



Diametrical modulation of tactile and visual perceptual thresholds during the rubber hand illusion: a predictive coding account

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Abstract

During the rubber hand illusion (RHI), the synchronous stroking of the participants' concealed hand and a visible rubber hand induces a conflict among visuo-tactile inputs, leading healthy subjects to perceive the illusion of being touched on the rubber hand, as if it were part of their body. The predictive coding theory suggests that the RHI emerges to settle the conflict, attenuating somatosensory inputs in favour of visual ones, which "capture" tactile sensations. Here, we employed the psychophysical measure of perceptual threshold to measure a behavioural correlate of the somatosensory and visual modulations, to better understand the mechanisms underpinning the illusion. Before and after the RHI, participants underwent a tactile (Experiment 1) and a visual (Experiment 2) task, wherein they had to detect stimuli slightly above the perceptual threshold. According to the predictive coding framework, we found a significant decrease of tactile detection (i.e. increased tactile perceptual threshold) and a significant increase of visual detection (i.e. decreased visual perceptual threshold), suggesting a diametrical modulation of somatosensory and visual perceptual processes. These findings provide evidence of how our system plastically adapts to uncertainty, attributing different weights to sensory inputs to restore a coherent representation of the own body.

Introduction

The *sense of body ownership* (SBO) has been defined as the feeling that a specific body part belongs to one's own body (Gallagher, 2000). It has been proposed that one of its core processes relies on the multisensory integration of exteroception, proprioception, and interoception into a single unitary percept (Tsakiris, 2017). Such integration would enable the brain to produce a coherent and non-conflicting representation of the body in the world. The sense of body ownership can be selectively impaired after brain-damage [as in somatoparaphrenia (Romano & Maravita, 2019) and pathological embodiment [(Fossataro et al., 2016, 2017; Pia et al., 2016, 2020); for a review see (Garbarini et al., 2020)] and it can be experimentally altered by means of well-known experimental paradigms such as the rubber hand illusion

(RHI; Botvinick & Cohen, 1998), the full-body illusion (Salomon et al., 2013; Serino et al., 2008) or the virtual arm illusion (Slater, 2008; Tieri et al., 2015), which exploit multisensory conflicts to induce the transient incorporation of a fake or a virtual body part. For instance, in the RHI, the experimenter synchronously strokes the participant's real hand (occluded from view) as well as a clearly visible human-like fake hand, congruently positioned with respect to the participant's posture and perspective. After about 10 s (della Gatta et al., 2016; Ehrsson et al., 2005), experimental subjects feel as if the fake hand were their own (the so-called *embodiment*) and their real hand were temporarily excluded from their body schema (the so-called *disembodiment*). This illusory experience is usually measured by means of the Embodiment and Disembodiment Questionnaires [see Table 1 and, e.g. (della Gatta et al., 2016; Fossataro et al., 2018; Longo et al., 2008)]. Since participants feel the tactile stimulation as originating from their own hand, but simultaneously see the dummy hand being stroked, a multisensory conflict among tactile, proprioceptive and visual inputs arises.

Within the framework of the predictive coding theory (Friston, 2005a, 2005b), the illusory experience associated

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with the RHI has been explained as the outcome of the top–down reduction of prediction errors resulting from this multisensory conflict, operated by multimodal brain areas (Apps & Tsakiris, 2014; Limanowski & Blankenburg, 2015; Zeller et al., 2016). According to this theory, conflicts emerge when predictions, based on internal models explaining sensory events, do not meet the sensory feedback, generating a prediction error. Since the own body is the only object in the world on whose surface visual touches generate tactile sensations, a prediction error emerges when, in the synchronous (experimental) condition of the RHI, the participant receives tactile (i.e. touches occurring onto the participant’s hand) and visual (i.e. touches occurring onto the fake hand) touches, occurring at the same time and spatial location on the two hands. Given its attitude to resist entropy, our brain tries to solve prediction errors, by modulating lower level sensory processing by feedback projections and by updating the existing internal models (Apps & Tsakiris, 2014; Friston, 2005b). Within this framework, the asynchronous (control) condition should not generate prediction errors, because tactile and visual stimuli are segregated in time and spatial location. Since the scenario of being touched and, in a separate moment, observing touch onto an external object is not in contrast with common sensory experience, it should be correctly predicted by internal models, thus, not eliciting prediction errors’ signals.

Converging evidence, coming from behavioural (Folegatti et al., 2009; Zopf et al., 2011) and physiological studies (Hornburger et al., 2019; Isayama et al., 2019; Limanowski & Blankenburg, 2016; Zeller et al., 2015, 2016), suggest that, during the synchronous RHI, multisensory brain areas receiving inputs from both somatosensory and visual systems decrease the influence of the somatosensory input coming from the real hand. By contrast, the role of the visual system has been less investigated, and whether multisensory areas upregulate or downregulate it to explain away the conflicting visual input coming from the rubber hand is still an open question.

Based on dynamic causal modelling of electrophysiological (EEG) data and Bayesian model comparison, Zeller et al. (2016) proposed that, during the RHI, the conflicting somatosensory input is downregulated, while greater precision is afforded to visual input. Indeed, they showed that the RHI is associated with (1) decreased intrinsic connectivity in the primary somatosensory cortex (S1) and (2) increased forward connectivity between visual regions and the premotor cortex (PMC). According to their interpretation, to reduce the prediction error signal emerging from feeling the touch on one’s own hand and seeing the fake hand being stroked, PMC is likely to downregulate proprioceptive and tactile inputs—as mirrored by the modulation of the intrinsic connectivity in S1—and to allocate greater weight to visual input—as mirrored by the upregulation of the connectivity

from visual regions to the PMC, suggesting an increased bottom–up influence of visual input onto the multisensory node, where the illusory feeling of ownership originates.

In this view, the downregulation of the somatosensory system during the RHI should result in worsened detection of tactile stimuli delivered over the real hand. In contrast, the increase of the connectivity between visual regions and PMC should result in improved detection of visual stimuli delivered near the fake hand.

In Experiment 1, we investigated the influence of the RHI in modulating the detection of near-threshold tactile stimulations delivered on the real hand. A tactile detection task in which unilateral and bilateral tactile stimuli were delivered to the participants’ hands was repeated twice, i.e. before and after the RHI (see Fig. 1). We predicted to replicate previous evidence of decreased tactile detection during unilateral stimulations (Zopf et al., 2011), also extending it to the bilateral stimulations. More precisely, if the alteration of body ownership that takes place during the RHI relies on the increase of the somatosensory threshold, we expected to find a decreased detection of tactile stimuli delivered over the participants’ hand exposed to the illusion, in both unilateral and bilateral trials.

