Acta Psychologica 229 (2022) 103672

Contents lists available at ScienceDirect

Acta Psychologica

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

Abrupt visibility modifications affect specific subjective (not objective) aspects of body ownership

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ARTICLE INFO

Keywords:
Multisensory
Rubber hand illusion
Visuo-tactile
Body representation

ABSTRACT

The sense of body ownership builds on proper multisensory integration mechanisms. The Rubber-Hand Illusion (RHI) paradigm exploits a visuo-tactile multisensory conflict to induce illusory body ownership toward a fake hand, assessed by multidimensional subjective ratings and univocal objective measurements. Considering the controversy as to whether viewing the rubber hand is necessary or not to induce the illusion, we investigated the effects of targeted manipulations of visibility on subjective and objective aspects of the RHI. To this aim, we collected questionnaire and proprioceptive drift data from thirty participants receiving visuo-tactile stimulation in a setup that allowed for increasing and decreasing the visibility (illumination) of the rubber hand. We found that specific subjective ratings (Movement and Loss of Ownership) were sensitive to the interaction between rubber hand's visibility and illusory ownership. The interaction was not significant for the Embodiment subjective component and for the objective one (proprioceptive drift). Since different degrees of visibility did not differentially affect the RHI, these findings highlight that relatively abrupt changes in the visibility of the rubber hand can differentially impact subjective versus objective components of body ownership. This understanding may be critical for neuroscientific theories on the relationship between multisensory integration and body consciousness.

1. Introduction

The human ability to combine information from different sensory sources (e.g., vision and touch) is one of the foundations of the sense of body ownership (Pamplona et al., 2021). Such a sense that “this” body is “my” body (Blanke & Metzinger, 2009; Haggard et al., 2003) is a fundamental aspect of daily living (Damasio, 1999; Jeannerod, 2006), but it cannot always be taken for granted. In fact, both neuropathological conditions [e.g. autoscopy (Devinsky et al., 1989), somatoparaphrenia (Nightingale, 1982), out-of-body experiences (Blanke et al., 2002)], or experimental manipulations of multisensory input (Ionta et al., 2011; Ionta et al., 2014) may hinder the sense of body ownership, including the misrecognition of one's body part as belonging to oneself.

Experimental manipulations of body ownership have been widely investigated with the so-called “Rubber-Hand Illusion” (RHI) paradigm (Botvinick & Cohen, 1998; Tsakiris & Haggard, 2005), whereby it is possible to induce the feeling that a fake hand belongs to us. In this paradigm, when participants observe a rubber hand being stroked in synchrony with the stroking of their own hidden hand, they report a feeling of ownership toward the rubber hand (self-attribution) and they tend to misjudge the location of their own hand toward the location of the rubber (mislocalization) (Longo et al., 2008; Tsakiris, 2010). However, the onset of the RHI depends on many experimental factors related to the relationship between the rubber and the real hand, including congruent positioning (Costantini & Haggard, 2007; Lloyd, 2007), general resemblance (IJsselsteijn et al., 2006; Preester & Tsakiris, 2009), anatomical plausibility (Ide, 2013; Ionta et al., 2013), and others. Paradoxically, the visibility of the rubber hand during the visuo-tactile stroking has been considered both a fundamental prerequisite (Fuchs et al., 2016) and a non-strictly necessary condition (Guterstam et al., 2013) for inducing illusory ownership. Such controversy might arise, at least partially, from methodological idiosyncrasies, such as the use of self-attribution questionnaires either as a whole or subdivided into components. These components may reflect different aspects of the overall subjective illusory experience (Longo et al., 2008), including “Embodiment” (the feeling that the rubber hand belongs to oneself),

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https://doi.org/10.1016/j.actpsy.2022.103672
Received 5 May 2022; Received in revised form 28 June 2022; Accepted 11 July 2022
Available online 20 July 2022

"Movement" (illusory feeling that either the rubber or the real hand move), and "Loss of Ownership" (the sense of being unable to control the real hand). Importantly, not all these components account for the same amount of variance in the subjective aspects of the RHI. Indeed, for the subjective evaluations of the RHI provided with reference to both the synchronous and asynchronous visuo-tactile stroking, the Embodiment component alone accounts for about 25 % of the variance of the reported illusion, followed by Loss of Ownership, and Movement (Longo et al., 2008).

Taking also into account that different body-related visual input can affect ownership-like neuro-behavioral responses (Ionta et al., 2020), the present study investigated the influence of the visibility of the rubber hand on different components of self-attribution (questionnaire scores) and mislocalization (proprioceptive drift) by systematically varying the visibility of the rubber hand during the illusion-inducing visuo-tactile stimulation. Considering the higher sensitivity (many components with different weight) of the multivariate subjective measure of the RHI (questionnaires) with respect to its univariate objective measure (proprioceptive drift), we hypothesized that variations in the visibility of the rubber hand may affect more strongly self-attribution (Embodiment, Loss of own hand, and Movement with respect to a control item) than objective mislocalization associated with the RHI. The implications of the obtained results may impact current models of the relationship between multisensory integration and body ownership, with potential insights for clinical practice and personalized assessment.

2. Methods

2.1. Subjects

Based on a power analysis of previous data, and in line with previous work (e.g., Guterstam et al., 2013), 30 right-handed and neuropsychologically healthy subjects (16 women; 23.9 ± 5.0 years old) took part to the study. All subjects had normal or corrected-to-normal vision and signed the informed consent form prior to their participation in the experiment, which was approved by the local ethics committee and carried out according to the Declaration of Helsinki (2013).

