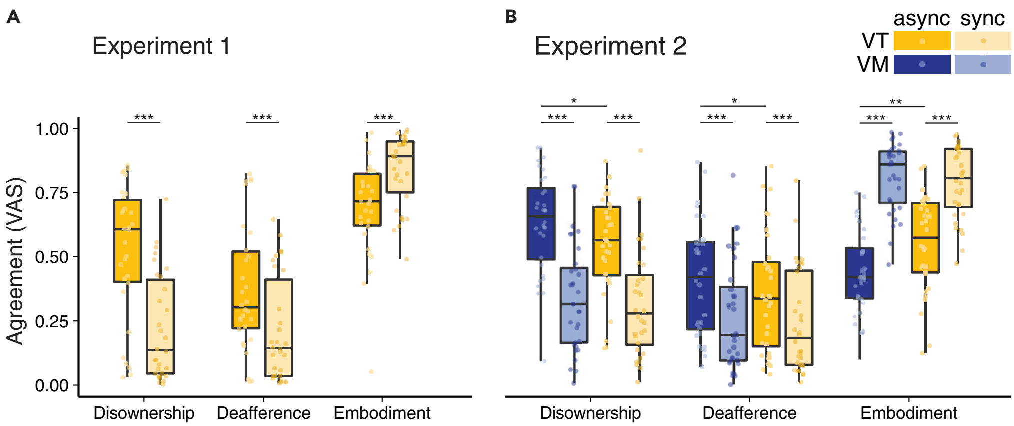

Figure 2. Questionnaire Responses Clustered by the PCA Factors Questionnaire data, medians, and interquartile ranges are displayed.

The three components of the questionnaire differed significantly between the synchronous (sync) and asynchronous (async) visuotactile (VT) stimulation in Experiment 1 (A). In Experiment 2 (B) there were significant differences between the synchronous and asynchronous stimulation for both the visuotactile, and visuomotor (VM) stimulation, as well as between visuotactile and visuomotor stimulation in the asynchronous, but not the synchronous, condition. *p < .05, ** p < 0.01, ***p < 0.001.

of disownership, deafference (though generally low [<0.5] in both conditions), and a relative reduction of embodiment (though generally still high [>0.5] in both conditions) after asynchronous visuotactile stimulation compared with synchronous stimulation. As expected, responses to the control item (q3) did not differ between conditions, and the manipulation check item (q2) differed between the synchronous and asynchronous condition, which confirmed that participants were able to perceive the manipulation.

Skin Conductance Response to Threat Is Not Altered

Previous studies demonstrated that SCRs to threats increased after synchronous stroking in rubber-hand–illusion-like paradigms (e.g. Armel and Ramachandran, 2003; Petkova and Ehrsson, 2008): a study showed reduced SCR to a threat after multisensory mismatching stimulation (Gentile et al., 2013), another a reduction of SCR after stimulating illusory dissapearance of the hand (Newport and Gilpin, 2011), and a similar pattern after asynchronous multimodal stimulation (Newport and Preston, 2010, 2011). As disownership was higher in the asynchronous condition, we hypothesized that SCRs would be reduced as compared to the synchronous condition. Even though we found an increase in skin conductance after threat, we did not observe significant differences between the synchronous and asynchronous condition in neither the short, (synchronous: *Mdn* = 1.13, IQR = 0.90–1.38; asynchronous: *Mdn* = 0.94, IQR = 0.71–1.16; $Z = -1.42$, p = .16) nor the long block (synchronous: *Mdn* = 1.01, IQR = 0.60–1.19; asynchronous *Mdn* = 0.94, IQR = 0.58–1.10; $Z = -0.48$, p = .63). This indicates that there was no evidence for a difference in the sympathetic activation in response to a threatening stimulus to the hand after asynchronous as compared to synchronous stimulation, even though participants subjectively experienced less embodiment and increased disownership over their own hand according to the questionnaire.

Skin Temperature Is Not Altered

Comparisons between synchronous and asynchronous conditions in the short block did not reveal any significant differences between conditions in temperature change for the neck (p = .76), right hand (p = .38), or left hand (p = .27). However, in the long block, there was a significantly smaller increase in skin temperature of the left hand across the trial in the asynchronous (*Mdn* = 0.038, IQR = −0.009–0.143) than synchronous condition (*Mdn* = 0.078, IQR = 0.012–0.158; $Z = -2.09$, p = .04, $r = -.30$). We further aimed to disentangle this small but significant effect for the left hand, by assessing differences between the conditions in each of the three minutes separately, but these analyses did not show any significant differences for any of these time periods (all ps> .48). There were no significant differences for the neck (p = .37) or the right hand (p = .72).

Heartrate Variability Is Not Altered

HRV, as quantified by the RMSSD, did not differ between the synchronous (*Mdn* = 30.62, IQR = 21.22–54.37) and the asynchronous condition (*Mdn* = 32.84, IQR = 24.61–45.30; $Z = -0.25$).

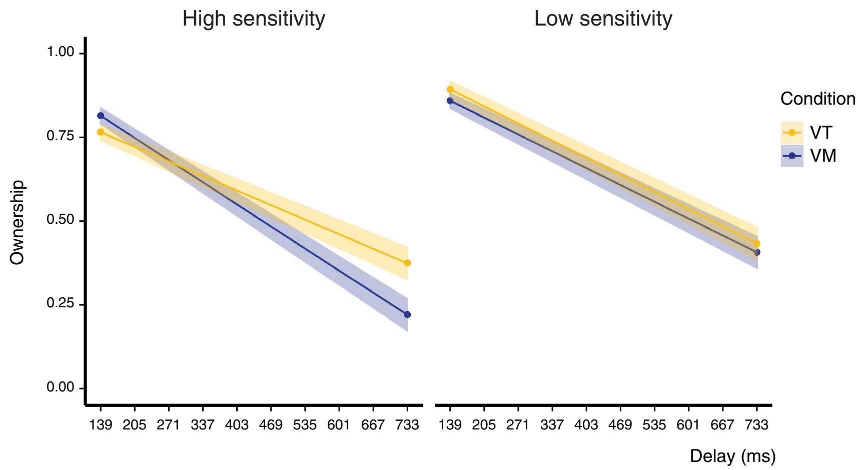

Figure 3. Predicted Ownership by Delay and Sensitivity to Delay

The three-way interaction of delay, modality (visuotactile [VT] and visuomotor [VM]), and sensitivity is displayed. Lines show predicted values from the model, where sensitivity was set to $M - 1$ *SD* for high sensitivity and $M + 1$ *SD* for low sensitivity for visualization purposes.

No Relation of Illusion Strength and Interoceptive Accuracy

Overall mean interoceptive accuracy was 0.62 ± 0.17, which is comparable to other studies (e.g. Garfinkel et al., 2015). We performed a median split on interoceptive accuracy scores to assess the differences in previously reported significant effects of synchrony between participants with high (*Mdn* = 0.77, IQR = 0.67–0.85) and low (*Mdn* = 0.46, IQR = 0.43–0.52) interoceptive accuracy. There was no significant difference between participants with high and low accuracy in the subjective strength of the illusion (difference between category average in synchronous and asynchronous) for the disownership ($Z = -0.48$, p = .63), deafference ($Z = -0.33$, p = .74), and embodiment ($Z = -0.63$, p = .53) category.

Summarized Results of Experiment 1

In this first experiment we showed that asynchronously shown stroking of one's own real hand using a video-based virtual reality setup leads, as predicted, to consistent and significant changes in the subjective sense of the bodily self as indicated by the responses to the questionnaire. According to the principal component analysis the response to this questionnaire can be clustered in three main components, namely disownership, deafference, and embodiment. During asynchronous as compared with synchronous stroking embodiment for one's own body is reduced, whereas the sense of disowernship and deafference is enhanced. In contrast to our prediction based on rubber-hand-illusion-like setups, despite these manipulations we did not evidence any physiological changes. There was no evidence for changes in the electrodermal response to threat, and the temperature measure only showed a mild trend toward a lesser increase in hand temperature in the asynchronous condition. Furthermore, we did not find the predicted relation between the individual strength of interoception and the subjective measures of the illusion.

Results of Experiment 2

Questionnaire Ratings Reveal Subjective Changes after Asynchronous Stimulation with a Stronger Effect of Visuomotor Than Visuotactile Signals

To assess the subjective experience of participants after 90 s of visuotactile or visuomotor stimulation, differences between responses to questionnaire items in the asynchronous and synchronous conditions were assessed (see Figure 3; and Tables S4 and S5 for descriptive statistics and results for each individual item). The results confirmed our hypothesis that asynchronous visuotactile and visuomotor stimulation induced a feeling of disownership for the seen body and followed a same pattern as in Experiment 1. There was a significant main effect of condition for the three illusion-related factors that were determined in the PCA (see section Principal Component Analysis Reveals Three Main Components of Disembodiment). Interestingly, the reduction of embodiment and increase in deafference and disownership were stronger in the asynchronous visuomotor than visuotactile condition. There were no significant differences between conditions for the control item (q3), and the differences in q2 confirmed that participants were able to perceive the manipulation.

Synchrony Judgements Did Not Differ between Modalities

To assess whether sensitivity to delay was affected by modality of stimulation, we compared the PSE in the visuomotor (M = 0.338, SE = 0.015) and visuotactile condition (M = 0.327, SE = 0.014). There was no significant difference between the two conditions (Z =−.55, p = .58). Sensitivity was also not correlated with relative changes in any of the questionnaire components between the synchronous and asynchronous stimulation in both the visuotactile (all ps> .59) and visuomotor (all ps> .44) conditions. Crucially, responses to only 2.3% of all trials in the visuotactile and 0.8% in the visuomotor condition stated that the 0 ms delay was asynchronous, thus indicating that stimulation with the intrinsic delay was generally perceived as synchronous.

VAS Body Ownership Ratings Drop with Increasing Delay

To assess the influence of delay, modality, and delay perception on ownership, we fitted mixed models in a stepwise procedure. First, we fitted a model that included fixed effects for delay and condition and their interaction (see Table S6 for model coefficients). To explore whether sensitivity to delay for the different modalities, as quantified by the PSE, explained additional variance, we added the main effect and the two- and three-way interactions with delay and condition in a second model. The model fit of the PSE-model was better than that of the initial model (BIC model 1 = −1676.7, BIC PSE-model = −1709.5), and the PSE-model explained 32% of the variance in VAS ownership ratings (pseudo R^2 = .32). Adding age as a predictor did not improve the model fit (BIC age-model: −1705.2) and was thus removed from the model. There was a significant three-way interaction of all predictors (delay × modality × PSE; b = 2.19, 95% CI: 1.15, 3.23, t(2213.7) = 4.13, p < .001; see Table S7 for all model coefficients). Overall, VAS ratings of ownership decreased with increasing delay. A stronger decrease in ownership was present especially in the visuomotor condition for participants with high sensitivity for delay. For lower sensitivity to delay there was no strong difference in the decrease of ownership between the visuotactile and visuomotor conditions (see Figure 3).