In a separate experiment (Experiment 2), we investigated the influence of the RHI in modulating the detection of near-threshold visual stimuli delivered around the fake hand. A visual detection task in which visual stimuli were displayed near the fake hand was repeated before and after the RHI (see Fig. 1). If somatosensory and visual systems are modulated in opposite directions to solve the multisensory conflict originated by the RHI as proposed by Zeller and colleagues (Zeller et al., 2016), we expected to observe an increased detection of visual stimuli delivered around the rubber hand.

Materials and methods

Participants

The sample size of each experiment was estimated with an a priori analysis employing G*Power software (www.psych.uni-duesseldorf.de/abteilungen/aap/gpower3) based on two different datasets in which tactile (Fossataro et al., *in preparation*) and visual (Ronga et al., 2018) detection modulations induced by prismatic adaptation trainings were measured in a between-subjects design where two groups performing real and sham prismatic adaptations were compared. The common effect of interest between these experiments and the present study is the modulation of detection accuracy following an experimental manipulation (i.e. prismatic adaptation there, RHI here). Hence, the effect size (d_z) was calculated on detection results before and after prismatic adaptation, as in Ronga et al., (2018). A sample of 18

participants was estimated by the analysis on tactile detection data [$\alpha=0.05$; power $(1 - \beta)=0.9$; $d_z=0.82$], whereas a sample of 15 participants was estimated by the analysis on the visual ones [$\alpha=0.05$; power $(1 - \beta)=0.9$; $d_z=0.92$]. Thus, to keep the sample size equal, we included 18 participants in both Experiment 1 [12 women; aged (mean \pm SD): 23.94 ± 0.99 years; mean years of education \pm SD: 16.89 ± 4] and Experiment 2 [14 women; aged 23.72 ± 1.27 years; mean years of education \pm SD: 16.33 ± 0.77], consistently with previous studies employing the RHI (Burin et al., 2017; Fossataro et al., 2018). All the participants were right handed according to the Edinburgh Handedness Inventory (Oldfield, 1971), had normal tactile sensitivity and normal (or corrected-to-normal) visual acuity. The two samples of participants were not different in terms of sex ($U=144$, $p=0.71$), age ($t_{34}=0.58$, $p=0.56$), or years of education ($t_{34}=1.14$, $p=0.26$). They all gave informed consent to participate in the study, which was approved by the Ethical Committee of the University of Turin (prot. n°122571).

Experiment 1

Experimental procedure and timeline

In Experiment 1, we investigated the modulations of the tactile sensory threshold following the RHI. To this aim, participants underwent 2 min of RHI to induce the illusory experience, immediately followed by a detection task of tactile stimuli, in which the administration of each stimulus was preceded by 13–15 s of RHI visuo-tactile stimulation. The 13–15 s of visuo-tactile stimulation were inserted to maintain the illusion throughout the task (della Gatta et al., 2016).

Participants underwent two sessions on different days, with at least a 1-week break in between. The sessions were identical except for the RHI procedure, which could be either synchronous (i.e. Synchronous condition) or asynchronous (i.e. Asynchronous control condition). The sessions' order was counterbalanced among subjects, so that half of the participants performed the Synchronous condition in the first session and the Asynchronous condition in the second session, and vice-versa for the other half. The counterbalancing

order was randomly assigned to subjects. Participants were comfortably seated with both hands lying on a desk. Their right hand was placed in the right compartment of a wooden box and a black piece of tissue covered the shoulders and the proximal parts of the arms (see “Rubber hand illusion”). After having determined the bilateral tactile threshold to set stimulation intensity (see “Electrical stimulation”), a tactile detection task was performed (TD Pre) to define a baseline. Then, a measure of the right hand's felt position (see below) was collected (Proprioceptive Judgement Pre) and the RHI procedure started with 2 min of synchronous or asynchronous stimulation, according to the session. After the 2-min stimulation, known to induce the illusory experience only in the Synchronous condition, we administered the experimental procedure combining 13–15 s of (synchronous or asynchronous) RHI stimulation with one trial of tactile detection (TD Post). This procedure was repeated for 45 trials. At the end of the procedure, RHI classical measures (Proprioceptive Judgement Post and subjective ratings to the Embodiment and Disembodiment Questionnaires, see Table 1) were collected (see Fig. 1).

Rubber hand illusion

The experimental materials used for the RHI procedure in Experiment 1 had already been employed in previous experiments (Bucchioni et al., 2016; Burin et al., 2017; Fossataro et al., 2018) and comprised a black wooden box (60 cm \times 40 cm \times 20 cm), a black piece of tissue and two realistic rubber hands (male and female). The box was divided into two compartments: the right one was covered by a black panel, while the top of the left compartment was open. At the beginning of the session, participants placed their right hand into the corresponding compartment so as to hide it from view, while the fake hand (male or female, according to the subject's biological gender) was positioned inside the left open compartment to make the fake hand visible. The participant's left hand was aligned with the left shoulder and the fake hand was aligned with the right shoulder, whereas the participant's right hand was externally

Table 1 Embodiment and Disembodiment Questionnaires (Fossataro et al., 2018; Longo et al., 2008). Participants were asked to rate their agreement with the following statements by assigning a

score to each item, using a 7 points Likert Scale (-3 = “strongly disagree”; $+3$ = “strongly agree”)

Embodiment Questionnaire

1. It seemed as if I were sensing the touch in the location where I saw the rubber hand touched
2. It seemed as if the touch I felt was caused by the paintbrush touching the rubber hand
3. I felt as if the rubber hand was my hand

Disembodiment Questionnaire

1. It seemed like I was unable to move my hand
2. It seemed like I could not really tell where my hand was
3. It seemed like my hand had disappeared