2.2. Experimental setup

All subjects sat comfortably in front of an RHI apparatus placed on a table (Ionta et al., 2013), horizontally centered on the subject's body

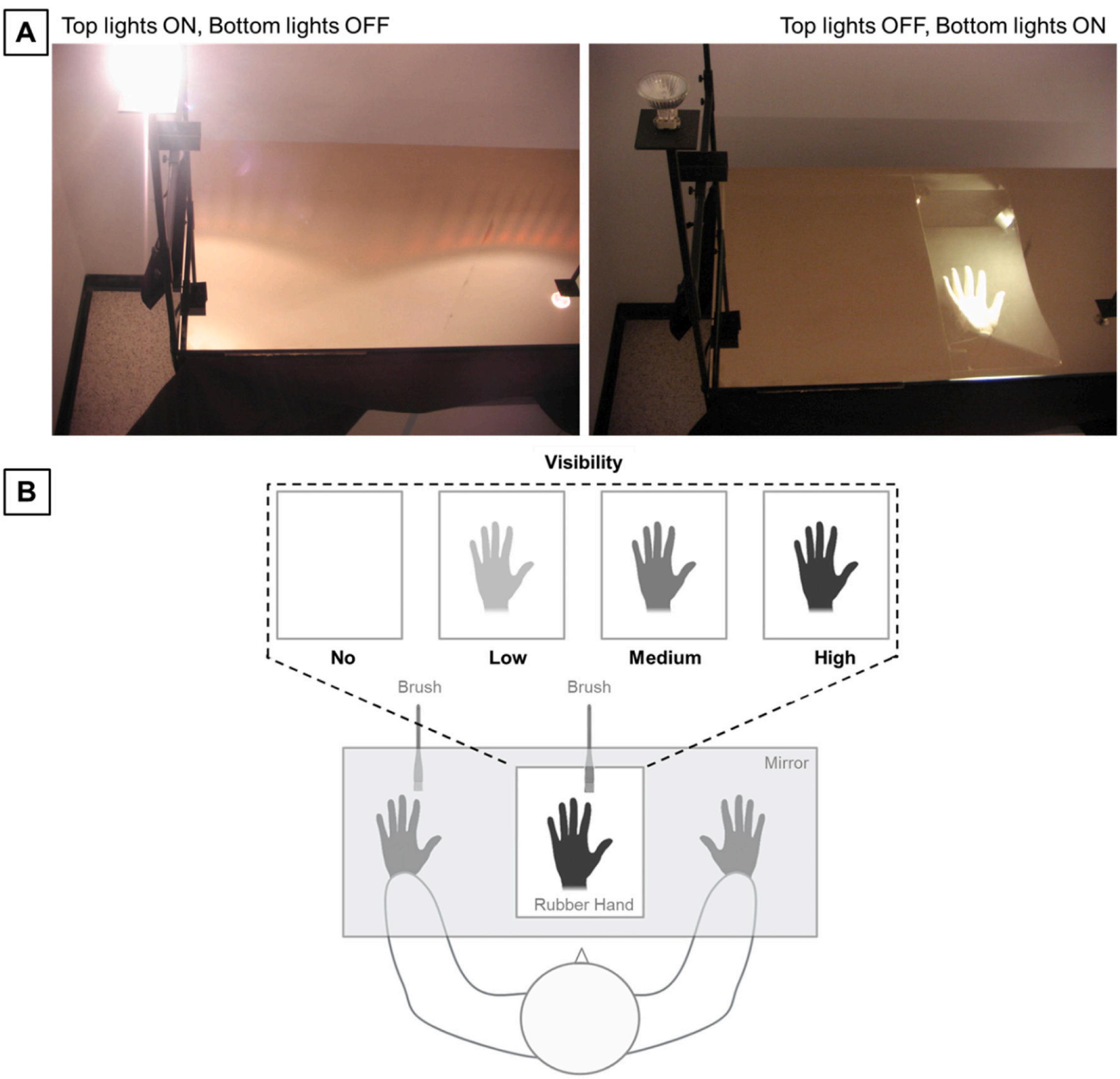

Fig. 1. (A) The RHI apparatus used for modulating visibility during visuo-tactile stimulation. Conditions of minimum and maximum visibility are shown, obtained by either switching the top lights on and the bottom lights off (left) or switching the top lights off and the bottom lights on (right). (B) Position of the participant with respect to the rubber hand. An experimenter used a brush to synchronously or asynchronously stimulate the real hand (haptic input) and the rubber hand (visual input).

midline (Fig. 1B). The RHI apparatus consisted of a wooden frame fully painted in black with two horizontal planes of dimensions 100×50 cm^2, placed one on top of the other with a gap of 20 cm between them. A two-way mirror constituted the upper plane. An opaque surface constituted the lower plane. Subjects placed their hands in the gap, on the lower plane. A black sheet attached to the edge of the two-way mirror covered the subjects' arms, ensuring that they could see their hand only through the two-way mirror. In addition, two black cardboards were positioned under the mirror, covering two fifths of the mirror on the left side and two fifths on the right side. This way, only the central fifth of the mirror was not covered. During the experiment, a rubber left hand was placed in the gap under the uncovered part of the mirror, in a position anatomically congruent with the subject's position (Riemer et al., 2019). Both the subjects' and the rubber hands were placed and kept still in a palm-down posture. The RHI apparatus was also equipped with two independent lighting systems. One lighting system (top lights), positioned on top of the mirror (outside the gap), could illuminate the room and comprised four 35 W/12 V halogen bulbs (left panel of Fig. 1A). The other lighting system (bottom lights), positioned under the mirror (inside the gap), could illuminate the rubber hand and comprised four 5 W/12 V incandescent bulbs (right panel of Fig. 1A). This setup allowed subjects to see the rubber hand during the visuo-tactile stimulation (bottom lights on and top lights off), but not during the following evaluations of the RHI (self-attribution and proprioceptive drift; bottom lights off and top lights on). In addition, the visibility of the rubber hand could be modulated by changing the power of the bottom lights (luminosity) with a dimmer switch. Specifically, the dimmer switch was used to generate four levels of visibility, which corresponded to the dimmer switch positioned at 0 % (no-visibility), 8 % (low visibility), 16 % (medium visibility), and 24 % (high visibility) (Fig. 1B) of the full power of the bottom lighting system.