Summarized Results of Experiment 2

The results from the long stimulation in Experiment 2 show that visuomotor asynchrony when actively moving the hand in the same setup as in Experiment 1 also induces a decrease in embodiment coupled with an increase in disownership and sense of deafference. These changes were significantly stronger during visuomotor than during visuotactile mismatch. In line with this, the results from the short time exposure to various delays show that although increasing delay attenuates embodiment in both modalities, in participants with high delay sensitivity visuomotor delays affected embodiment already at smaller delays. Together these results might suggest a stronger contribution of visuomotor as compared to visuotactile synchrony in maintaining embodiment of the own hand or/and a heightened sensitivity to mismatch during active body movements as compared with passive touch. It should be noted, however, that the visuomotor task included a tactile component when participants put their hand on the table after each movement trajectory, in which case it may be the trimodal interaction that affects disembodiment more strongly.

DISCUSSION

In two separate experiments and a PCA for a larger sample, we set out to assess how mismatching multimodal signals about one's own body alter the sense of embodiment in healthy participants. For this, the participant's hand was passively stroked or actively moved while their own body was seen from a first-person perspective on an HMD in a realistic video-based environment. The visual signals were either delayed (asynchronous; experimental condition) or presented simultaneously (synchronous; control condition; although including the system delay of ∼139 ms) compared to the bodily signals (i.e. tactile or motor related). We used a (dis)embodiment questionnaire as well as physiological measures that have previously reported to correlate with body ownership (Experiment 1) and a series of synchrony and embodiment judgements across different visuotactile and visuomotor delays (Experiment 2). The two studies revealed three main findings. First, both visuotactile and visuomotor mismatches led to increased disembodiment, which predominantly involved the feelings of disownership, deafference, and embodiment (PCA results Experiment 1 and Experiment 2). Second, visuomotor delay when actively moving the hand led to a stronger feeling of disembodiment than visuotactile delay during passive touch. In participants with high delay sensitivity this was also evidenced by a steeper decay of body ownership with increased delay for visuomotor signals (Exp 2). Third, implicit measures of body ownership such as SCR and skin temperature showed overall no evidence of being modulated by the illusion, except for a small difference in the hand temperature that should be taken with caution because it was only significant for the whole duration of the long-stimulation block and not for shorter periods within that block (Experiment 1).

Multimodal Temporal Mismatches from the Own Hand Alter the Bodily Self

Subjective changes in embodiment were measured with a questionnaire given to the participants after a stroking period. In line with previous studies (e.g. Gentile et al., 2013; Kannape et al., 2019) asynchronous stimulation generally reduced the feeling of embodiment, suggesting that synchronous multisensory inputs are crucial not only to induce embodiment over a fake body (e.g. Botvinick and Cohen, 1998) but also to maintain the sense of embodying one's own body. In a PCA based on the asynchronous visuotactile stroking, we identified three main factors of the subjective disembodiment experience. These are disownership corresponding to the experience of not belonging of the body, alienation, and perceiving the body as an image rather than as an actual body; deafference, which, in accordance to Longo et al. (2008) includes numbness and vividness, plus in our case disappearance of the own body; and embodiment, consisting of the experience of body ownership, agency, and the feeling of looking at one's own body. Our results show that both visuotactile and visuomotor mismatches lead to increased disownership, deafference, and decreased embodiment respectively, when compared to synchronous stimulation.

In the case of synchronous stimulation, only two main factors were identified in the PCA, namely embodiment and disownership, together accounting for 71% of the variance (see Table S3). These results exclude the deafference component found for asynchronous stimulation. Although this might be expected because our bodily experience is not generally accompanied by a sense of deafference, it should be noted that asynchronous signals led not only to a disruption of the components found for synchronous signals but also to a new phenomenal component (see Longo et al., 2008 for similar results using a rubber hand illusion). This suggests that disembodiment does not only vary along the dimensions of embodiment and disownership, but also includes a sense of deafference.

As mentioned in the Introduction, the direct study of disembodiment in contrast to embodiment of a fake limb is not trivial, as important conceptual (e.g. de Vignemont, 2011; Folegatti et al., 2009) and neuroanatomical (Martinaud et al., 2017; Zeller et al., 2011) differences between these two mechanisms have been suggested. Furthermore, there is only indirect, sparse, and non-conclusive evidence of embodiment of a fake limb altering disembodiment (de Vignemont, 2011; Folegatti et al., 2009). Thus the currently most common way to study disembodiment, namely in RHI-like paradigms (Barnsley et al., 2011; Longo et al., 2008; Moseley et al., 2008), is problematic, as it (1) does not necessarily apply to some disturbances in body ownership and (2) may not actually induce the phenomena of interest. In this sense, the direct stimulation of disembodiment by altering own-body related signals may be important and more ecologically valid than using fake limbs. Several experimental setups for stimulating disembodiment on the own body exist, using mirror-based (e.g. McCabe et al., 2005), MIRAGE (e.g. Newport et al., 2010; Newport and Gilpin, 2011; Newport and Preston, 2011), infrared camera feed (Kannape et al., 2019), or pre-recorded setups (Gentile et al., 2013), yet we add to this palette the capacity to show the full body and the natural environment from a first-person perspective and alter it in real time (see Stanton et al., 2018 for a similar setup for manipulating non-temporal aspects of the body).

The Effect of Visuomotor as Compared with Visuotactile Mismatch on the Phenomenology of Disembodiment

Our questionnaire data from Experiment 2 replicated and extended the findings of Experiment 1 by showing that both asynchronous visuotactile signals as well as asynchronous visuomotor signals lead to increased disembodiment. Moreover, prolonged asynchronous visuomotor signals had a stronger effect on disembodiment compared with that of visuotactile signals. Although previous studies using foreign bodies or body parts have suggested that the tolerance for asynchronous visuotactile versus visuomotor stimulation during embodiment might differ (Kalckert and Ehrsson, 2012; Kokkinara and Slater, 2014; Roel Lesur et al., 2018; Tsakiris et al., 2006) and the specific contribution of actively moving on the bodily self has been intensively discussed (Grechuta et al., 2019; Pia et al., 2019), we here compared the relative contribution of these couplings by directly manipulating signals explicitly related to the own body. Although it is known that in the clinical population both alterations in the sensory and motor systems might correlate with feelings of disembodiment, our results suggest that there may be a stronger contribution of the latter to disembodiment. On these lines, for example the rubber hand illusion has been related to activity in the premotor cortex (Ehrsson et al., 2005; Ehrsson et al., 2004); and in clinical cases

Burin et al. (2015) found that participants with left upper-limb hemiplegia experienced a greater rubber hand illusion in their affected hand when compared with both their unaffected hand and a control group, arguing that the reduction of efferent signals in these participants contributed to weakening their own body ownership, resulting in a more plastic sense of body. Our results further extend these findings showing that in healthy participants, breaking visuomotor synchrony facilitates the sense of disembodiment.

The data from the short trials of different delay steps might provide a more sensitive measure of the relation between small multimodal mismatches and its subjective interpretation and disembodiment. As hypothesized, the results generally showed better asynchrony detection and a decreased sense of ownership over one's own body with increased delay. This finding was true for both the tactile and the motor modality, and there were no significant differences in terms of perceived delay between multimodal couplings. This is surprising as previous literature suggested a greater delay sensitivity depending on the strength of efferent signals (Hoover and Harris, 2012; Lau et al., 2004; Winter et al., 2008; the latter however without a statistically significant difference). A possible reason for this difference to previous literature is that our protocol might not have had a high enough temporal resolution to assess small differences in synchrony judgments, as previous literature has found it varying between 22 ms (Hoover and Harris, 2012) and 29 ms (Winter et al., 2008). Moreover, theoretical models would suggest that with the presence of efferent signals, there would be a stronger expectation of afferent signals (Wolpert, 1997), thus affecting the perception of the afferent stimuli.

High sensitivity to delay, however, predicted overall lower ownership ratings and especially in the visuomotor condition a faster decay. Although previous studies have shown that greater temporal binding windows (TBW) of multisensory integration increase susceptibility to illusory embodiment of a rubber hand (Costantini et al., 2016), our results show that participants with high delay sensitivity have an overall stronger tendency to lose body ownership with increased delay between visuotactile or visuomotor signals than participants with lower sensitivity. A recent study found that the binding of incongruent multisensory signals in the ventriloquist effect (an effect where the location of an auditory stimulus is mapped to that of a visual stimulus: Pick et al., 1969; Talsma et al., 2010) drops after active movements (Zierul et al., 2019), i.e., incongruent signals are more easily bound when no efferent signals are involved. Zierul et al. (2019) expected, following a predictive coding account, that action would modulate the predictions and therefore bind incongruent stimuli more with action than without; however, their results showed the contrary. The authors thus hypothesize that action did form a *stronger* prediction, yet resulting mismatches were more salient and therefore multisensory incongruences were more evident. In our results, a similar explanation could be applied, i.e. expectations based on the motor-prediction were broken, whereas for the only visuotactile signals these expectations were not present. Moreover, in the visuomotor task, there is, next to matching between the motor command and the seen visual consequence, an additional mismatch of proprioceptive and visual signals that is not present during purely visuotactile tasks. This might explain the steeper decay of body ownership with increased delay. In this sense, the matching of motor predictions with their sensory consequences is important not only for the sense of agency but also for the maintenance of a healthy sense of ownership (perhaps even more than the temporal coherence of somatosensory signals).

Importantly, low sensitivity to delay did not differently influence ownership sensation in the visuomotor and visuotactile tasks but rather generally predicted higher ownership. This could suggest that the effect might be mediated by stronger visual dependence: participants with stronger visual dependence would not be so sensitive to incongruencies to other senses because they rely stronger on vision as compared to other senses (Witkin and Asch, 1948). Indeed visual dependence has shown to be correlated with susceptibility to various multisensory illusions (David et al., 2014; Rothacher et al., 2018). A stronger dependence on visual signals could thus explain why there was no difference in the decay of ownership for visuomotor and visuotactile tasks for participants with low delay sensitivity; however, we did not objectively assess such dependence.