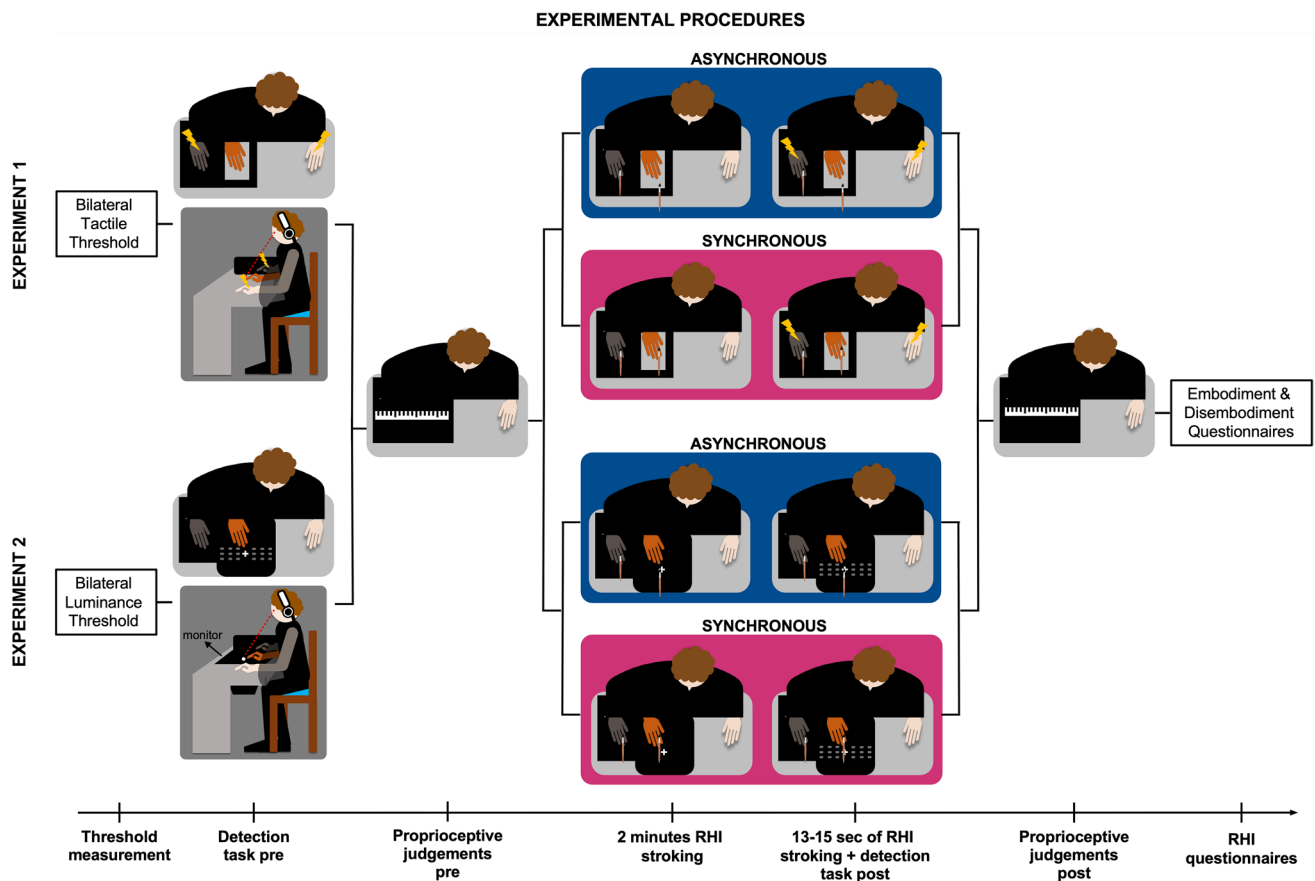


Fig. 1 Experimental procedure of Experiments 1 and 2. After the bilateral threshold was estimated, participants underwent a *detection task pre* (Experiment 1: TD Pre; Experiment 2: VD Pre), wherein stimuli were administered with a jittering inter-trial-interval (13–15 s). Then, after five proprioceptive judgements about the right-hand index finger position were given by the subject, the 2-min (synchronous or asynchronous) RHI procedure was performed. Participants then underwent the *detection task post* (Experiment 1: TD Post; Experiment 2: VD Post), which was identical to the detection task

pre, except that 13–15 s of RHI stimulation preceded each trial. Subsequently, five more proprioceptive judgements were performed by the participants. Finally, Embodiment and Disembodiment Questionnaires were administered. Note that, in Experiment 1, tactile stimuli were delivered on the participant's hands (20 bilateral, 10 on the right hand, 10 on the left hand, plus 5 catch trials), whereas in Experiment 2, visual stimuli could appear in 9 possible positions around the rubber hand (27 bilateral, 27 on the right side and 27 on the left side of the monitor, plus 5 catch trials)

positioned, 20 cm to the right of the fake hand. We took care that the fake hand was placed in an anatomically congruent position from the participant's egocentric perspective and that the black piece of tissue covered the shoulders and the proximal portions of the real and the dummy hand.

Before performing the RHI procedure, we covered the box with a wooden panel and collected five proprioceptive judgements (Proprioceptive Judgement Pre) about the perceived position of the right index finger. A ruler was positioned over the box, at the same gaze level of the fake hand, and participants were asked to judge the location of their index finger by verbally reporting the number on the ruler which corresponded to the felt location of their right index finger. For each proprioceptive judgement, the ruler was positioned on the box so that the number corresponding to its left limit was always different, in order that the participant

could not anchor the judgement on a given number. The experimenter took note not only of the number reported by the participant, but also of the number corresponding to the left limit of the box, and we considered the delta between the two numbers (i.e. the distance between the left angle of the box and the index position reported by the participant) as a proprioceptive judgement. Afterwards, the wooden panel was removed, and the participant's right hand and the dummy hand were continuously stroked for 2 min by the experimenter. In the Synchronous condition, wherein RHI generally occurs, the stroking was synchronous in its timing and spatial location on the two hands. Conversely, in the Asynchronous condition, wherein RHI generally does not occur (i.e. control condition), the stroking was delayed and was, therefore, asynchronous in its timing and spatial location between the two hands.

The 2-min RHI procedure was immediately followed by the tactile detection task (TD Post, see “[Tactile detection task](#)”), wherein each tactile stimulus was preceded by 13–15 s of RHI visuo-tactile stimulation. At the end of the tactile detection task, to measure the effectiveness of such procedure in inducing the illusion, we covered the box again and five more proprioceptive judgements were collected (Proprioceptive Judgement Post). In conclusion, participants were asked to rate their subjective feeling of ownership over the fake hand by answering to three items of the Embodiment Questionnaire (Botvinick & Cohen, 1998; Fossataro et al., 2018, see Table 1) and to rate their subjective feeling of disownership over their real hand by answering to three items of the Disembodiment Questionnaire (Longo et al., 2008; Fossataro et al., 2018, see Table 1). Participants were asked to rate their agreement with these items on a 7 points Likert Scale, ranging from “– 3” (“strongly disagree”) to “+3” (“strongly agree”).