2.3. Procedure

Subjects' hands were hidden from view and always kept in the same position throughout the experiment (on the bottom plane, under the mirror). At the beginning of the experimental session, the top lights were on and the bottom lights were off (i.e., no-visibility). A removable ruler was placed parallel to and above the mirror, perpendicular to the subjects' left index finger; its readings were reflected by the mirror and visible to the subjects. Then, before the visuo-tactile stimulation, subjects were instructed on the proprioceptive drift task: they were asked to verbally indicate the ruler reading, as reflected in the mirror, corresponding to the perceived position of their left index finger. Thus, the reading indicated by the subject before visuo-tactile stimulation was defined as the baseline value for the following proprioceptive drift assessment. The ruler was then removed, all lights were switched off, and subjects also closed their eyes for 1 min to adapt to darkness. Next, the bottom lights were switched on and subjects opened their eyes, being able to see through the mirror where the rubber hand was placed.

To induce the RHI in the subject's left (non-dominant) hand, the real and rubber hands were synchronously stroked with two brushes by an experimenter for 2 min. A left rubber hand was used because of reports of higher subjective ratings and proprioceptive drifts compared to a right hand (Dempsey-Jones & Kritikos, 2019; Riemer et al., 2019; Smit et al., 2017). Thus, subjects viewed the rubber hand being stroked (visual stimulation) while their left hand was also stroked (tactile stimulation). During synchronous visuo-tactile stimulation (RHI condition), the subject's hand and the rubber hand were stroked at the same locations and time. As a control condition, during asynchronous visuo-tactile stimulation (noRHI condition), the real and rubber hands were stroked but at different locations and at different times. In both synchronous and asynchronous stimulations, the real and rubber hands were stroked on the fingers, dorsum, and knuckles. According to this approach, the illusory ownership for the rubber hand should be induced only or more strongly in the RHI compared to the noRHI condition. To assess illusory ownership, after the visuo-tactile stimulation, subjects underwent a proprioceptive drift task and completed dedicated questionnaires (see next paragraph). After these measurements, subjects removed their hands from the RHI apparatus, moved them freely, and rubbed them together to cancel eventual carry-over proprioceptive effects. Then, they returned their hands to the original position in the RHI apparatus for the next experimental trial. Considering the two types of stimulation (RHI, noRHI) and the four types of visibility (no, low, medium, high), the experiment comprised eight possible combinations of stimulation and visibility, presented once each in randomized order.

2.3.1. Subjective measures of RHI (questionnaire)

After the proprioceptive drift task, subjects rated the strength of RHI-related subjective sensations according to specific statements derived from extensive RHI questionnaires (Longo et al., 2008). While the proprioceptive drift is an objective measurement of the proprioceptive recalibration due to the RHI (Tsakiris, 2010), the RHI questionnaire is used to measure aspects of the subjective experience associated with the RHI (Longo et al., 2008). In particular, the RHI statements on which the present study is based comprised three components of the subjective RHI experience (Table 1): three statements referred to the perceived “Embodiment” of the rubber hand into the subject's own body (S1, S2, S3); two statements assessed the illusory sense of “Movement” of the subject's hand (S4, S5); one statement concerned the feeling of “Loss of Ownership” of the subject's own hand (S6); and one statement was used as “Control” item to assure effect specificity and control for attention and compliance (S7). These statements were selected as a function of their principal component analysis loadings (“factor Loading”) for the related component in both the synchronous and asynchronous visuo-tactile stimulation. In particular, based on Table 1 of the paper by Longo et al. (2008), for the Embodiment component we selected the statement S1, S2, and S3 because they had the highest factor Loadings in both the synchronous (0.854, 0.878, 0.838, respectively) and asynchronous (0.845, 0.858, 0.802, respectively) visuo-tactile stimulation. Similarly, Longo et al. (2008) showed that the statements S4 and S5 used in the present study had the highest factor Loadings for the Movement component in both the synchronous (0.747 and 0.667, respectively) and the asynchronous (0.718 and 0.640, respectively) conditions. Finally, we selected S7 as a control statement, because in Longo et al. (2008) it had the lowest possible value in Communalities (0), indicating that this particular statement is not related to the RHI in either the synchronous or asynchronous conditions. An additional statement addressed the sensation of “Deafference” of the subject's hand but, since this component accounts for the variance of the subjective RHI only after asynchronous, not synchronous, visuo-tactile stimulation (Longo et al., 2008), the data related to this statement were not considered in the definitive analysis of the present study.

Subjects indicated their level of agreement with each statement according to a 7-point symmetric Likert scale (from −3 to 3), where the minimum and the maximum values corresponded to “strongly disagree” and “strongly agree”, respectively. Questionnaire scores addressing the same component (i.e., as in the “Embodiment” and “Movement”

Table 1
RHI statements and associated components rated by the participants for each trial.

Component	Statement
Embodiment	S1 - *It seemed like the rubber hand began to resemble my real hand*
	S2 - *It seemed like the rubber hand was my hand*
	S3 - *It seemed like the touch I felt was caused by the paintbrush touching the rubber hand*
Movement	S4 - *It seemed like my hand was moving toward the rubber hand*
	S5 - *It seemed like the rubber hand was moving toward my hand*
Loss of ownership	S6 - *It seemed like my hand had disappeared*
Control	S7 - *I found myself liking the rubber hand*

components) were averaged within each component prior to analysis. Subjects kept their hands under the mirror while answering to the questionnaire and provided their answers verbally, recorded using the PsychoPy software (http://www.psychopy.org/).

2.3.2. Objective measure of RHI (proprioceptive drift)

After 2 min of visuo-tactile stimulation (synchronous or asynchronous), the rubber hand was hidden by turning off the bottom lights and turning on the top lights, and subjects performed the proprioceptive drift task. For this purpose, the ruler was placed back above the mirror, but in a different position with respect to baseline (proprioceptive drift task performed before the visuo-tactile stimulation). In particular, to avoid any potential carry-over bias for the several proprioceptive drift tasks performed throughout the experiment, for each repositioning the ruler was randomly placed in one out of sixteen reference readings distributed along the ruler (relative zeros). This way, during each proprioceptive drift task the physical position of the subject's left index finger was the same, but it corresponded to a different reading on the ruler. The location of the index finger perceived by each subject (perceived location) was established by computing the distance in centimeters from the ruler reading indicated by the subject and the specific reference reading used in that specific trial. The subtraction of the perceived location at baseline (before the visuo-tactile stimulation) from the perceived location after the visuo-tactile stimulation indicated the magnitude (cm) and direction (left, right) of the proprioceptive drift. From this subtraction, positive values indicated a rightward proprioceptive drift: a biased perception of the real hand's position toward the rubber hand. Conversely, negative values indicated a leftward proprioceptive drift: a biased perception of the real hand's position away from the rubber hand. By defining a baseline value for each trial and subject, the proprioceptive drift was controlled for individual perceptual differences and avoided carry-over effects.