No Evidence for Physiological Changes

The generally strong effect in the subjective measures of the illusion was not mirrored in the chosen implicit measures (skin temperature, SCR, HRV), where no evidence for, or only weak effects, were found. Only the temperature measure tentatively suggests a condition-specific effect by revealing a significantly smaller increase of temperature for asynchronous compared with synchronous stroking. This is in line with literature suggesting that a decrease in body temperature links to own-body disembodiment during illusory embodiment of a fake body (Moseley et al., 2008; Salomon et al., 2013; but see also de Haan et al., 2017) or in neurological damage (Moseley et al., 2008; but see also Lenggenhager et al., 2015). As in previous literature, such relatively lower temperature was in our data specifically found for the stimulated hand (Macauda et al., 2015) and only after longer stimulation (cp. Macauda et al., 2015; Moseley et al., 2008, both reporting a drop in temperature only after more than a minute of stimulation), which might be related to the adaptation time homeostatic processes might need. However, when comparing temperature for different time periods of the long stimulation block, we found no significant differences between time periods. Thus, these results should be taken with caution. Moreover, an increasing amount of literature doubts a meaningful relationship between body ownership and body temperature (de Haan et al., 2017).

SCR is an indicator of physiological reactions to threat (Armel and Ramachandran, 2003; Ehrsson, 2007). Previous studies have linked embodiment of an external body part to an SCR when such body part is threatened (Armel and Ramachandran, 2003; Ehrsson, 2007), a study has found a weaker SCR with decreased embodiment of the own body in a setup similar to ours (Gentile et al., 2013), and other studies using the MIRAGE illusion box for stimulating the hand found a significantly weaker SCR after illusory disappearance of the hand (Newport and Gilpin, 2011) and asynchronous multimodal stimulation (Newport and Preston, 2010, 2011). Following this, we hypothesized to find a weaker response in the asynchronous compared with the synchronous stimulation condition. However, such an effect was not evident in our data, with both conditions showing a response to threat. On the other hand, given that HRV has been suggested to be a measure of homeostatic processes (Berntson et al., 1997), we expected to find lower HRV during asynchronous stimulation due to a homeostatic disturbance, which was however not evidenced in our analysis.

So far, we can only speculate on the reasons for this lack of significant results in the chosen threat-related implicit measures. Although generally the relationship between explicit and implicit measures of embodiment manipulations has been questioned (de Haan et al., 2017; Rohde et al., 2011; Rohde et al., 2013), and in the case of HRV a recent study found no differences after altering embodiment in a full-body illusion (Park et al., 2016), it may be that the ecological congruency of the seen environment and body might have impeded an effect on our implicit measures. That is, in our setup participants are actually seeing their own hand and surroundings, with a higher degree of ecological plausibility compared with previous setups (e.g. Gentile et al., 2013). From an ecological point of view, it makes sense that participants would more readily extend the physiological reaction (protective space) to an external object than diminishing it. Additionally, although there is a significant increase of subjective disembodiment following the asynchronous stimulation, the degree of the embodiment component is still relatively high (>0.5 on the scale), which may account for the sustained physiological response. Alternatively, it may be that even if there is an increase of disembodiment of one's own body during asynchronous stimulation, it might be too fragile and that body perception may be immediately restored when attention is shifted away from the asynchronous stroking, regardless of limb-related multisensory synchrony. Along these lines it has been proposed a low degree of ownership does not necessarily result in disownership but that attention to the lack of ownership may (de Vignemont, 2011).

Lastly, although not directly linked to physiological changes but to conscious monitoring of physiological changes, high interoceptive accuracy has previously been related to lower malleability of the bodily self in the context of the rubber hand illusion paradigm (Monti et al., 2019; Tsakiris et al., 2011). We thus expected interoceptive accuracy as measured by a heartbeat counting task to predict the degree of disembodiment after asynchronous stimulation. Yet, interoceptive accuracy did not predict the strength of disembodiment in the current study. Our findings are in line with recent studies showing no relation between interoception and suggestibility to bodily illusions (Crucianelli et al., 2018; David et al., 2014).

General Considerations, Challenges, and Outlook

Setups involving the own body to manipulate embodiment in contrast to requiring supernumerary body parts (such as the rubber hand illusion) may be more directly related to the loss of ownership described in certain psychiatric and neurological conditions and may thus be important for understanding such disorders. The use of an HMD for showing and manipulating the full body viewed from a first-person perspective, and not exclusively a limb, may offer additional advantages. The protocol used in Experiment 2 allows for a sensitive assessment of the contribution of various multimodal mismatches to the loss of body ownership and can be expanded to measure the temporal thresholds in relation to body ownership for other multimodal couplings. In contrast to illusory supernumerary ownership, which has described to occur after 11 s in visuotactile rubber hand setups (Ehrsson et al., 2004), 22.8 s in active visuomotor (Kalckert and Ehrsson, 2017), 36 s in a visuotactile virtual hand setups (Perez-Marcos et al., 2012), and 20 s in MIRAGE mixed reality setups (e.g. Newport et al., 2010; Newport and Preston, 2011; Preston and Newport, 2011), our Experiment 2 shows that even after short periods of stimulation (7 s), it is possible to manipulate the sense of one's own body consistently and reliably cp. also (Kannape et al., 2019). Such a procedure can be sensitive for comparing individual differences as well as between different populations. Future studies comparing populations and multisensory mismatches are encouraged to shed light on the concept of bodily self plasticity. On these lines, a direct comparison between the rubber hand or a virtual hand illusion and our setup would offer important insights.

Although the plasticity of the bodily self has traditionally been measured as the susceptibility to illusory supernumerary embodiment, there is currently no consensus on whether higher delay sensitivity in terms of own-body embodiment is a result of a more or less plastic bodily self or vice-versa. Motivating the question of whether there is a "general body plasticity" or promptness to own-body disembodiment and to supernumerary embodiment may be separate components of such plasticity. Costantini et al. (2016) found that a small TBW leads to lower susceptibility to illusory embodiment of a rubber hand, whereas we found that small TBWs lead to higher susceptibility to own-body disembodiment. This may seem paradoxical, because the same condition (small TBW) leads to both lower susceptibility to supernumerary embodiment and higher to own-body disembodiment. Such a contrast may suggest the need of separate components of bodily self plasticity, say one for supernumerary embodiment and one for own-body disembodiment. This would follow neuroanatomical findings in patients with disorders of embodiment (Martinaud et al., 2017; Zeller et al., 2011). This differentiation could help to explain the different results in implicit measures between previous literature and our study. However, it could also be that more proneness to a disembodiment illusion is actually a result of a less plastic bodily self, thus a weaker susceptibility to supernumerary embodiment. In this scenario, participants with a highly plastic sense of body would still maintain embodiment even during stronger multimodal mismatches, adapting their bodily sense to the ongoing mismatching signals. Although our data are inconclusive regarding this point, we propose that this is an important debate in the field of bodily self consciousness, which in our view has not received enough attention. We hope to encourage future experimental inquiries that disentangle these questions; studies directly comparing our protocol with the rubber hand illusion may offer additional insights.

With the increasing availability of mixed reality technologies, and in particular with the growing availability of augmented reality, understanding how our sense of body may change through our interactions with a mediated view of reality and the temporal mismatches that this may entail is of great importance. Again, the study of bodily self consciousness would benefit of studying more on how seeing one's own body, instead of fake or virtual bodies, through digital visual manipulations affects embodiment. This is thus not only important at a theoretical and clinical level but may imply relevant practical knowledge for a near future where mixed reality technologies may be ubiquitous and thus constantly manipulate our sense of body. The study of disembodiment is relevant for various clinical conditions and has been studied rather indirectly in the general population. Our disembodiment protocol may be important for the scientific study of bodily self consciousness, both to induce a sense of disembodiment and as an assessment tool. In particular, it may be a useful method to measure the degree and sensory weighting of bodily self plasticity in the general as well as clinical populations. The results of the two experiments presented here extend the previous literature showing that mismatching multisensory signals contribute to increased disembodiment of one's own body as expressed by the phenomenal dimensions of disownership, deafference, and embodiment. Moreover, they provide evidence for the differential contribution of sensorimotor signals compared to somatosensory in maintaining our sense of body. Lastly, we promote a debate regarding the concept of bodily self plasticity, proposing either that it has two independent dimensions for supernumerary embodiment and for disembodiment respectively or that strong susceptibility to disembodiment is a reflection of low bodily self plasticity.

Limitations of the Study

Readers should note that in our visuomotor task, participants were instructed to start and end every movement trajectory with their hand on the table during the visuomotor task; therefore the procedure also involved touch. Along these lines, the presence of an acoustic metronome may be an additional source of multisensory binding. Future studies should aim at constraining to the modalities in question. The experimenter was not blinded to the condition when performing the threats in Experiment 1, and neither speed nor kinematics were controlled for. Lastly, our short trials of Experiment 2 do not allow us to disentangle whether the explicit judgment of synchrony may affect the participants' subsequent response regarding body ownership. Future studies should address this point.

METHODS

All methods can be found in the accompanying Transparent Methods supplemental file.

SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at https://doi.org/10.1016/j.isci.2020.100901.

ACKNOWLEDGMENTS

M.R.L., M.L.W., and B.L. were supported by the Swiss National Science Foundation (grant number: PP00P1_170511).

AUTHOR CONTRIBUTIONS

M.R.L., M.L.W., and B.L. contributed to the experimental design and the writing of the manuscript. M.R.L., M.L.W., and C.S. collected the data. M.L.W. and C.S. performed the statistical analysis. O.A.K. contributed with a thorough revision of the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

Received: July 30, 2019
Revised: November 12, 2019
Accepted: January 20, 2020
Published: March 27, 2020

REFERENCES

Aglioti, S., Smania, N., Manfredi, M., and Berlucchi, G. (1996). Disownership of left hand and objects related to it in a patient with right brain damage. NeuroReport *8*, 293.

Armel, K.C., and Ramachandran, V.S. (2003). Projecting sensations to external objects: evidence from skin conductance response. Proc. R. Soc. B: Biol. Sci. *270*, 1499–1506.

Asai, T. (2015). Feedback control of one's own action: self-other sensory attribution in motor control. Conscious.Cogn. *38*, 118–129.