Tactile detection task

The Tactile Detection task (TD) consisted of 40 randomised tactile stimuli delivered by the experimenter who manually activated the stimulator with a jittering inter-trial-interval (ITI) of 13–15 s. We chose such a long ITI to match the timing of the tactile detection task performed before the RHI (TD Pre) with that of the tactile detection task performed in conjunction with the RHI (TD Post), wherein a long ITI (greater than 12 s) was required for the RHI stroking performed before each stimulus delivery to be effective in inducing the illusion (della Gatta et al., 2016). Hence, stimuli were delivered within a 13–15 s time-window with a jittering onset and without any starting cue signalling stimulus delivery, to avoid expectancy effects.

During the tactile detection task, participants laid their arms on a desk, with their right hand into the right compartment of the black wooden box and were asked to gaze at the fake hand (see Fig. 1). Moreover, they were made to listen to a white noise track through headphones, whose intensity was adjusted (in a range between 60 and 80 decibels) to prevent them from hearing the “click” noise produced by the stimulator; otherwise, this noise could have anticipated to the participants the occurrence of a stimulation. Importantly, the sound intensity was set at the beginning of the experimental session, during threshold estimation (see details in “[Electrical stimulation](#)”), and it was kept constant throughout the session, to avoid possible related confounds. Electrical stimuli were delivered over the hand dorsum and participants were asked to verbally report any tactile sensation and to indicate its location (i.e. “Right hand”, “Left hand”, “Both hands”). Indeed, 20 stimuli were administered simultaneously to both hands (i.e. bilateral), 10 were administered to the right hand (i.e. unilateral right) and 10

were administered to the left hand (i.e. unilateral left). Note that, since the tactile detection task (as well as the visual detection task, see “[Visual detection task](#)”) was specifically designed to test the effect of the experimental manipulation on detection accuracy as in previous studies (Ronga et al., 2018; Swinkels et al., 2020), we added only 5 catch trials in which no stimulation was delivered, to ensure that participants did not respond automatically. During catch trials, the error rate was very low [i.e. in the entire sample (18 participants), only 7 false alarms (4 in the TD Pre and 3 in the TD Post) occurred, leading to 173 correct rejections out of 180 catch trials; moreover, false alarms were present only in 3 participants].

The tactile detection task was performed before the RHI procedure (i.e. TD Pre) to acquire a baseline measure. Then, the RHI procedure started, and after the 2-min stimulation (synchronous or asynchronous), the tactile detection task was combined with an RHI stimulation block (13–15 s of synchronous or asynchronous stimulation), so that after each RHI stimulation block, one tactile detection trial was performed (i.e. TD Post), for a total of 40 trials (plus 5 catch trials).

Electrical stimulation

Transcutaneous electrical stimulation consisted of constant current square-wave pulses (DS7A, Digitimer) delivered to the hand dorsum, using a pair of surface bipolar electrodes attached to a Velcro strap, as in previous studies (Fossataro et al., 2020a, 2020b). The stimulus duration was 200 μ s. Since, during the tactile detection task, we delivered stimuli to the right, to the left or to both hands, we chose to measure the bilateral threshold to set the stimulation intensity so that stimuli would be perceived by both the hands. Moreover, we enhanced this intensity by 7% to prevent habituation effects, which are normally observed after repetitive stimulation at sensory threshold (Thompson & Spencer, 1966).

To identify participants’ bilateral tactile threshold, we employed the method of limits (Gescheider, 1997). Starting from very low-magnitude stimulations (1.5–2 mA), the experimenter gradually increased intensity by steps of 0.02 mA until the subject reported a bilateral tactile stimulation. Then, the experimenter lowered the intensity by 0.2 mA until the participant did not report the bilateral stimulation. Hence, the experimenter enhanced the current intensity again, and so on until the electric stimulation intensity which caused participants to report exactly 5 stimuli out of 10 on both hands was determined. The number of trials needed to estimate the threshold varied depending on the subject. During the threshold estimation, as during the tactile detection task, participants wore headphones delivering a white noise as in the TD tasks. The average stimulus intensity of the bilateral threshold in Experiment 1 was (mean \pm SD):

3.887 ± 0.972 mA, range 2.41–5.65 mA in the Synchronous condition; 4.092 ± 0.98 mA, range 2.66–5.98 mA in the Asynchronous condition. Importantly, the intensity was not different between the conditions ($t_{17} = 1.641$; $p = 0.119$).

Experiment 2

Experimental procedure and timeline

Experiment 2 was identical to Experiment 1 except that we investigated the modulations of the visual detection following the RHI. To render the results comparable, the two experiments were designed as closely as possible. However, for the detection tasks, we chose to employ different procedures (e.g. different apparatus, target numbers, target positions) that had been previously devised in our lab for the two modalities (Fossataro et al., *in preparation*; Ronga et al., 2018).

Participants were seated at a desk facing a 21-inches horizontally oriented CRT monitor levelled with the desk plane, at a distance of 50 cm, with each hand resting on the desk, respectively, on the left and right sides of the monitor. First, they put their right hand into the covered compartment of the RHI box, and a black tissue covered their shoulders and the proximal parts of their arms (see “[Rubber hand illusion](#)”). Second, participants’ luminance detection threshold was estimated and a visual detection task (VD Pre) was performed. Afterwards, the proprioceptive judgments were collected (Proprioceptive Judgment Pre), and then, the 2-min RHI (synchronous or asynchronous according to the session) was delivered. Immediately after, the procedure combining the detection task (VD Post) with the 13–15 s of RHI stroking was performed (see “[Visual detection task](#)”). During the detection tasks and the RHI procedures, participants were asked to look at a central fixation cross on the monitor, below which the rubber hand was placed. Finally, the proprioceptive judgements (Proprioceptive Judgment Post) and the Embodiment and Disembodiment Questionnaires were administered, to measure whether the procedure was effective in inducing the RHI (see Fig. 1).

Rubber hand illusion

The RHI procedure was the same as in Experiment 1, except that participants sat with their arms laying on either side of the horizontally oriented monitor on which the visual stimuli were displayed during the visual detection tasks. The room was scarcely lit so that the same lighting could be used for the visual detection task (see “[Visual detection task](#)”). A different kind of RHI box was designed ad hoc for this experiment. The right hand was covered from view by a dark box (34 cm × 20 cm × 25 cm) while a black piece of tissue concealed the subjects’ shoulders and the proximal end of

their hands and of the rubber hand. As in Experiment 1, the participants’ left hand was aligned with the left shoulder and the fake hand was aligned with the right shoulder, whereas the participant’s right hand was externally positioned, 20 cm to the right of the dummy. The fake hand was placed on the monitor so that its index finger laid right below the middle of the screen, where the fixation cross was displayed during the visual detection tasks.