2.4. Data analysis

Data analysis was conducted with RStudio (https://rstudio.com/). We defined as factors of interest Stimulation (levels: RHI and noRHI) and Visibility (levels: no, low, medium, and high).

To investigate whether there were effects of Stimulation and Visibility on the subjective components of the RHI (questionnaire), we used a two-way repeated ordinal regression with cumulative link mixed models (Mangiafico, 2016) to handle nonparametric, ordinal data (library 'ordinal'). We tested the significance of the main effects of each factor and the interaction between them with an analysis of deviance approach (library 'car'). We used Nagelkerke pseudo-R^2 (Nagelkerke, 1991) to evaluate effect sizes of main effects and interactions (library 'rcompanion'). Post-hoc analyses following significant main effects and interactions were conducted using pairwise ordinal comparisons (library 'lsmeans').

To investigate whether there were effects of Stimulation and Visibility on the objective index of the RHI (proprioceptive drift), we used a two-way repeated-measures ANOVA, in which we tested the significance of the main effects and interaction. We also applied Greenhouse-Geisser correction to adjust for sphericity after a Mauchly's test (library 'rstatix'). Three participants were considered outliers (data values were more than three times the interquartile range below the first quartile or above the third quartile) and were excluded from the following analyses. We used partial eta-squared to evaluate effect sizes of main effects and interaction (library 'DescTools'). Post-hoc analyses following significant effects were conducted using pairwise comparisons (library 'emmeans'). Significance was determined according to a level of significance of 0.05. The *p*-values in post-hoc analyses were corrected for multiple comparisons using the Šidák correction (library 'rstatix'). Post-hoc pairwise comparison effect sizes were evaluated by z-scores (i.e., dividing the estimated differences by the standard deviation for the fitted model).

3. Results

3.1. Subjective components measured by the RHI questionnaire

We observed significant interactions Visibility × Stimulation in the Movement and Loss of Ownership, but not in the Embodiment component [Movement: LR $\chi^2(3) = 25.5$ (likelihood ratio chi-square), $p < 0.0001$, $R^2 = 0.53$; Loss of Ownership: LR $\chi^2(3) = 10.9$, $p = 0.012$, $R^2 = 0.42$; Embodiment: $p = 0.21$]. The absence of significance in the Control statement ($p = 0.4$) confirmed that the effect of the Visibility × Stimulation interactions was specific for Movement and Loss of Ownership (Fig. 2). The relatively high scores provided to the Control statement suggest that participants paid attention to and complied with the experimental task. For the interactions in Movement and Loss of Ownership components, post-hoc analyses indicated higher questionnaire scores for RHI compared to noRHI at low, medium, and high levels of visibility. In addition, for both Movement and Loss of Ownership, higher questionnaire scores were found in the RHI condition for low, medium, and high visibility compared to no-visibility. Finally, in the component Loss of Ownership, also in the noRHI condition the questionnaire scores were significantly higher in low, medium, and high visibility with respect to no-visibility (Tables 2 and 3).

For all statements, we observed the main effects of Stimulation [Embodiment: LR $\chi^2(1) = 39.1$, $p < 0.0001$, $R^2 = 0.11$; Movement: LR $\chi^2(1) = 102.6$, $p < 0.0001$, $R^2 = 0.30$; Loss of Ownership: LR $\chi^2(1) = 53.1$, $p < 0.0001$, $R^2 = 0.17$; Control: LR $\chi^2(1) = 17.2$, $p < 0.0001$, $R^2 = 0.07$] and Visibility [Embodiment: LR $\chi^2(3) = 104.6$, $p < 0.0001$, $R^2 = 0.33$; Movement: LR $\chi^2(3) = 65.40$, $p < 0.0001$, $R^2 = 0.17$; Loss of Ownership: LR $\chi^2(3) = 72.2$, $p < 0.0001$, $R^2 = 0.23$; Control: LR $\chi^2(3) = 7.89$, $p = 0.048$, $R^2 = 0.03$], meaning higher questionnaire scores for RHI compared to noRHI and for low, medium, and high compared to no-visibility (Tables 2 and 3).

3.2. Objective index measured by the proprioceptive drift task

Regarding the proprioceptive drift measures, we observed the main effects of Stimulation [$F(1,26) = 8.73$, $p = 0.007$, $\eta_p^2 = 0.10$] and Visibility [$F(3,78) = 2.79$, $p = 0.046$, $\eta_p^2 = 0.25$] (Fig. 3), for which post-hoc analysis showed higher drift for RHI compared to noRHI (Tables 2 and 3). The interaction between Stimulation and Visibility was not statistically significant ($p = 0.24$).

4. Discussion

The present study provides evidence that, when the RHI occurs (synchronous visuo-tactile stimulation; not asynchronous) and independently from the degree of visibility, making the rubber hand visible affects some specific subjective components of illusory body ownership, namely Movement and Loss of Ownership (significant Stimulation × Visibility interactions). Conversely, the other subjective component (Embodiment) and the objective aspect (proprioceptive drift) of illusory body ownership were not modulated by the interaction between Visibility and Stimulation. These findings suggest that (1) some components of the subjective RHI (Movement and Loss of Ownership) are more sensitive to visibility than others (Embodiment), at least for relatively abrupt visibility changes (no- vs. low-visibility), as subjects report the illusion as soon as the rubber hand is even barely visible, and (2) relatively gross visibility manipulations do not differentially affect the RHI, as there were no significant differences between the conditions where the rubber hand was visible (low, medium, high visibility). These interpretations hint at Bayesian causal inference models, in that, specifically for subjective aspect of body ownership, once the multisensory binding reached the minimal conditions (e.g. low visibility) to be "approved" by causal inference mechanisms, increasing the sensory input (e.g. medium and high visibility) does not affect the RHI.