Barnsley, N., McAuley, J.H., Mohan, R., Dey, A., Thomas, P., and Moseley, G.L. (2011). The rubber hand illusion increases histamine reactivity in the real arm. Curr.Biol. *21*, R945–R946.

Berntson, G.G., Bigger, J.T., Jr., Eckberg, D.L., Grossman, P., Kaufmann, P.G., Malik, M., Nagaraja, H.N., Porges, S.W., Saul, J.P., Stone, P.H., and Van Der Molen, M.W. (1997). Heart rate variability: origins, methods, and interpretive caveats. Psychophysiology *34*, 623–648.

Blanke, O. (2012). Multisensory brain mechanisms of bodily self-consciousness. Nat. Rev. Neurosci. *13*, 556–571.

Blanke, O., Slater, M., and Serino, A. (2015). Behavioral, neural, and computational principles of bodily self-consciousness. Neuron *88*, 145–166.

Blom, R.M., Hennekam, R.C., and Denys, D. (2012). Body integrity identity disorder. PLoSOne *7*, e34702.

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

Brugger, P., and Lenggenhager, B. (2014). The bodily self and its disorders: neurological, psychological and social aspects. Curr.Opin.Neurol. *27*, 644.

Burin, D., Livelli, A., Garbarini, F., Fossataro, C., Folegatti, A., Gindri, P., and Pia, L. (2015). Are movements necessary for the sense of body ownership? Evidence from the rubber hand illusion in pure hemiplegic patients. PLoSOne *10*, e0117155.

Costantini, M., Robinson, J., Migliorati, D., Donno, B., Ferri, F., and Northoff, G. (2016). Temporal limits on rubber hand illusion reflect individuals' temporal resolution in multisensory perception. Cognition *157*, 39–48.

Crucianelli, L., Krahé, C., Jenkinson, P.M., and Fotopoulou, A.K. (2018). Interoceptive ingredients of body ownership: affective touch and cardiac awareness in the rubber hand illusion. Cortex *104*, 180–192.

David, N., Fiori, F., and Aglioti, S.M. (2014). Susceptibility to the rubber hand illusion does not tell the whole body-awareness story. Cogn.AffectiveBehav.Neurosci. *14*, 297–306.

Davidson, P.W. (1966). Depersonalization phenomena in 214 adult psychiatric in-patients. Psychiatr. Q. *40*, 702–722.

de Haan, A.M., van Stralen, H.E., Smit, M., Keizer, A., Van der Stigchel, S., and Dijkerman, H.C. (2017). No consistent cooling of the real hand in the rubber hand illusion. ActaPsychol. *179*, 68–77.

de Vignemont, F. (2011). Embodiment, ownership and disownership. Conscious.Cogn. *20*, 82–93.

Ehrsson, H.H. (2007). The experimental induction of out-of-body experiences. Science *317*, 1048.

Ehrsson, H.H. (2012). The concept of body ownership and its relation to multisensory integration. In The New Handbook of Multisensory Processes, B.E. Stein, ed. (MIT Press), pp. 775–792.

Ehrsson, H.H., Holmes, N.P., and Passingham, R.E. (2005). Touching a rubber hand: feeling of body ownership is associated with activity in multisensory brain areas. J. Neurosci. *25*, 10564–10573.

Ehrsson, H.H., Spence, C., and Passingham, R.E. (2004). That'smy hand! Activity in premotor cortex reflects feeling of ownership of a limb. Science *305*, 875–877.

Folegatti, A., Vignemont, F., dePavani, F., Rossetti, Y., and Farnè, A. (2009). Losing one's hand: visual-proprioceptive conflict affects touch perception. PLoSOne *4*, e6920.

Garfinkel, S.N., Seth, A.K., Barrett, A.B., Suzuki, K., and Critchley, H.D. (2015). Knowing your own heart: distinguishing interoceptive accuracy from interoceptive awareness. Biol. Psychol. *104*, 65–74.

Gentile, G., Guterstam, A., Brozzoli, C., and Ehrsson, H.H. (2013). Disintegration of multisensory signals from the real hand reduces default limb self-attribution: an fMRI study. J. Neurosci. *33*, 13350–13366.

Graham, K.T., Martin-Iverson, M.T., Holmes, N.P., and Waters, F.A. (2015). The projected hand illusion: component structure in a community sample and association with demographics, cognition, and psychotic-like experiences. Attention Percept. Psychophys. *77*, 207–219.

Grechuta, K., Ulysse, L., Rubio Ballester, B., and Verschure, P.F.M.J. (2019). Self beyond the body: action-driven and task-relevant purely distal cues modulate performance and body ownership. Front. Hum. Neurosci. *13*, https://doi.org/10.3389/fnhum.2019.00091.

Hoover, A.E.N., and Harris, L.R. (2012). Detecting delay in visual feedback of an action as a monitor of self recognition. Exp. Brain Res. *222*, 389–397.

Kalckert, A., and Ehrsson, H.H. (2012). Moving a rubber hand that feels like your own: a dissociation of ownership and agency. Front. Hum. Neurosci. *6*, https://doi.org/10.3389/fnhum.2012.00040.

Kalckert, A., and Ehrsson, H.H. (2014). The moving rubber hand illusion revisited: comparing movements and visuotactile stimulation to induce illusory ownership. Conscious.Cogn. *26*, 117–132.

Kalckert, A., and Ehrsson, H.H. (2017). Theonset time of the ownership sensation in the moving rubber hand illusion. Front. Psychol. *8*, https://doi.org/10.3389/fpsyg.2017.00344.

Kannape, O.A., Smith, E.J.T., Moseley, P., Roy, M.P., and Lenggenhager, B. (2019). Experimentally induced limb-disownership in mixed reality. Neuropsychologia *124*, 161–170.

Kilteni, K., Maselli, A., Kording, K.P., and Slater, M. (2015). Over my fake body: body ownership illusions for studying the multisensory basis of own-body perception. Front. Hum. Neurosci. *9*, https://doi.org/10.3389/fnhum.2015.00141.

Kokkinara, E., and Slater, M. (2014). Measuring the effects through time of the influence of visuomotor and visuotactile synchronous stimulation on a virtual body ownership illusion. Perception *43*, 43–58.

Lane, T., Yeh, S.-L., Tseng, P., and Chang, A.-Y. (2017). Timing disownership experiences in the rubber hand illusion. Cogn. Res. Princ.Implic. *2*, 4.

Lau, H.C., Rogers, R.D., Haggard, P., and Passingham, R.E. (2004). Attention to intention. Science *303*, 1208–1210.

Lenggenhager, B., Hilti, L., and Brugger, P. (2015). Disturbed body integrity and the "rubber foot illusion.". Neuropsychology *29*, 205–211.

Lenggenhager, B., Tadi, T., Metzinger, T., and Blanke, O. (2007). Video ergo sum: manipulating bodily self-consciousness. Science *317*, 1096–1099.

Loetscher, T., Regard, M., and Brugger, P. (2006). Misoplegia: a review of the literature and a case without hemiplegia. J. Neurol. Neurosurg. Psychiatry *77*, 1099–1100.

Löffler, A., Kleindienst, N., Cackowski, S., Schmidinger, I., and Bekrater-Bodmann, R. (2019). Reductions in whole-body ownership in borderline personality disorder – a phenomenological manifestation of dissociation. J. Trauma Dissociation, 1–14, https://doi.org/10.1080/15299732.2019.1678213.

Longo, M.R., and Haggard, P. (2009). Sense of agency primes manual motor responses. Perception *38*, 69–78.

Longo, M.R., Schüür, F., Kammers, M.P.M., Tsakiris, M., and Haggard, P. (2008). What is embodiment? A psychometric approach. Cognition *107*, 978–998.

Macauda, G., Bertolini, G., Palla, A., Straumann, D., Brugger, P., and Lenggenhager, B. (2015). Binding body and self in visuo-vestibular conflicts. Eur. J. Neurosci. *41*, 810–817.

Martinaud, O., Besharati, S., Jenkinson, P.M., and Fotopoulou, A. (2017). Ownership illusions in patients with body delusions: different neural profiles of visual capture and disownership. Cortex *87*, 174–185.

McCabe, C.S., Haigh, R.C., Halligan, P.W., and Blake, D.R. (2005). Simulating sensory–motor incongruence in healthy volunteers: implications for a cortical model of pain. Rheumatology *44*, 509–516.

Monti, A., Porciello, G., Tieri, G., and Aglioti, S.M. (2019). "Embreathment" illusion reveals hierarchical influence of respiratory, visual and spatial signals on corporeal awareness. https://doi.org/10.31234/osf.io/cn9s3.

Moseley, G.L., Olthof, N., Venema, A., Don, S., Wijers, M., Gallace, A., and Spence, C. (2008). Psychologically induced cooling of a specific body part caused by the illusory ownership of an artificial counterpart. Proc. Natl. Acad. Sci. USA *105*, 13169–13173.

Newport, R., Pearce, R., and Preston, C. (2010). Fake hands in action: embodiment and control of supernumerary limbs. Exp. Brain Res. *204*, 385–395.

Newport, R., and Gilpin, H.R. (2011). Multisensory disintegration and the disappearing hand trick. Curr.Biol. *21*, R804–R805.

Newport, R., and Preston, C. (2010). Pulling the finger off disrupts agency, embodiment and peripersonal space. Perception *39*, 1296–1298.

Newport, R., and Preston, C. (2011). Disownership and disembodiment of the real limb without visuoproprioceptive mismatch. Cogn.Neurosci. *2*, 179–185.

Osumi, M., Nobusako, S., Zama, T., Taniguchi, M., Shimada, S., and Morioka, S. (2018). Sensorimotor incongruence alters limb perception and movement. Hum. Mov. Sci. *57*, 251–257.

Otsuru, N., Hashizume, A., Nakamura, D., Endo, Y., Inui, K., Kakigi, R., and Yuge, L. (2014). Sensory incongruence leading to hand disownership modulates somatosensory cortical processing. Cortex *58*, 1–8.

Park, H.-D., Bernasconi, F., Bello-Ruiz, J., Pfeiffer, C., Salomon, R., and Blanke, O. (2016). Transient modulations of neural responses to heartbeats covary with bodily self-consciousness. J. Neurosci. *36*, 8453–8460.

Perez-Marcos, D., Sanchez-Vives, M.V., and Slater, M. (2012). Is my hand connected to my body? The impact of body continuity and arm alignment on the virtual hand illusion. Cogn.Neurodyn. *6*, 295–305.