First, an additional box (75 cm × 20 cm × 25 cm) was placed over the previous box and five proprioceptive judgements (Proprioceptive Judgements Pre) were collected. Then, the 2-min (synchronous or asynchronous) RHI procedure was performed as in Experiment 1. Immediately after the 2-min RHI, the visual detection task (VD Post, see “[Visual detection task](#)”) was carried out, wherein each visual stimulus was preceded by 13–15 s of RHI visuo-tactile stimulation. At the end of the VD Post, five proprioceptive judgements (Proprioceptive Judgment Post) and the Embodiment and Disembodiment Questionnaires (for details, see “[Rubber hand illusion](#)”) were collected to measure the effectiveness of such combined procedure in inducing the RHI.

Visual detection task

The visual detection task (VD) consisted of 86 randomised trials administered via E-Prime 2.0 software (Psychology Software Tools Inc., Pittsburgh, PA) with a jittering ITI of 13–15 s, as in Experiment 1. Subjects were asked to gaze at a white fixation cross displayed in the centre of the screen during the whole task. Visual stimuli (see “[Visual stimuli](#)”) could appear either on the left, on the right or on both sides of the fixation cross, which remained right above the fake hand for the whole task. Before the detection tasks, the fixation cross and the stimuli were displayed on the monitor and we asked participants if they could be detected on screen. Participants were instructed to report the perceived stimuli and to indicate their location on the screen (“Right side”, “Left side”, and “Both sides”). The task consisted of two blocks, which comprised 27 right, 27 left and 27 bilateral trials. Furthermore, we added 5 catch trials, wherein a red fixation cross appeared on screen, and we asked participants to report them by saying “Red”. These stimuli were added to control that participants gazed at the fixation cross throughout the task. While performing the task, participants listened to a white noise track whose intensity was adjusted (in a range between 60 and 80 decibels), as in Experiment 1.

The detection task was performed before the RHI procedure (VD Pre) to collect a baseline measure of the participants’ performance. Afterwards, the RHI procedure began with 2 min of RHI visuo-tactile stimulation to induce the illusion. Immediately after, the visual detection task (VD Post) was performed in conjunction with 13–15 s of RHI

stimulation, so that each trial of the detection task was preceded by 13–15 s of RHI stimulation.

Visual stimuli

Visual stimuli consisted of grey rectangles (1 cm × 0.5 cm) appearing on the horizontally oriented 21-inch Sony CRT monitor which was embedded in the desk where participants' hands rested throughout Experiment 2. Stimuli were displayed for 50 ms in 9 different positions: 3 on the left, 3 on the right or bilaterally with respect to a white fixation cross centred on the screen lying right above the fake hand for the entire duration of the experiment. Importantly, for the RHI to emerge, the participants' gaze must be directed towards the rubber hand. Hence, in Experiment 2, stimuli were not lateralized with respect to the participants' hands (as in Experiment 1), but, instead, they appeared near the fake hand. We set the luminance intensity slightly above the bilateral threshold level, as in Experiment 1. To identify the bilateral luminance threshold, participants performed a visual detection task adapted from Ronga et al., (2018), which comprised 220 visual stimuli divided into 10 successive blocks [for a similar paradigm see also (Sarasso et al., 2018)]. Each block consisted of 18 bilateral and 4 unilateral (randomly left or right) stimuli. The level of luminance across blocks was progressively decreasing (from 2.32% in the first to 1.6% of 226 lx in the last block in steps of 0.08%), so that the difficulty of the task was progressively increasing. Participants were asked to respond by pressing a pedal with their right foot only to bilateral stimuli, ignoring unilateral ones which served as catch trials. Differently from Experiment 1, wherein the experimenter could calibrate the intensity manually, in Experiment 2 the luminance increased in fixed steps across different levels of the threshold visual task. Hence, we decided to define the visual bilateral threshold as the luminance level at which participants reported 60% of bilateral stimuli, to avoid habituation effects. If detection accuracy was higher than 60% in all levels, we adjusted the monitor contrast and brightness and repeated the task to estimate the luminance threshold.

Data analysis

Experiment 1

Rubber hand illusion

To assess whether the RHI procedures successfully modulated the sense of body ownership, we calculated the subjective rating average at the Embodiment and Disembodiment Questionnaire items in both conditions (i.e. Synchronous and Asynchronous). Mean ratings were separately compared

between the two conditions as in previous studies [e.g. (della Gatta et al., 2016)], by means of Wilcoxon matched pairs tests.

Furthermore, we calculated the Proprioceptive drift, namely the shift of the felt position of the participant's right hand towards the fake hand (Tsakiris & Haggard, 2005), an additional measure of the RHI that has been demonstrated to be dissociable from the illusory *feeling* measured by questionnaires (Holmes et al., 2006; Rohde et al., 2011; Tamè et al., 2018). To do so, we averaged the five proprioceptive judgements for each time-point (Proprioceptive Judgment Pre, Proprioceptive Judgment Post) in both conditions (i.e. Synchronous and Asynchronous), and we subtracted the mean of the Proprioceptive Judgments-Post to the mean of the Proprioceptive Judgments-Pre, obtaining a measure of the proprioceptive drift in the Synchronous and in the Asynchronous conditions. Higher values of proprioceptive drift indicated a greater shift towards the fake hand (i.e. a stronger RHI effect). We compared proprioceptive drift values between Synchronous and Asynchronous conditions with a matched pairs *t* test. Statistical threshold level was set at $\alpha=0.05$. The RHI analyses, as well as all the following statistical analyses, were performed using Statistica Software (StatSoft, release 8). Note that, following a reviewer's suggestion, for both Experiments 1 and 2, we ran non-parametric tests for discrete measures (i.e. questionnaires) and parametric ones for continuous measures (i.e. proprioceptive drift, detection accuracy—see as follows).

Tactile detection task

Detection accuracy analysis. Statistical analyses were performed on the percentage of correct responses (i.e. detection accuracy).