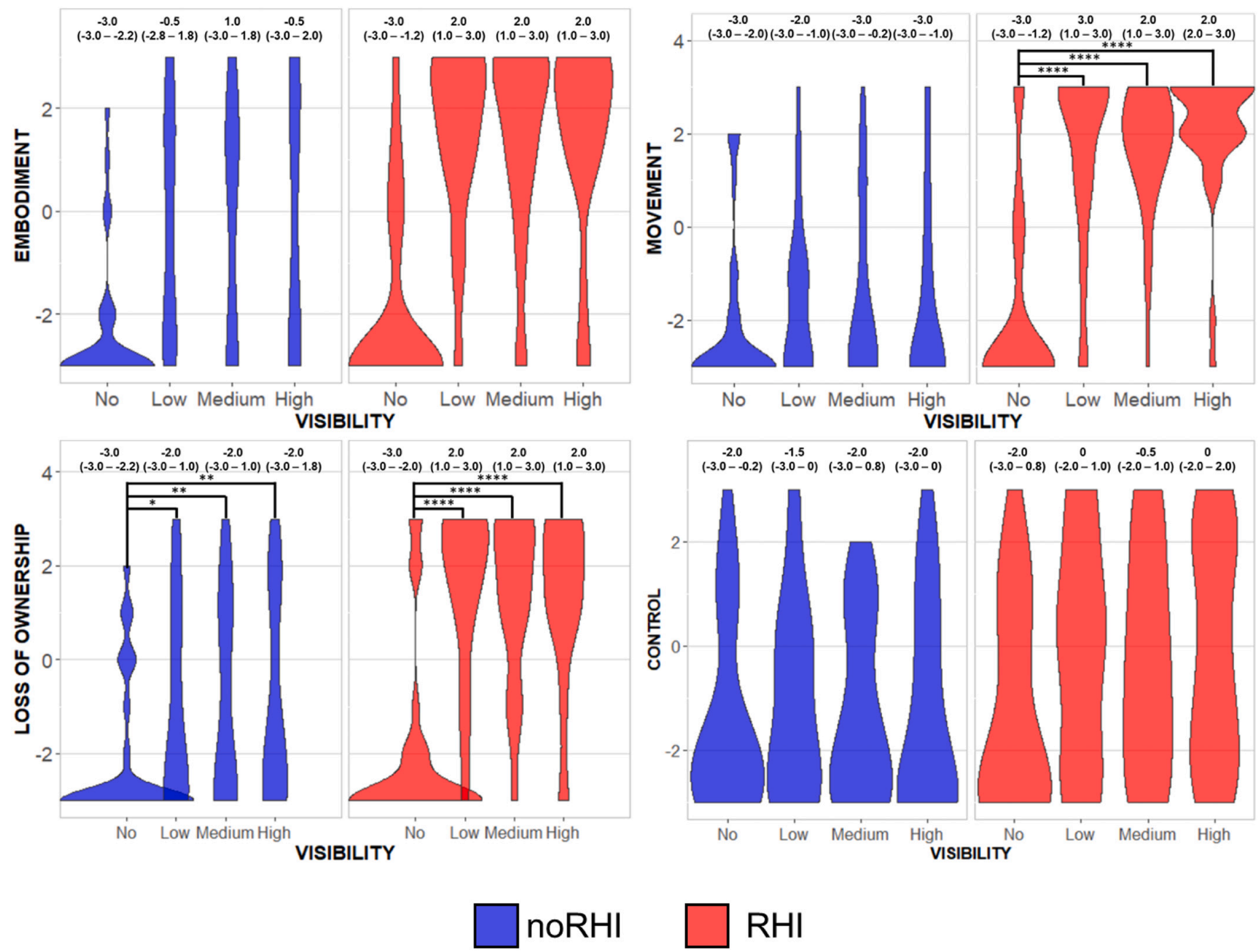

Fig. 2. Questionnaire scores as a function of Stimulation (noRHI, RHI) and Visibility (no, low, medium, high) for all RHI components. The interaction Stimulation × Visibility was significant only for Movement and Loss of ownership. The noRHI and RHI conditions are represented in blue and red, respectively. Following ordinal regression models, asterisks represent significant differences in post-hoc tests corrected for multiple comparisons (****$p < 0.0001$, **$p < 0.01$, *$p < 0.05$). Medians and interquartile intervals (between parentheses) are shown on top of the graphs. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 2
Descriptive statistics for each combination of conditions (Vis = visibility, Stim = stimulation) – for the questionnaire measures, the median and interquartile interval (between parentheses) is reported; whereas for the proprioceptive drift measure the mean ± standard deviation is reported.

Vis	Stim	Questionnaire				Proprioceptive drift
		Embodiment	Movement	Loss of ownership	Control	
No	noRHI	−3.0 (−3.0 to −2.2)	−3.0 (−3.0 to −2.0)	−3.0 (−3.0 to −2.2)	−2.0 (−3.0 to −0.2)	0.00 ± 1.52
Low		−0.5 (−2.8–1.8)	−2.0 (−3.0 to −1.0)	−2.0 (−3.0–1.0)	−1.5 (−3.0–0)	−0.37 ± 2.11
Mid		1.0 (−3.0–1.8)	−3.0 (−3.0 to −0.2)	−2.0 (−3.0–1.0)	−2.0 (−3.0–0.8)	0.70 ± 2.70
High		−0.5 (−3.0–2.0)	−3.0 (−3.0 to −1.0)	−2.0 (−3.0–1.8)	−2.0 (−3.0–0)	0.19 ± 2.35
No	RHI	−3.0 (−3.0 to −1.2)	−3.0 (−3.0 to −1.2)	−3.0 (−3.0 to −2.0)	−2.0 (−3.0–0.8)	0.07 ± 1.88
Low		2.0 (1.0–3.0)	3.0 (1.0–3.0)	2.0 (1.0–3.0)	0 (−2.0–1.0)	1.07 ± 2.30
Mid		2.0 (1.0–3.0)	2.0 (1.0–3.0)	2.0 (1.0–3.0)	−0.5 (−2.0–1.0)	1.52 ± 2.64
High		2.0 (1.0–3.0)	2.0 (2.0–3.0)	2.0 (1.0–3.0)	0 (−2.0–2.0)	1.70 ± 2.25