Petkova, V.I., and Ehrsson, H.H. (2008). If I were you: perceptual illusion of body swapping. PLoSOne *3*, e3832.

Pia, L., Garbarini, F., Kalckert, A., and Wong, H.Y. (2019). Editorial: owning a body + moving a body = me? Front. Hum. Neurosci. *13*, https://doi.org/10.3389/fnhum.2019.00088.

Pick, H.L., Warren, D.H., and Hay, J.C. (1969). Sensory conflict in judgments of spatial direction. Percept.Psychophys. *6*, 203–205.

Preston, C., and Newport, R. (2011). Differential effects of perceived hand location on the disruption of embodiment by apparent physical encroachment of the limb. Cogn.Neurosci. *2*, 163–170.

Roel Lesur, M., Gaebler, M., Bertrand, P., and Lenggenhager, B. (2018). The plasticity of the bodily self: head movements in bodily illusions and their relation to gallagher's body image and body schema. Constructivist Foundations *14*, 94–105.

Rohde, M., Luca, M.D., and Ernst, M.O. (2011). The rubber hand illusion: feeling of ownership and proprioceptive drift do not go hand in hand. PLoSOne *6*, e21659.

Rohde, M., Wold, A., Karnath, H.-O., and Ernst, M.O. (2013). Thehuman touch: skin temperature during the rubber hand illusion in manual and automated stroking procedures. PLoSOne *8*, e80688.

Rothacher, Y., Nguyen, A., Lenggenhager, B., Kunz, A., and Brugger, P. (2018). Visual capture of gait during redirected walking. Sci. Rep. *8*, 17974.

Salomon, R., Lim, M., Pfeiffer, C., Gassert, R., and Blanke, O. (2013). Full body illusion is associated with widespread skin temperature reduction. Front. Behav.Neurosci. *7*, https://doi.org/10.3389/fnbeh.2013.00065.

Shaqiri, A., Roinishvili, M., Kaliuzhna, M., Favrod, O., Chkonia, E., Herzog, M.H., Blanke, O., and Salomon, R. (2018). Rethinking body ownership in schizophrenia: experimental and meta-analytical approaches show no evidence for deficits. Schizophr. Bull. *44*, 643–652.

Sierra, M., Baker, D., Medford, N., and David, A.S. (2005). Unpacking the depersonalization syndrome: an exploratory factor analysis on the Cambridge Depersonalization Scale. Psychol. Med. *35*, 1523–1532.

Slater, M., Spanlang, B., Sanchez-Vives, M.V., and Blanke, O. (2010). First person experience of body transfer in virtual reality. PLoSOne *5*, e10564.

Smit, M., van Stralen, H.E., van den Munckhof, B., Snijders, T.J., and Dijkerman, H.C. (2018). The man who lost his body: suboptimal multisensory integration yields body awareness problems after a right temporoparietal brain tumour. J. Neuropsychol. https://doi.org/10.1111/jnp.12153.

Stanton, T.R., Gilpin, H.R., Edwards, L., Moseley, G.L., and Newport, R. (2018). Illusory resizing of the painful knee is analgesic in symptomatic knee osteoarthritis. PeerJ *6*, https://doi.org/10.7717/peerj.5206.

Talsma, D., Senkowski, D., Soto-Faraco, S., and Woldorff, M.G. (2010). The multifaceted interplay between attention and multisensory integration. Trends Cogn. Sci. *14*, 400–410.

Thakkar, K.N., Nichols, H.S., McIntosh, L.G., and Park, S. (2011). Disturbances in body ownership in schizophrenia: evidence from the rubber hand illusion and case study of a spontaneous out-of-body experience. PLoSOne *6*, e27089.

Tsakiris, M., Jiménez, A.T., and Costantini, M. (2011). Just a heartbeat away from one's body: interoceptive sensitivity predicts malleability of body-representations. Proc. R. Soc. Lond. B: Biol. Sci. *278*, 2470–2476.

Tsakiris, M., Longo, M.R., and Haggard, P. (2010). Having a body versus moving your body: neural signatures of agency and body-ownership. Neuropsychologia *48*, 2740–2749.

Tsakiris, M., Prabhu, G., and Haggard, P. (2006). Having a body versus moving your body: how agency structures body-ownership. Conscious.Cogn. *15*, 423–432.

Vallar, G., and Ronchi, R. (2009). Somatoparaphrenia: a body delusion. A review of the neuropsychological literature. Exp. Brain Res. *192*, 533–551.

van Stralen, H.E., van Zandvoort, M.J.E., Kappelle, L.J., and Dijkerman, H.C. (2013). The rubber hand illusion in a patient with hand disownership. Perception *42*, 991–993.

White, R.C., and AimolaDavies, A.M. (2017). Asynchrony in the rubber hand paradigm: unexpected illusions following stroke. Cortex *93*, 224–226.

Winter, R., Harrar, V., Gozdzik, M., and Harris, L.R. (2008). The relative timing of active and passive touch. Brain Res. *1242*, 54–58.

Witkin, H.A., and Asch, S.E. (1948). Studies in space orientation. IV. Further experiments on perception of the upright with displaced visual fields. J. Exp. Psychol. *38*, 762–782.

Wolpert, D.M. (1997). Computational approaches to motor control. Trends Cogn. Sci. *1*, 209–216.

Zeller, D., Gross, C., Bartsch, A., Johansen-Berg, H., and Classen, J. (2011). Ventral premotor cortex may be required for dynamic changes in the feeling of limb ownership: a lesion study. J. Neurosci. *31*, 4852–4857.

Zierul, B., Tong, J., Bruns, P., and Röder, B. (2019). Reduced multisensory integration of self-initiated stimuli. Cognition *182*, 349–359.

iScience, Volume *23*

Supplemental Information

Psychometrics of Disembodiment and Its Differential Modulation by Visuomotor and Visuotactile Mismatches

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Supplementary figures and tables

Table S1 related to Table 1

Descriptive statistics and pairwise comparisons of additional questionnaire data used in the PCA, N = 15.

	Visuotactile Synchronous		Visuotactile Asynchronous				
	Median	IQR	Median	IQR	*Z*	*p*	*r*
Disownership	0.13	0.04 - 0.27	0.55	0.46 - 0.63	-3.74	<.001	-.68
q4	0.07	0.03 -0.16	0.67	0.38 - 0.76	-4.01	<.001	-.73
q6	0.10	0.03 -0.26	0.60	0.33 - 0.70	-3.01	.003	-.55
q9	0.17	0.03 - 0.39	0.58	0.37 - 0.70	-2.71	.007	-.49
Deafference	0.04	0.03 - 0.11	0.58	0.27 - 0.63	-3.52	<.001	-.64
q10	0.06	0.02 - 0.13	0.72	0.36 - 0.77	-3.33	<.001	-.61
q8	0.06	0.03 - 0.10	0.53	0.09 - 0.67	-2.64	.008	-.48
q7	0.04	0.02 - 0.09	0.34	0.06 - 0.65	-3.74	<.001	-.68
Embodiment	0.90	0.85 - 0.96	0.58	0.41 - 0.73	-4.01	<.001	-.73
q1	0.95	0.90 - 0.98	0.70	0.28 - 0.81	-4.01	<.001	-.73
q11	0.94	0.83 - 0.97	0.63	0.52 - 0.78	-3.42	<.001	-.63
q5	0.92	0.71 - 0.96	0.39	0.17 - 0.69	-3.33	<.001	-.61
Control item and manipulation check							
q3	0.96	0.94 - 0.99	0.93	0.85 - 0.97	-2.23	.026	-.41
q2	0.96	0.84 - 0.98	0.68	0.24 - 0.72	-2.57	.010	-.47
Components based on the PCA in the synchronous condition							
Component 1	0.21	0.17 - 0.31	0.50	0.39 - 0.56	-4.01	<.001	-.73
Component 2	0.94	0.87 - 0.97	0.70	0.44 - 0.79	-4.01	<.001	-.73

Note: VAS ratings on q5 were inversed, so that higher scored indicate higher embodiment.

Table S2 Related to Table 1

Descriptive statistics and pairwise comparisons of questionnaire data in Experiment 1, N = 30.

	Visuotactile Synchronous		Visuotactile Asynchronous				
	Median	IQR	Median	IQR	*Z*	*p*	*r*
Disownership	0.14	0.05 - 0.41	0.61	0.40 - 0.72	-5.08	<.001	-0.66
q4	0.11	0.03 – 0.30	0.59	0.25 – 0.78	-4.59	.005	-0.59
q6	0.07	0.03 – 0.23	0.54	0.18 – 0.70	-4.96	<.001	-0.64
q9	0.20	0.05 – 0.53	0.61	0.31 – 0.78	-4.34	<.001	-0.56
Deafference	0.14	0.04 - 0.41	0.30	0.22 - 0.52	-5.83	<.001	-0.75
q10	0.11	0.03 – 0.43	0.29	0.12 – 0.69	-4.17	<.001	-0.53
q8	0.26	0.04 – 0.40	0.52	0.21 – 0.70	-4.20	<.001	-0.54
q7	0.07	0.03 – 0.17	0.18	0.07 – 0.46	-4.34	<.001	-0.56
Embodiment	0.89	0.75 - 0.95	0.72	0.62 - 0.82	-3.81	<.001	-0.49
q1	0.91	0.88 – 0.98	0.78	0.67 – 0.86	-4.17	<.001	-0.54
q11	0.94	0.79 – 0.96	0.76	0.67 – 0.84	-3.58	<.001	-0.46
q5	0.90	0.72 - 0.96	0.73	0.38 - 0.87	-2.78	<.001	-0.36
Control item and manipulation check							
q3	0.93	0.84 – 0.97	0.91	0.81 – 0.97	-1.31	.191	-0.16
q2	0.85	0.57 – 0.97	0.51	0.28 – 0.75	-3.28	.001	-0.42
Components based on the PCA in the synchronous condition							
Component 1	0.25	0.18 - 0.45	0.48	0.39 - 0.57	-5.57	<.001	-.72
Component 2	0.93	0.84 - 0.96	0.78	0.67 - 0.82	-3.84	<.001	-.50

Note: VAS ratings on q5 were inversed, so that higher scored indicate higher embodiment.