In our *main analysis*, we investigated the presence of a RHI-dependent effect on tactile accuracy and whether such a modulation was circumscribed to the hand subjected to the illusion, including both unilateral and bilateral trials in a single analysis, by categorising the data as follows. When participants responded “left hand” to a left-hand unilateral stimulation, we considered that as a correct response for left-hand trials. When participants responded “right hand” to a right-hand unilateral stimulation, we considered that as a correct response for right-hand trials. When participants responded “left hand” to a bilateral stimulation, we considered that as a correct response for left-hand trials and as an incorrect response for right-hand trials. When participants responded “right hand” to a bilateral stimulation, we considered that as a correct response for right-hand trials and as an incorrect response for left-hand trials. When participants did not respond to a unilateral (left- or right-hand) stimulation, we considered that as an incorrect response for the corresponding trial. When participants did not respond to

a bilateral stimulation, we considered that as an incorrect response for both right-hand and left-hand trials. Hence, we entered tactile detection accuracy in a $2 \times 2 \times 2$ repeated-measures ANOVA with Condition (Synchronous, Asynchronous), Time (TD Pre, TD Post) and Side (Left-hand, Right-hand) as within subject factors. Post hoc comparisons were carried out by means of Newman–Keuls' test. Statistical threshold level was set at $\alpha=0.05$.

Furthermore, we run *additional analyses*, performed separately on unilateral and bilateral tactile detection accuracy, with the aim of investigating whether the modulatory effects were present both in unilateral and bilateral trials. Specifically, we performed two $2 \times 2 \times 2$ repeated-measures ANOVA with Condition (Synchronous, Asynchronous), Time (TD Pre, TD Post) and Side (Left hand, Right hand) as within subject factors on each dataset. Post hoc comparisons were carried out by means of Newman–Keuls' test. Since the data were split in two separate analyses, statistical threshold level was set at $\alpha=0.025$.

Note that our main analyses were performed following a Reviewer suggestion, whereas the additional analyses were planned a priori.

Correlational analysis. We ran Spearman correlations between RHI measures (Embodiment and Disembodiment Questionnaires' mean ratings, proprioceptive drift values) and a modulation index, calculated as the % of tactile detection accuracy in the TD Post – % TD Pre on the Right-hand trials of the Synchronous and Asynchronous conditions.

Experiment 2

Rubber hand illusion

To compare the RHI measures (mean of subjective ratings to the Embodiment and Disembodiment Questionnaires, proprioceptive drift) between Synchronous and Asynchronous conditions, we employed the very same analyses of Experiment 1 (see “[Rubber Hand Illusion](#)”). Statistical threshold level was set at $\alpha=0.05$.

Visual detection task

Detection accuracy analysis. To investigate the RHI effect on visual stimuli detection, we calculated the percentage of correct responses (i.e. visual detection accuracy) for each condition in the VD Pre and in the VD Post task. We then entered these values in a repeated-measures 2×2 ANOVA with Condition (Synchronous, Asynchronous) and Time (VD Pre, VD Post) as within-subject factors. Post hoc comparisons were carried out by means of Newman–Keuls' test. Statistical threshold level was set at $\alpha=0.05$.

Correlational analysis. We ran Spearman correlations between RHI measures (Embodiment and Disembodiment Questionnaires' mean ratings, proprioceptive drift values) and a modulation index, calculated as the % of visual detection accuracy in the VD Post – % VD Pre of the Synchronous and Asynchronous conditions.

Results

Experiment 1

Rubber hand illusion

The Wilcoxon tests comparing Synchronous vs Asynchronous conditions revealed a significant difference both for the Embodiment ($T=0$; $p=0.0003$; effect size $r=0.604$; Fig. 2A) and the Disembodiment Questionnaire ($T=18$; $p=0.017$; $r=0.384$; Fig. 2B), showing, as expected, greater values in the Synchronous as compared to the Asynchronous condition (see Table 2). Note that, although participants showed a general tendency to give lower ratings to the items of the Disembodiment than to those of the Embodiment Questionnaire, overall they attributed higher scores in the Synchronous as compared to the Asynchronous condition in both the cases. Furthermore, the t test between Synchronous and Asynchronous conditions on the proprioceptive drift measures revealed a significant difference between the conditions ($t=2.198$; $p=0.042$; $d_z=0.516$; Fig. 2C). Indeed, as expected, the Synchronous condition's shifts were greater than the Asynchronous' ones (see Table 2).

Tactile detection task

Detection accuracy analyses. The *main analysis* showed a significant main effect of Time ($F_{1,17}=14.633$; $p=0.001$; $\eta_p^2=0.463$) and a significant Condition \times Time interaction ($F_{1,17}=17.808$; $p=0.001$; $\eta_p^2=0.512$). Crucially, we also found a significant Condition \times Time \times Side interaction ($F_{1,17}=11.175$; $p=0.004$; $\eta_p^2=0.397$). In particular, the Synchronous TD Post right-hand condition showed a significantly lower tactile detection accuracy relative to the Synchronous TD Pre right-hand ($p=0.0003$; $d_z=1.063$) and all the other conditions (p always <0.0005 ; see Fig. 2D; Table 3). Conversely, no significant difference resulted between Asynchronous conditions, nor between Synchronous Pre and Asynchronous Pre or Post conditions (p always >0.514).

When separate analyses were run on unilateral and bilateral trials (*additional analyses*), similar results were found. Specifically, results of unilateral data highlighted not only a significant main effect of Time ($F_{1,17}=9.142$; $p=0.008$; $\eta_p^2=0.350$), but also a Condition \times Time \times Side