4.1. Rubber hand visibility affects subjective aspects of illusory body ownership

In typical conditions, we use multisensory-matching mechanisms to combine different sensory inputs originating from one object/event (Halje et al., 2015). During the RHI subjects experience an alteration of body ownership, due to a distortion of such a multisensory (visuo-tactile) binding. The spatial conflict between visual and tactile inputs (synchronous but in different locations) is resolved through a proprioceptive re-adaptation in favor of vision, resulting in an increased sense of ownership for the rubber hand (Botvinick & Cohen, 1998; Ehrsson et al., 2004; Longo et al., 2008) and a mislocalization of the perceived position of one's own hand toward the rubber hand (Ehrsson et al., 2005; Kammers et al., 2009; Shimada et al., 2009). As participants are

Table 3
Statistically significant differences following post-hoc pairwise comparisons for all components of the questionnaire scores and the proprioceptive drift.

	Visibility	Stimulation	z-Ratio	p-Value
Embodiment	Low/no	–	7.9	<0.0001
	Mid/no		8.02	<0.0001
	High/no		8.05	<0.0001
	–	RHI/noRHI	5.55	<0.0001
Movement	Low	RHI/noRHI	6.38	<0.0001
	Mid		6.56	<0.0001
	High		7.22	<0.0001
	Low/no	RHI	7.1	<0.0001
	Mid/no		7.01	<0.0001
	High/no		7.61	<0.0001
Loss of ownership	Low/low	RHI/noRHI	5.07	<0.0001
	Mid/mid		4.61	<0.0001
	High/high		4.45	<0.0001
	Low/no	noRHI	2.87	0.024
	Mid/no		3.25	0.007
	High/no		3.19	0.008
	Low/no	RHI	6.75	<0.0001
	Mid/no		6.85	<0.0001
	High/no		6.71	<0.0001
Control	–	RHI/−noRHI	4.01	<0.0001
Proprioceptive drift	–	RHI−/noRHI	3.11	0.0022

instructed to not move their hidden hands, proprioception updating is prevented, and vision becomes dominant over proprioception, promoting the illusion (Lewis & Lloyd, 2010). Rather than a unitary subjective measure, self-report questionnaires are deemed to reflect multidimensional aspects of the illusory experience (Longo et al., 2008).

Considering the centrality of vision in the RHI, in the present study we followed the logic assumption that, since vision is an important aspect in the RHI experience, changing the visibility of the rubber hand setup could alter the strength of the RHI. The significant interactions indicated that subjects felt stronger illusory Movement and Loss of Ownership as soon as the rubber hand was even barely visible (low visibility) and that this feeling did not change as a function of increased visibility (no difference between low, medium, high visibility). Conversely, the Embodiment component was not affected by visibility, in that the questionnaire scores were similar among all the experimental conditions. It is worth noting that, in the present study, the statements used to assess the Movement component of the RHI referred to an illusory movement of the real to the rubber hand or vice-versa (S4, S5), the statement for evaluating the Loss of Ownership component referred to the feeling of illusory disappearance of the hand (S6), and the statements to measure the Embodiment component concerned the visual resemblance between the real and the rubber hand (S1, S2), as well as the similarity of the haptic sensations derived from them (S3). In other words, while the Movement statements concerned proprioceptive aspects of the RHI illusion and the Loss of Ownership regarded visual aspects, the Embodiment statements comprised both proprioceptive (S1, S2) and visual (S3) aspects of the RHI. It is therefore plausible that only the unimodal components (proprioceptive or visual) of the RHI are sensitive enough to be affected by the visual presentation of the rubber hand (visibility conditions) or not (no-visibility). Conversely, for multimodal components (visuo-proprioceptive) such as Embodiment, the effects induced by variating the visibility of the rubber hand might be too weak or divergent to result in a straightforward result. Along this line, it has been reported that for the Embodiment component also the asynchronous condition may induce illusory ownership, due the mere visual perception of the rubber hand (Longo et al., 2008). Such an alteration of illusory ownership during the asynchronous condition may have prevented or hindered the interaction between Visibility and Stimulation for the Embodiment component.

Interestingly, Loss of Ownership was the only RHI component for which subjects' evaluations were significantly different between the no-visibility and the other three conditions also after the asynchronous visuo-tactile stimulation. This suggests that some sort of illusory ownership can occur also following the asynchronous condition. It is worth noting that the statement we used to assess this component (S6) is the only one that, unlike all other statements, refers uniquely to the subject, not comprising mentions of the rubber hand. Such a relative cognitive detachment from the rubber hand, or minor attentional demand toward the rubber hand, or greater focus on subjective sensations, might explain why subjects reported increased illusory Loss of Ownership also when the visual and tactile stimulations were incongruent. In other words, since the focus of the statement was the subject in isolation without reference to the rubber hand, it might be that the weight of the mismatch between the visual and tactile inputs in the process of