Table S3 Related to Table 1

Results of the PCA on questionnaire responses in the synchronous condition

	Varimax rotated factor loadings		
	Component 1	Component 2	commonalities
q4	**0.87**	0.27	0.83
q10	**0.87**	0.06	0.76
q7	**0.81**	0.27	0.73
q6	**0.79**	**0.44**	0.82
q8	**0.72**	0.38	0.66
q9	**0.71**	0.41	0.67
q5	**0.67**	0.12	0.46
q11	0.10	**0.87**	0.77
q1	0.34	**0.72**	0.64
Eigenvalues	4.39	1.95	
% of variance	49	22	

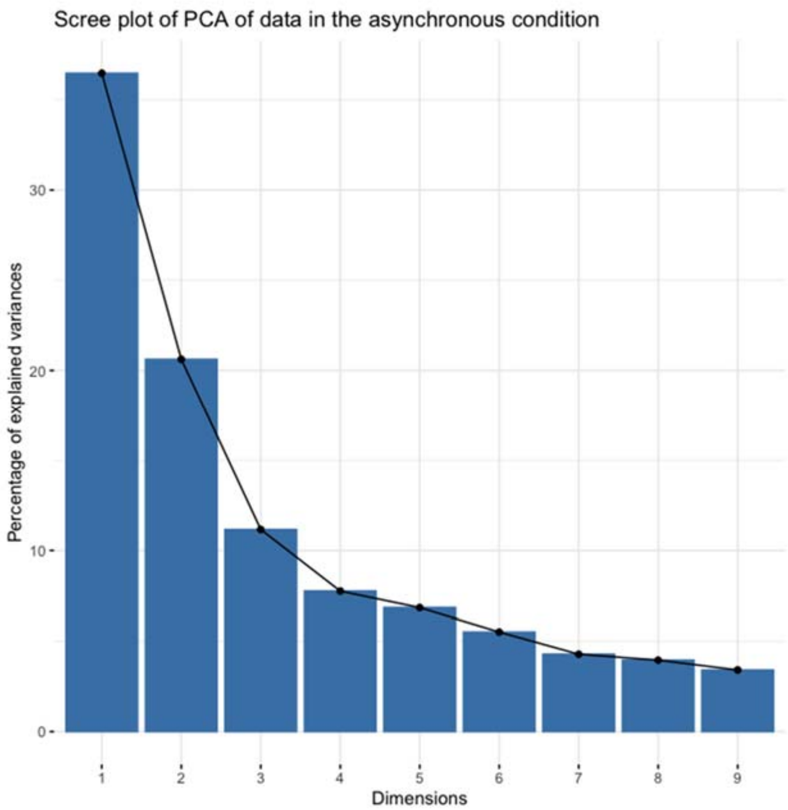

Figure S1 Related to Table 1: The scree plot of the PCA in the asynchronous condition justifies retaining three components for the secondary PCA.

Table S4 Related to Figure 2

Descriptive statistics of questionnaire data in Experiment 2, N = 32

	Visuotactile Synchronous		Visuotactile Asynchronous		Visuomotor Synchronous		Visuomotor Asynchronous	
	Median	IQR	Median	IQR	Median	IQR	Median	IQR
Disownership	0.28	0.16 - 0.43	0.57	0.43 – 0.70	0.32	0.17 – 0.46	0.66	0.49 – 0.77
q4	0.17	0.09 - 0.36	0.60	0.34 - 0.69	0.20	0.10 - 0.30	0.72	0.56 - 0.82
q6	0.21	0.09 - 0.29	0.62	0.32 - 0.73	0.18	0.07 - 0.33	0.69	0.57 - 0.85
q9	0.50	0.24 - 0.68	0.67	0.40 - 0.76	0.58	0.26 - 0.74	0.62	0.33 - 0.80
Deafference	0.19	0.08 – 0.45	0.34	0.15 – 0.48	0.20	0.10 – 0.38	0.42	0.22 – 0.56
q10	0.16	0.06 - 0.30	0.25	0.17 - 0.43	0.17	0.08 - 0.41	0.38	0.22 - 0.64
q8	0.19	0.10 - 0.59	0.4	0.14 - 0.69	0.24	0.08 - 0.61	0.37	0.19 - 0.66
q7	0.12	0.06 - 0.28	0.23	0.06 - 0.40	0.10	0.05 - 0.28	0.31	0.15 - 0.48
Embodiment	0.81	0.70 - 0.93	0.58	0.44 – 0.71	0.86	0.71 - 0.91	0.43	0.34 - 0.54
q1	0.90	0.81 - 0.97	0.65	0.41 - 0.78	0.91	0.81 - 0.95	0.42	0.28 - 0.68
q11	0.85	0.78 - 0.93	0.7	0.37 - 0.82	0.89	0.80 - 0.96	0.54	0.29 - 0.69
q5	0.81	0.59 - 0.91	0.43	0.26 - 0.66	0.81	0.61 - 0.92	0.31	0.15 - 0.54
Control item and manipulation check								
q3	0.91	0.84 - 0.97	0.86	0.80 - 0.94	0.89	0.78 - 0.97	0.86	0.68 - 0.96
q2	0.85	0.57 - 0.95	0.53	0.18 - 0.69	0.89	0.77 - 0.95	0.66	0.56 - 0.81
Components based on the PCA in the synchronous condition (see Table S3)								
Component 1	0.30	0.22 - 0.47	0.48	0.36 - 0.56	0.34	0.24 - 0.44	0.49	0.42 - 0.61
Component 2	0.87	0.80 - 0.93	0.64	0.47 - 0.75	0.89	0.82 - 0.93	0.47	0.34 - 0.60

Note: VAS ratings on q5 were inversed, so that higher scored indicate higher embodiment.

Table S5 Related to Figure 2

Results of Friedman tests and post-hoc comparisons of questionnaire in Experiment 2, using Wilcoxon Signed-Rank tests, FDR corrected p-values

	Friedman test			VTsyn - VTasyn			VMsyn - VMasyn			VTsyn - VMsyn			VTasyn - VMasyn		
	χ^2	df	p	Z	$p_{corrected}$	r	Z	$p_{corrected}$	r	Z	$p_{corrected}$	r	Z	$p_{corrected}$	r
Disownership	35.51	3	<.001	-4.42	<.001	-0.55	-5.12	<.001	-0.64	-0.05	.963	-0.01	-2.31	.021	-0.29
q4	39.38	3	<.001	-4.19	<.001	-0.52	-5.09	<.001	-0.63	-0.06	.949	-0.01	-2.52	.016	-0.31
q6	43.46	3	<.001	-4.72	<.001	-0.59	-5.30	<.001	-0.66	-0.25	.803	-0.03	-3.04	.003	-0.38
q9	7.76	3	.051												
Deafference	26.78	3	<.001	-3.36	<.001	-0.42	-3.77	<.001	-0.47	-0.69	.488	-0.09	-1.98	.048	-0.25
q10	28.56	3	<.001	-3.63	.001	-.045	-3.41	.001	-0.43	-1.71	.087	-0.21	-3.50	.001	-0.44
q8	5.66	3	.129												
q7	19.95	3	<.001	-2.16	.062	-0.27	-4.72	<.001	-0.59	-0.10	.919	-0.01	-1.94	.069	-0.24
Embodiment	59.36	3	<.001	-4.58	<.001	-0.57	-5.92	<.001	-0.74	-0.97	.331	-0.12	-2.85	.005	-0.36
q1	55.65	3	<.001	-4.19	<.001	-0.52	-5.86	<.001	-0.73	-0.05	.963	-0.01	-2.54	.015	-0.05
q11	52.46	3	<.001	-4.24	<.001	-0.53	-6.23	<.001	-0.78	-1.54	.139	-0.19	-1.48	.139	-0.19
q5	49.24	3	<.001	-3.63	.001	-0.45	-4.90	<.001	-0.61	-0.18	.861	-0.02	-2.76	.008	-0.34
Control item and manipulation check															
q2				-3.61	<.001	-0.45	-3.68	<.001	-0.46						
q3	9.19	3	.027	-1.96	.100	-0.24	-2.46	.056	-0.31	-0.05	.963	-0.01	-1.69	.121	-0.21
Components based on the PCA in the synchronous condition (see Table S3)															
Component 1	30.41	3	<.001	-3.87	<.001	-.48	-4.31	<.001	-.54	-.92	.36	-.11	-2.22	.04	-.28
Component 2	60.86	3	<.001	-4.81	<.001	-.60	-6.23	<.001	-.78	-1.37	.17	-.17	-2.48	.02	-.31

Table S6 Related to Figure 3

Summary of the initial mixed model, including the fixed effects for delay and modality, and their two-way interaction

		Confidence interval					
fixed effects	*b*	lower	upper	*SE*	*df*	*t*	*p*
intercept	0.923	0.866	0.981	0.029	46.29	31.49	<.001
Delay	-0.718	-0.772	-0.665	0.027	2525	-8.84	<.001
Modality	0.038	0.002	0.074	0.018	2525	2.29	.04
Delay x Modality	-0.154	-0.230	-0.079	0.039	2525	-4.47	<.001

Notes: Modality (0 = Visuotactile, 1 = Visuomotor)

Table S7 Related to Figure 3

Summary of the final mixed model, including the predictors delay, modality, and PSE, and the two-way and three-way interactions.

		Confidence interval					
fixed effects	*b*	lower	upper	*SE*	*df*	*t*	*p*
intercept	0.830	0.788	0.871	0.027	37.23	34.32	<.001
Delay	-0.717	-0.880	-0.553	0.082	33.82	-8.69	<.001
Modality	0.007	-0.017	0.031	0.017	2473.88	1.84	.066
PSE	0.790	0.485	1.099	0.210	1393.73	4.24	<.001
Delay x Modality	-0.164	-0.232	-0.096	0.035	2471.39	-4.73	<.001
Delay x PSE	-0.724	-1.609	0.149	0.446	1633.18	-1.62	.105
Modality x PSE	-0.511	-0.878	-0.148	0.251	2086.97	-3.26	.001
Delay x Modality x PSE	2.188	1.153	3.233	0.530	2213.69	4.13	<.001

Notes: Modality (0 = Visuotactile, 1 = Visuomotor), PSE was mean-centered around 0, lower values correspond to high sensitivity, and higher values to low sensitivity.

Transparent Methods

Experiment 1

Participants. Thirty healthy volunteers participated in Experiment 1 (10 males; *M* = 25, *SD* = 3.8 years). Participants provided informed consent and received either course credit or financial compensation.