EXPERIMENT 1

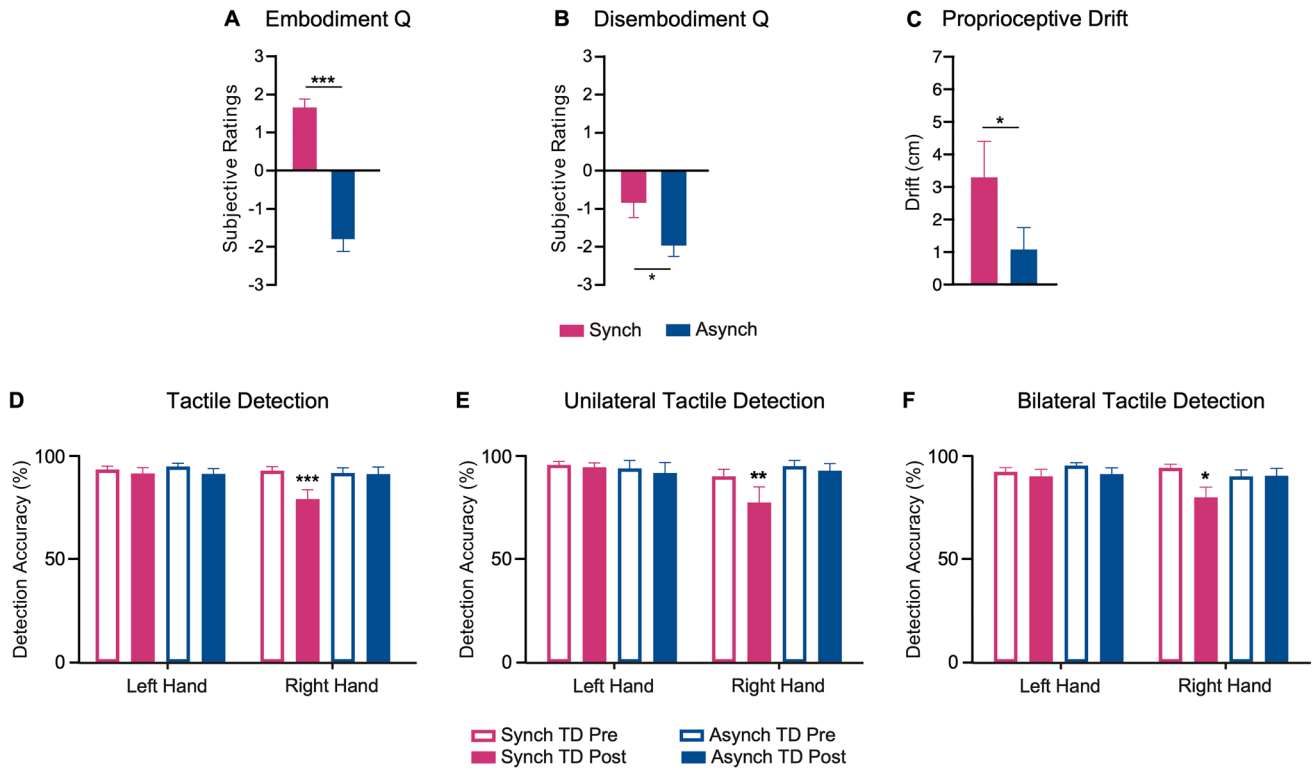


Fig. 2 Results of Experiment 1. **A** Embodiment Questionnaire results: mean embodiment ratings (Likert Scale – 3/+3). **B** Disembodiment Questionnaire results: mean disembodiment ratings (Likert Scale – 3/+3). **C** Proprioceptive drift results: mean drift (cm) towards the fake hand. Note that in **A** and **B**, higher values indicate a greater agreement with the questionnaire items, and in **C**, higher values indicate greater shifts towards the fake hand. In **A**, **B**, and **C**, a significant difference is present between Synchronous and Asynchronous conditions, with greater values in the former than in the latter. **D**, **E**, and **F**, respectively, show tactile detection accuracy (%) calculated merging unilateral and bilateral data (**D**), unilateral tactile detec-

tion accuracy (%) (**E**), and bilateral tactile detection accuracy (%) (**F**) in the Synchronous (pink) and Asynchronous (blue) conditions, in the TD Pre (empty plot) and in the TD Post (solid plot) for the right- and left-hand stimulations. In **D**, **E**, and **F**, detection accuracy of right hand’s stimuli is significantly lower, after the Synchronous RHI. Note that, when correction for multiple comparison was applied, the results of the analysis performed on unilateral data (**E**) did not reach statistical significance (Condition×Time×Side interaction: $p = 0.049$; $\alpha = 0.025$). * $p < 0.05$; ** $p < 0.005$ *** $p < 0.0005$ (uncorrected). Bars indicate standard errors of the mean (SEM)

Table 2 Rubber hand illusion results of Experiments 1 and 2. Embodiment and Disembodiment Questionnaires values for each condition expressed as median ratings±quartile range. Proprioceptive drift values for each condition expressed as mean shift (cm)±SD. Proprioceptive drift values for each condition expressed as mean shift (cm)±SD

	Experiment 1	Experiment 2
Embodiment Q		
Synchronous	1.833 ± 1	1.5 ± 2
Asynchronous	- 2.583 ± 2	- 2.667 ± 0.667
Disembodiment Q		
Synchronous	- 1.167 ± 2.667	- 1 ± 3.333
Asynchronous	- 2.667 ± 1.667	- 2.667 ± 1
Proprioceptive drift		
Synchronous	3.278 ± 4.686	5.267 ± 5.362
Asynchronous	1.078 ± 2.889	1.544 ± 4.478

interaction ($F_{1,17} = 4.503$; $p = 0.049$; $\eta_p^2 = 0.209$), with the Synchronous TD Post right-hand condition showing significantly lower tactile detection accuracy relative to the Synchronous TD Pre right-hand ($p = 0.0004$; $d_z = 0.650$) and all the other conditions (p always < 0.001 ; see Fig. 2E). Conversely, no differences were highlighted between Asynchronous conditions, nor between Synchronous Pre and Asynchronous Pre or Post conditions (p always > 0.480). Furthermore, results of bilateral data highlighted not only a significant main effect of Time ($F_{1,17} = 7.630$; $p = 0.013$; $\eta_p^2 = 0.310$) and a significant a Condition×Time interaction ($F_{1,17} = 14.647$; $p = 0.001$; $\eta_p^2 = 0.463$), but, crucially, also a significant Condition×Time×Side interaction ($F_{1,17} = 7.692$; $p = 0.013$; $\eta_p^2 = 0.312$). Post hoc tests revealed that the Synchronous TD Post right-hand condition showed significantly lower

Table 3 Detection task results of Experiments 1 and 2. Tactile and visual detection values expressed as mean accuracy (%) \pm SD

Experiment 1				
Tactile detection (accuracy %)	Synchronous	TD Pre	Right-hand: 93.889 \pm 8.498 Left-hand: 94.444 \pm 7.14	
		TD Post	Right-hand: 80 \pm 19.647 Left-hand: 92.59 \pm 11.802	
	Asynchronous	TD Pre	Right-hand: 92.778 \pm 10.981 Left-hand: 95.926 \pm 6.817	
		TD Post	Right-hand: 92.222 \pm 14.731 Left-hand: 92.407 \pm 10.895	
	Unilateral tactile detection (accuracy %)	Synchronous	TD Pre	Right-hand: 91.11 \pm 14.91 Left-hand: 96.67 \pm 7.67
			TD Post	Right-hand: 78.33 \pm 31.22 Left-hand: 95.56 \pm 9.22
Asynchronous		TD Pre	Right-hand: 96.11 \pm 11.95 Left-hand: 95 \pm 16.89	
		TD Post	Right-hand: 93.89 \pm 14.61 Left-hand: 92.78 \pm 21.91	
Bilateral tactile detection (accuracy %)	Synchronous	TD Pre	Right-hand: 95.278 \pm 7.568 Left-hand: 93.333 \pm 8.911	
		TD Post	Right-hand: 80.833 \pm 21.506 Left-hand: 91.111 \pm 14.808	
	Asynchronous	TD Pre	Right-hand: 91.111 \pm 13.672 Left-hand: 96.389 \pm 5.893	
		TD Post	Right-hand: 91.389 \pm 15.416 Left-hand: 92.222 \pm 13.309	
Experiment 2				
Visual detection (accuracy %)	Synchronous	VD Pre	62.001 \pm 10.939	
		VD Post	70.932 \pm 12.92	
	Asynchronous	VD Pre	62.408 \pm 17.001	
		VD Post	62.627 \pm 19.9	