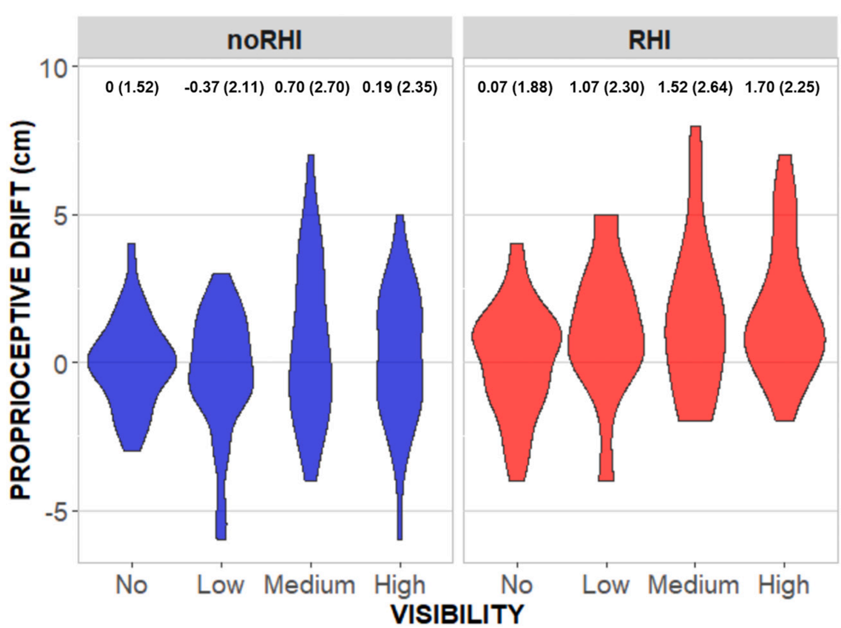

Fig. 3. Distribution of proprioceptive drifts as a function of Stimulation (noRHI, RHI) and Visibility (no, low, medium, high) conditions. Blue and red colors indicate noRHI and RHI conditions, respectively. Means and standard deviations (between parentheses) are shown on top of the graph. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

providing the evaluation was smaller than for other statements where subjects were required to focus the relationship between their hand and the rubber hand. This would mean that the mismatch brought by the asynchronous conditions would have had a smaller impact on subjects' evaluations, resulting in similar score profiles about Loss of Ownership following both synchronous and asynchronous conditions.

Altogether, it can be proposed that, while viewing or not the rubber hand modulated the illusory experience only for the subjective aspects linked to proprioceptive or visual aspects of the RHI, separately, this interaction was not observed for components that linked visuo-proprioceptive representations. De Vignemont (2011) suggested that perceptual embodiment is related to visually-based mental representations of the body, while motor embodiment relies more on sensorimotor-based representations of the body (de Vignemont, 2011). Thus, the components referred here as Movement and Loss of Ownership could be classified as “motor” and “perceptual” embodiment, respectively. This interpretation that motor and perceptual embodiment separately, but not in conjunction, are sensitive to the visual presence of the rubber hand, corroborates previous suggestions that the RHI likely “displaces” the proprioceptive input related to the real hand (de Vignemont, 2011; Longo et al., 2008) and that and this shift can be detected also through visual misrepresentations. Importantly, while visibility changes correspond to the modulation of a bottom-up element (perception of light), RHI-induced illusory changes are a top-down phenomenon (Longo et al., 2008; Matsumuro et al., 2019). Therefore, the embodiment experience related to the RHI would emerge from an interplay between immediate bottom-up bodily sensations and top-down updating and comparison with stored body representations (Lewis & Lloyd, 2010; Longo et al., 2008). Since the low visibility condition was already sufficient to induce illusory Movement and Loss of Ownership with respect to no-visibility, and the strength of these illusions remained stable across different visibility conditions (low, medium, high), we propose that the strong dominance of vision over proprioception was present as soon as the rubber hand was visible and remained stable across all conditions with a certain degree of visibility.

Previous studies reported that illusory body ownership can decrease with the visibility (transparency) of the rubber hand (Martini et al., 2015; Matsumuro et al., 2019), and that illusory ownership can occur even if the rubber hand/body-part is not visible (D'Angelo et al., 2017; D'Angelo et al., 2020; Guterstam et al., 2013; Guterstam et al., 2015). However, in Martini et al. (2015) the evaluation of the RHI was limited to only one Embodiment statement, corresponding to S2 of the present study. Conversely, Matsumuro et al. (2022) seemed to implement more ownership statements (Matsumuro et al., 2022), but irrespective to the factor Loadings described in Longo et al. (2008). In addition, none of these previous studies comprised both the manipulation of visibility and the visual absence of the rubber hand. It is therefore unclear whether the onset of the RHI as a function of the visibility of the rubber hand is a gradual or abrupt progressing. Our setting allowed to show that at least illusory Movement and Loss of Ownership occur as soon as the rubber hand is visible. We nevertheless note that it remains unclear whether illusory ownership can be induced gradually of abruptly, given that the difference between the no-visibility and low visibility condition was already large enough to induce in the latter effects similar to those observed in the other visibility conditions (medium, high). Our results are inconclusive in this direction, as the effect sizes in Table 2 do not seem to increase consistently with visibility for the analyzed subjective aspects. This absence of modulation of any RHI component as a function of increased visibility (medium and high visibility) supports that the illusory experience is of the “all-or-nothing” type when it comes to visibility (de Vignemont, 2011). However, this trend might be due to the fact that already the low visibility condition (8 % of luminance) was strong enough to let participants see (or internally complete) the image of the rubber hand (as in Martini et al., 2015) and therefore experience the illusion. To directly investigate the possible gradual impact of visibility on the RHI, future investigations shall address implement smaller visibility changes (perhaps steps of 1 % or 2 %) limited to the rubber hand.