For the PCA of the questionnaire responses after synchronous versus asynchronous stroking, we additionally included the participants of Experiment 2 (see section *Participants* for Experiment 2), as well as 15 participants (3 males; *M* = 22.2, *SD* = 2.4 years) from a previously unpublished experiment resulting in a total of 77 participants (27 males; *M* = 22.9, *SD* = 4.0 years). These were recorded in the same setting and using the same experimental materials as the other studies, with the only difference being that for 5 individuals the stroking lasted 60 s and for ten individuals 90 s. The participants were not included in the general analysis as we did not record the physiological measures in that sample.

All protocols were approved by the Ethics Committee of the Faculty of Arts and Social Sciences at the University of Zurich (Approval Number 17.12.15). The studies were performed in accordance with the ethical standards of the Declaration of Helsinki.

Apparatus for stimulation. An Oculus CV1 HMD (Oculus VR, Irvine, CA, USA) was used for the visual stimulation. An ELP 180˚ webcam (Ailipu Technology Co., Ltd, Guangdong, China) was positioned on the front of the HMD, set to 30 frames per second and resolution of 1024 x 768 pixels. The camera was positioned with the wide side of view (1024 pixels) on the vertical axis in order to more clearly show the full-body. The control system was designed using Unity 2017 for delaying the camera feed, rotating the image, mapping it to a 3D model approximately matching the distortion of the camera-lens, and projecting the image on the HMD. A qualitative calibration was done before the experiment to approximately match the visual field of view in the HMD to that without the HMD as well as to the seen and felt (proprioceptive) position of the body. The questionnaires and randomization were also built within Unity 2017. The system was run on an Alienware 15 R3 computer (Nvidia Geforce GTX 1080 8GB; 16GB RAM; Intel Core i7; Windows 10). The mean intrinsic delay of the camera feed added by the system was of 139.1ms (*SD* = 18.3 ms).

Procedure.

Heartbeat counting task. At the beginning of the experiment, participants performed a heartbeat counting task (Schandry, 1981), see Figure 1a (in the main text) for general procedure and order of the experiment. Participants were instructed to count their heartbeats, without taking their pulse. They were informed that the time of the intervals would vary, to prevent them relying on time estimation instead of actual counting of the heartbeats. Three intervals of 25, 35, and 45 s were presented in randomized order, and the start and end of each interval was indicated by a tone. During the task, electrocardiograms (ECG) were recorded with a Biopac MP150 system and ECG100C amplifier (Goleta, USA) at 1000 Hz sampling rate. Three ECG electrodes (Red Dot, 3M, Neuss, Germany) were placed on the left and right clavicle and on the lowest left rib. The electrodes were left to measure ECG throughout the experimental procedure.

The heartbeat perception score, which reflects the normalized difference between recorded and perceived heartbeats in a way that higher scores indicate higher accuracy, was calculated using the following equation:

$$\text{heartbeat perception score} = 1/3 \sum 1 - \frac{|\text{recorded heartbeats} - \text{perceived heartbeats}|}{\text{recorded heartbeats}}$$

Data from 10 participants were excluded due to technical difficulties with the ECG recording equipment, missing markers, or because they did not understand the task.

Visuotactile stimulation. After performing the heartbeat counting task, the thermocouples and additional electrodes for measuring electrodermal activity were put on. Participants received verbal instructions about the visuotactile stimulation procedure and were helped to put on the HMD. After reading instructions on the HMD, they performed a test trial where they selected “strongly agree” on a visual analogue scale (VAS) from “strongly disagree” to “strongly agree” to indicate that they were ready. A few seconds of exposure to a synchronous video feed of their own bodies on the table followed to acquaint participants with the task and the virtual environment. For the experiment participants were instructed to not move and keep especially the head in a fixed position.

First a block with synchronous and asynchronous visuotactile stimulation of 60 s each was presented. Asynchrony was achieved by adding a 594 ms delay to the ~139 ms intrinsic delay, we refer to the synchronous condition as such despite the fact that it included the system delay of ~139 ms. The stroking in both conditions was performed by the experimenter following the same strategy with a stroking rate of approximately 1 Hz in randomized directions for all fingers while monitoring the participant's perspective on a computer screen. The order of synchrony was counterbalanced across participants. After the 60 s of stimulation, the experimenter threatened the participant’s left hand with a plastic knife in a stabbing motion, which was followed by a 30 s rest period where the video feedback was displayed without any tactile stimulation, to assess change in heartrate. Participants were informed about the knife threat before starting the experiment, but did not know when it would occur. Both the synchronous and asynchronous condition were followed by the (dis)embodiment questionnaire. A block of 180 s of synchronous and asynchronous visuotactile stimulation followed. After 180 s of visuotactile stimulation, the experimenter threatened the participant’s left hand with the plastic knife in a sliding motion. The 30 s rest period followed again. The 180 s blocks were aimed at assessing HRV during the manipulation of embodiment, and were not followed by the embodiment questionnaire. Again, the order of synchrony was counterbalanced across participants.

The experiment was concluded with a brief semi-structured interview on the experiences of the participant and a short debriefing. The full procedure took about 45 minutes.

Measures of illusion strength.

(Dis)embodiment questionnaire. The subjective experience of the illusion was assessed with a questionnaire (see Table 1 for illusion related questions, and additional control questions). Two questions were used as control items, respectively q2 (It felt as if the stroking I felt on my hand was due to the seen stroking) and q3 (It seemed as if the seen hand resembled my own hand in terms of its shape and structure). For the former we expected changes between conditions given that it was foreseen to change with the manipulation, but not in respect of body perception; while for the latter we expected no changes between conditions. The questionnaire was based on other studies, including the original rubber hand illusion (Botvinick & Cohen, 1998), a full-body illusion (Lenggenhager, Tadi, Metzinger, & Blanke, 2007), the psychometric approach developed by Longo and colleagues ((Longo, Schüür, Kammers, Tsakiris, & Haggard, 2008), other psychometric approaches (Dobricki & Rosa, 2013) and additional new items to specifically assess disembodiment. Participants indicated on a VAS scale ranging from "completely disagree" to "completely agree" (respectively mapped to values ranging between 0 and 1) how much they agreed with each of the 11 statements. Based on the PCA (see section *The effect of visuomotor as compared to visuotactile mismatch on the phenomenology of disembodiment* in the main text), three subscales of disownership, deafference, and embodiment were identified. The questionnaire was displayed in the HMD and participants responded by means of head movements: they would select the corresponding position on the scale by looking at it for 1 s, after which they had to look at another button for 1 s to proceed to the next item.

Skin temperature. Skin temperature was measured with an HH309A Data Logger thermometer (Omega, Stanford, CT, USA) at a 0.5 Hz sampling rate with a resolution of 0.1° C per thermocouple. Such device has been previously used to assess changes in skin temperature in embodiment-related experimental paradigms (Macauda et al., 2015; Salomon, Lim, Pfeiffer, Gassert, & Blanke, 2013). Two thermocouples were placed on the left and right ventral side of the wrist, and a third on the back of the neck. A fourth thermocouple was used to monitor room temperature. While not systematically measured, the time since entering the room, setting up the equipment and doing the tasks previous to the temperature recording, served for the participant's adaptation to the room temperature. Temperature was measured for the full length of the visuotactile stimulation in each condition. For each thermocouple, a baseline was calculated as the average temperature of the first 6 s of recording. This average value was subtracted from the subsequent recordings to represent the relative change in skin temperature across the stimulation period. In the short conditions, average temperature change was computed over 54 s (60 – 6 s baseline). In the long conditions, the average temperature change was computed over 174 s. One participant had to be excluded from the analyses due to technical problems. Two additional participants in the 60 s-blocks, and four in the 180 s-blocks were excluded due to missing data. We controlled for changes in room temperature by assessing differences in room temperature change between the asynchronous and synchronous condition, which were not significant in both the short block ($p = .54$) and the long block ($p = .33$).

Skin conductance responses. Threat evoked SCRs were recorded with a Biopac MP150 system and EDA100C amplifier (Goleta, USA) at a 1000 Hz sampling rate. Two electrodes with electrode paste were placed on the participant's index and middle finger of the non-stimulated right hand. The experimenters threatened the left hand of the participant, by making a stabbing motion in the short block, and a sliding motion in the long block, without touching the hand. A sound signal on the experimenter's headphones indicated the onset of the threat at the corresponding time depending on the condition, and a manual marker was placed in the raw data file immediately after presenting the threat. The data was processed in Acqknowledge software (Version 4.1, Biopac, Goleta, USA). The SCR was identified as the maximum peak-to-peak value in electrodermal activity between 2 s before, to 6 s after the marker. The 2 s before were taken into account, as it reflects the time from the threat to the actual manual pressing of the marker. The SCR response was then computed as a relative value, taking into account the average raw SCR of all four threat responses. It was computed by dividing the SCR in each condition, by the average SCR of all four conditions in order to standardize the values. The data was gathered separately by two experimenters, blindly analyzed and compared. Absent responses were registered as missing values. Data from five participants were excluded from the analysis due to missing responses or technical difficulties.

Heart Rate Variability. A synchronous and asynchronous block of three-minute-long visuotactile stimulation was added to the procedure to assess HRV. ECG was recorded with the Biopac MP150 system as described previously. 160 seconds of recording were used, with an onset 10 s after the stimulation onset up to 10 s before the threat marker. The R-package RHRV (Rodriguez-Linares et al., 2017) was used to detect R-peaks and extract the Root Mean Square of the Successive Differences (RMSSD) as a measure of HRV. Data from four participants were excluded from the analysis due to technical difficulties.

Data analysis. Data were analyzed with R (R Core Team, 2018) version 3.5.1. Alpha level was set at 0.05, or 95% confidence intervals, excluding 0, and p-values were adjusted for multiple comparisons using false discovery rate (FDR) corrections (Benjamini & Hochberg, 1995). Data were tested for normality, and appropriate tests were used accordingly. Details of preprocessing of the physiological data are described above.

Principal Component Analysis. A PCA was used to investigate the structure of participants' experience, and to quantify the complex experience during this illusion. The PCA was conducted on the questionnaire data after synchronous or asynchronous visuotactile stimulation. In order to maximize the number of participants we took the questionnaire data from Experiment 1 and questionnaire data from the long visuotactile stroking of Experiment 2 (see below) as well as additional data of 15 participants in an unpublished experiment (see Table S1, for descriptive statistics and item comparisons of these additional participants). Exposure time was 60 s in experiment 1 ($n = 30$), 90 s in experiment 2 ($n = 32$), and differed for the additional data between 60 s ($n = 6$) and 90 s ($n = 9$).