4.2. Causal inference and visual sensory uncertainty

The consideration of the strength of visibility as a triggering factor in the onset of the RHI has links to recent views on the decisional mechanisms responsible for the combination/segregation of multisensory inputs. Over the last two decades, a large body of studies exploited the RHI protocol to reveal the neuro-behavioral correlates of body ownership (review in Riemer et al., 2019). However, very little is known about the way we combine different sensory signals to create a coherent sense of owning our body. Recent studies have addressed this issue by using Bayesian causal inference models to understand the decisional mechanisms underlying the selection/exclusion of relevant/irrelevant multisensory inputs to be bound/segregated in the process of creating a coherent sense of body ownership. For instance, it has been shown that Bayesian causal inference models can account for the binding of spatial (proprioceptive) and temporal (visuo-tactile) inputs to induce the RHI, further predicting that the illusion can occur even in absence of tactile stimulation (Samad et al., 2015). According to similar causal inference models related, although indirectly (Henrik & Marie, 2019), to body-ownership-specific multisensory binding in the brain (Wen et al., 2019), it is possible to explain how this spatiotemporal binding builds on the judged causal similarity between different sources of information. In particular, up to a certain degree of incongruence, the brain can combine different inputs to infer, for example, common origins/causes (Blanke et al., 2015). However, if these inputs become too uncorrelated, the brain stops the integration process and reaches the decision that the inputs derive from different origins (Rohe & Noppeney, 2015). In this context, and along the line of the present study, recent reports indicate that Bayesian causal inference models can account for a decrease of visibility in a RHI setup (sensory uncertainty), accommodating decisions as a function of the available sensory input and therefore outperforming fixed criterion models (Chancel et al., 2021). Adopting a similar Bayesian perspective, it is possible to infer that the present study shows that relatively small changes in visibility (no- vs. low-visibility) are sufficient to induce the binding of visuo-tactile-proprioceptive inputs during the RHI protocol and therefore provide the illusory sense of ownership for the rubber hand. On the other hand, once the causal inference mechanism supports the multisensory binding and therefore the illusory ownership, further augmentations of the visibility do not improve the process which is supposed to be already optimal. This interpretation is in line with the finding that, despite an overall advantage for larger visual noise, different levels of visual sensory uncertainty do not systematically affect self-reported evaluations of Embodiment (corresponding to the S2 statement of the present study) at specific time gaps between the visual and tactile stimulation (Chancel et al., 2021). However, the relatively abrupt increase of visibility (8 %) between the conditions of our experimental protocol does not allow to assume whether/how a Bayesian model would accommodate higher levels of visual sensory uncertainty and/or subjective completion/ abstraction in the context of subjective/objective aspects of body-ownership-related multisensory binding. Future studies may clarify the potential role of increasing visibility by smaller steps.

4.3. Dissociation between subjective and objective measures of the RHI

In the present study, while the objective measures of the RHI (proprioceptive drift) were modulated by the type of visuo-tactile Stimulation and Visibility, separately, there was no interaction between these two factors. Therefore, while our data confirm previously reported increases in illusory ownership associated with augmented visibility (Martini et al., 2015; Matsumuro et al., 2022) and visuo-tactile synchrony (Botvinick & Cohen, 1998; Tsakiris & Haggard, 2005), this finding was unspecific. The dissociation between visibility/stimulation-affected subjective (questionnaire) and visibility/stimulation-unaffected objective aspects of the RHI (proprioceptive drift) found in the present study is in line with previous evidence that questionnaires and proprioceptive do not necessarily correlate (Gallagher et al., 2021; Holle et al., 2011; Rohde et al., 2011). This dissociation indicates that self-report questionnaires and proprioceptive drift account for different processes, i.e., conscious cognitive aspects and automatic integration of multisensory cues, respectively (Gallagher et al., 2021). Considering such subjective/objective difference in the context of Bayesian causal inference models, it might be proposed that the presence of visibility effects on questionnaire, together with the absence of visibility-related changes in proprioceptive drift, suggest that the same amount of visual sensory change (no-to-low visibility) is sufficient to trigger causal inference mechanisms for at least some components of subjective self-attribution, but is not powerful enough to pass the combination/segregation threshold for objective mislocalization. However, further studies would we necessary to accurately address this point, including the implementation of smaller changes of sensory inputs with respect to the present study.

4.4. Limitations

First, it might be argued that the visibility conditions comprised both visual and tactile stimulations, while the no-visibility condition concerned only tactile stimulation. This difference might result in the risk that the data obtained in the no-visibility condition are independent from the experimental manipulations. However, if this bias would have affected our data, it might be expected that it would generally/unspecifically impact all data sets (questionnaire statements and proprioceptive drift), and therefore should always (or never) result in significant differences between the no-visibility and the other three conditions. In this framework, it is worth noting that subjects' statements showed that the experimental manipulations determined different effects in different components of the RHI, showing significant differences between the no-visibility and the other visibility conditions specifically for Movement and Loss of Ownership, but not Embodiment. On this basis, it is likely that the obtained data exclude the risks of effect unspecificity, which would result is equal data profiles for all questionnaire statements.

Second, the manipulation of the visibility did not affect only the rubber hand, but also the brush and the experimenter's hand. From an experimental standpoint it could be argued that this approach does not allow to disentangle the effect of visually manipulating the target object (rubber hand) versus the environment (brush, experimenter's hand, background, etc.). Nevertheless, we note that the main aim of the study was assess the impact of degraded visual input on the plasticity of body ownership. For this reason, and in line with recent work on the effects of manipulating the whole scene during the RHI protocol (Chancel et al., 2021), we aimed at experimentally reproducing the conditions most possible ecologically similar to common visual deficits, such as low luminance deficit, which affect the whole visual input, not only parts of the visual field.

Third, visibility was modulated relative to the maximum power of the light system, not using an absolute measure (e.g. luxmeter). Therefore, visibility was defined as a qualitative and ordinal measure. Future studies could help determine the effects of manipulating visibility with respect to absolute units, which would be useful in elucidating the minimum visual input required for inducing the RHI.

4.5. Conclusions

Gross changes of the visibility of the rubber hand (minimal visibility) affected some subjective indexes of visual and proprioceptive aspects of body ownership, separately. In contrast, we did not observe visibility effects on subjective indexes related to visual-and-proprioceptive integration, nor on objective indexes as measured by the proprioceptive drift. Together with the observation that different degrees of visibility did not modulate the RHI, these findings indicate that even relatively abrupt changes in the visibility of the rubber hand can differentially impact subjective versus objective components of body ownership. Understanding how we interact with the environment under degraded perceptual visibility conditions and compensatory mechanisms may be critical for neuroscientific theories of visuomotor integration and relevant for clinical interventions.

Declaration of competing interest

The present study was funded by the Swiss National Science Foundation through the grant PP00P1_202665 / 1 to Silvio Ionta. All authors declare no conflict of interest.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.actpsy.2022.103672.

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