Before running the PCA, the ratings of q1 and q11 were inversed, so that all items were coded in the same direction, with higher ratings indicating decreased embodiment. Two PCAs were separately run for the asynchronous and synchronous conditions. Adequacy of using PCA was assessed by Bartlett's test of sphericity, which was highly significant for both the asynchronous ($X^2(55) = 238.6$, $p < .0001$), and synchronous condition ($X^2(55) = 506.9$, $p < .0001$), indicating that correlations between individual items were sufficiently large for PCA. The overall Kayser-Meyer-Olkin (KMO) measure verified that the sample size was adequate, both for the asynchronous (KMO = 0.71), and synchronous (KMO = 0.85) condition. The two control items (q2 and q3) were excluded from the PCA, based on the low expected correlation with any of the other questionnaire items in the asynchronous conditions, as well as their poor individual KMO (both < 0.55) (Kaiser, 1974). An initial PCA was computed with 9 components. Inspection of the eigenvalues of each component and the scree plot (Figure S1) justified retaining three components for the secondary PCA. For subsequent comparisons between conditions component scores were calculated as the mean of q4, q6, and q9 for Component 1; q7, q8, and q10 for Component 2; and q1, q11, and (1 -

q5) for Component 3. For the component scores, q5 was inversed to ensure that higher ratings correspond to increased embodiment for all items within Component 3.

Experiment 2

Participants. Thirty-two healthy volunteers participated in Experiment 2 (7 males; *M* = 21.2, *SD* = 3.9 years old). None of the participants took part in Experiment 1, and all gave informed consent and received either course credits or a financial compensation. The protocol was approved by the Ethics Committee of the Faculty of Arts and Social Sciences at the University of Zurich (Approval Number 17.12.15). The study was performed in accordance with the ethical standards of the Declaration of Helsinki.

Apparatus for stimulation. The apparatus to present visual stimulation was identical to Experiment 1 (*Apparatus for stimulation* for Experiment 1). An additional laptop was used to play a metronome sound with its built-in speakers.

Procedure. The experiment consisted of two different parts: first, two blocks with multiple trials of short stimulation, either visuotactile or visuomotor were presented, then four conditions of longer stimulations, either visuomotor or visuotactile both either synchronous or delayed were presented (see Figure 1b in the main text for an overview of the procedure). When participants were ready, they were helped to put on the HMD and read instructions on the screen. Similar to Experiment 1, the testing procedure was preceded by a test trial to practice giving responses on the VAS scale, and exposure to a synchronous image of the participant's body with their hands on the table for a few seconds.

For the visuotactile block, participants were asked to fix their left hand between the two markers on the table while they were stroked with a small paintbrush outwards from their arm on their index and middle fingers at a rate of approximately 0.5 Hz with the aid of a metronome set to 1 Hz. The first click of the metronome would be to stroke down the finger and release, and the second click to go back without touching to start the next stroke. This would be repeated across the whole trial. For the visuomotor block they were asked to move their left hand horizontally from the left to the right marker (set at a distance of approximately 60 cm from each other) and back repeatedly, following the rhythm of a metronome (set to 1 Hz), each back-and-forth movement would last 0.5 Hz. Participants started and ended each trajectory with their hand touching the table. Each trial lasted 7 s and was followed by the question “Was the touch/movement you saw and felt synchronous?”, which could be answered by either selecting *yes* or *no*. This question was followed by the statement “It felt as if the hand that I saw was my own”, which could be answered on a VAS scale ranging from *strongly disagree* to *strongly agree.* The first two blocks consisted of 40 trials with four repetitions of 10 possible delay steps of 66 ms each, resulting in a range from 139 to 733 ms (including the intrinsic delay). The order of the visuomotor and visuotactile blocks were counterbalanced across participants.

Finally, a block of longer stimulation followed, where we presented four conditions (synchronous visuotactile, synchronous visuomotor, asynchronous visuotactile and asynchronous visuomotor) in counterbalanced order. The asynchronous conditions had a delay of 594 ms (plus the intrinsic 139.1 ms delay). During the visuomotor conditions, participants moved their hands as in the previous block but for a longer period; similarly, for the visuotactile condition, participants were stroked on their hand with a paintbrush randomly over the full hand at a rate of approximately 1 stroke per second for a period of 90 s, the stroking was monitored on the computer screen by the experimenter to prevent the overlap of the previous seen stroke with the ongoing tactile stroke in the asynchronous condition. After each condition, they were asked to answer the (dis)embodiment questionnaire (see section *(Dis)embodiment questionnaire*).

Participants could take breaks and remove the HMD in between blocks. The experiment was concluded with a brief semi-structured interview on the experiences of the participant and a short debriefing. The overall procedure took about 50 minutes.

Measures of illusion strength. The assessment for the short stimulation was based on simultaneity judgment methods used to measure temporal windows of multisensory integration (Engel & Dougherty, 1971; Hirsh & Fraisse, 1964; Hoover & Harris, 2012, 2016), and an embodiment question derived from several studies (Botvinick & Cohen, 1998; Dobricki & Rosa, 2013; Lenggenhager et al., 2007). After each block of 90 s, participants completed an identical questionnaire as in Experiment 1. Item 3 corresponded to a control item and differed between conditions, and was “It felt as if the movement I felt was due to the seen movement” in the visuomotor condition, and “It felt as if the stroking I felt on my hand was due to the seen stroking” in the visuotactile condition.

Data analysis. The same software and parameters for significance were used as in Experiment 1. The questionnaire was analyzed using Wilcoxon signed-rank tests to assess the effect of synchrony (visuotactile synchronous vs. visuotactile asynchronous and visuomotor synchronous vs. visuomotor asynchronous) and the effect of modality (visuotactile synchronous vs. visuomotor synchronous and visuotactile asynchronous vs. visuomotor asynchronous).

Sensitivity to delay was assessed by determining the Point of Subjective Equality (PSE) for each participant in the visuomotor and visuotactile condition separately. To this end, logistic psychometric functions were fitted to the forced choice synchrony judgements of each participant, using a binomial Generalized Linear Model (glm) with delay as a predictor. The estimated coefficients of the glm were used to calculate the PSE: $-\beta_0 / \beta_1$, where β_0 corresponds to the intercept and β_1 to the slope. Goodness of fit was assessed with the Hosmer-Lemeshow test, and data of one participant in the visuotactile condition was excluded due to bad fit of the glm. All other psychometric curves did not yield a significant test result, and corresponding PSEs were thus used for further analyses.

Generalized linear mixed models were fitted with the lme4 package in R (Bates, Mächler, Bolker, & Walker, 2015). A generalized linear mixed model was fitted to the VAS ownership ratings in the short block, across different delays, which ensured for adequate power while considering the repeated measures within individuals. The intraclass correlation demonstrated that observations within individuals were non-independent (ICC(1) = .27, F(31, 2528) = 31, p < .001), thus justifying the use of a mixed model. Visual inspection of diagnostic plots of the residuals showed that these were normally distributed. The model that included both a random intercept and slope for individuals, where VAS ratings were explained as a function of delay, fitted the data better than the model that included only the random intercept and no random slope ($X^2(2) = 470$, p < .001). Therefore, we used the random intercept and slope model for further hypothesis testing.

Supplemental References

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 67(1). https://doi.org/10.18637/jss.v067.i01

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society*, *57*(1), 289–300. https://doi.org/10.2307/2346101

Botvinick, M., & Cohen, J. (1998). Rubber hands “feel” touch that eyes see. *Nature*, *391*(6669), 756. https://doi.org/10.1038/35784

Dobricki, M., & Rosa, S. de la. (2013). The Structure of Conscious Bodily Self-Perception during Full-Body Illusions. *PLoS ONE*, *8*(12), e83840. https://doi.org/10.1371/journal.pone.0083840

Engel, G. R., & Dougherty, W. G. (1971). Visual-Auditory Distance Constancy. *Nature*, *234*(5327), 308. https://doi.org/10.1038/234308a0

Hirsh, I.-J., & Fraisse, P. (1964). Simultanéité et succession de stimuli hétérogènes. *L'Année psychologique*, *64*(1), 1–19. https://doi.org/10.3406/psy.1964.27144

Hoover, A. E. N., & Harris, L. R. (2012). Detecting delay in visual feedback of an action as a monitor of self recognition. *Experimental Brain Research*, *222*(4), 389–397. https://doi.org/10.1007/s00221-012-3224-3

Hoover, A. E. N., & Harris, L. R. (2016). Inducing ownership over an 'other' perspective with a visuo-tactile manipulation. *Experimental Brain Research*, *234*(12), 3633–3639. https://doi.org/10.1007/s00221-016-4760-z

Kaiser, H. F. (1974). An index of factorial simplicity. Psychometrika, 39(1), 31–36. https://doi.org/10.1007/BF02291575

Lenggenhager, B., Tadi, T., Metzinger, T., & Blanke, O. (2007). Video Ergo Sum: Manipulating Bodily Self-Consciousness. *Science*, *317*(5841), 1096–1099. https://doi.org/10.1126/science.1143439

Longo, M. R., Schüür, F., Kammers, M. P. M., Tsakiris, M., & Haggard, P. (2008). What is embodiment? A psychometric approach. *Cognition*, *107*(3), 978–998. https://doi.org/10.1016/j.cognition.2007.12.004

Macauda, G., Bertolini, G., Palla, A., Straumann, D., Brugger, P., & Lenggenhager, B. (2015). Binding body and self in visuo-vestibular conflicts. *The European Journal of Neuroscience*, *41*(6), 810–817. https://doi.org/10.1111/ejn.12809

R Core Team. (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing (Version 3.5.1). Retrieved from https://www.R-project.org/

Rodriguez-Linares, L., Vila, X., Lado, M. J., Mendez, A., Otero, A., & Antonio, C. (2017). RHRV: Heart Rate Variability Analysis of ECG Data (Version 4.2.3). Retrieved from https://CRAN.R-project.org/package=RHRV

Salomon, R., Lim, M., Pfeiffer, C., Gassert, R., & Blanke, O. (2013). Full body illusion is associated with widespread skin temperature reduction. *Frontiers in Behavioral Neuroscience*, *7*. https://doi.org/10.3389/fnbeh.2013.00065

Schandry, R. (1981). Heart Beat Perception and Emotional Experience. *Psychophysiology*, *18*(4), 483–488.