tactile detection accuracy relative to the Synchronous TD Pre right-hand ($p = 0.003$; $d_z = 0.860$) and all the other conditions (p always < 0.01 ; see Fig. 2F). Conversely, no differences were found between Asynchronous conditions, nor between Synchronous Pre and Asynchronous Pre or Post conditions (p always > 0.480).

However, while the results of bilateral data highlighted significant results, the Condition \times Time \times Side interaction found in the unilateral data analysis did not reach statistical significance when the correction for multiple comparison was applied ($\alpha = 0.025$). We reasoned that this result could be due to the lower number of unilateral trials (20 total: 10 right-hand, 10 left-hand), and thus, recommend a minimum of 40 trials (40 total: 20 right-hand, 20 left-hand) for future studies that will capitalise on detection paradigms like the one employed here.

Correlational analysis. No significant correlation was found between RHI measures and the modulation index (p

always > 0.05), highlighting that the relationship between the changes in ownership and tactile downregulation was not linear.

Experiment 2

Rubber hand illusion

The Wilcoxon tests comparing the Embodiment and Disembodiment Questionnaire's mean ratings between conditions showed a significant difference (Embodiment: $T = 1$; $p = 0.0002$; $r = 0.613$; Disembodiment: $T = 20.5$; $p = 0.014$; $r = 0.409$; Fig. 3A, B) with higher values in the Synchronous than in the Asynchronous condition (see Table 2). Coherently, the t test which compared PD measures in the Synchronous and Asynchronous conditions revealed a significant difference between conditions ($t = 3.164$; $p = 0.0140$;

EXPERIMENT 2

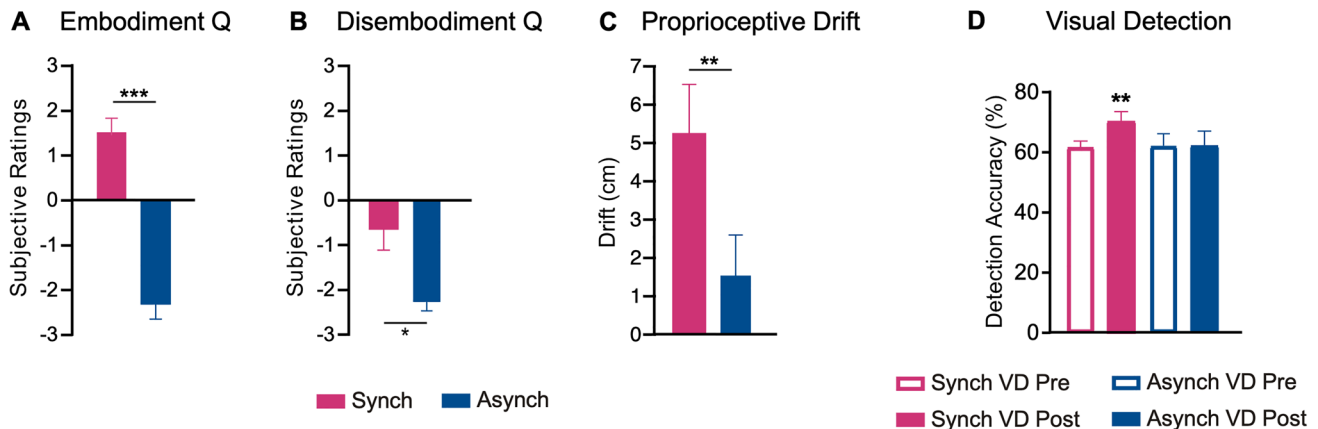


Fig. 3 Results of Experiment 2. **A** Embodiment Questionnaire results: mean embodiment ratings (Likert Scale – 3/+3). **B** Disembodiment Questionnaire results: mean disembodiment ratings (Likert Scale – 3/+3). **C** Proprioceptive drift results: mean drift (cm) towards the rubber hand. In **A–C**, a significant difference is present between Synchronous and Asynchronous conditions, with greater val-

ues in the former than in the latter. **D** The visual detection accuracy (%) in the Synchronous (in pink) and Asynchronous (in blue) conditions, in the VD Pre (empty plot) and in the VD Post (solid plot). Detection accuracy is significantly higher after the Synchronous RHI. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.0005$. Bars indicate standard errors of the mean (SEM)

$d_z = 0.746$; Fig. 3C), with the former showing greater values than the latter (see Table 2).

Visual detection task

Detection accuracy analysis. The repeated-measures ANOVA showed a significant main effect of Time ($F_{1,17} = 4.527$; $p = 0.048$; $\eta_p^2 = 0.210$), with higher accuracy in VD Post than in VD Pre. Crucially, we also found a significant Condition \times Time interaction ($F_{1,17} = 9.078$; $p = 0.008$; $\eta_p^2 = 0.348$). In particular, the Synchronous VD Post condition showed a significantly higher visual detection accuracy relative to the Synchronous VD Pre condition ($p = 0.002$, $d_z = 0.756$) and all the other conditions (p always < 0.003 ; see Fig. 3D; Table 3). Conversely, the Asynchronous VD Post condition did not differ from the Asynchronous VD Pre condition ($p = 0.916$; $d_z = 0.023$).

Correlational analysis. No significant correlation was found between RHI measures and the modulation index (p always > 0.05), pinpointing that the relationship between dis(embodiment) and visual upregulation was not linear.

Discussion

In this study, we investigated whether, after the RHI, a modulation of tactile and visual processing occurs using a perceptual threshold stimulation paradigm, to better understand the mechanisms underpinning the updating of the SBO. To manipulate the sense of body ownership in healthy participants, we employed the RHI paradigm (Botvinick & Cohen,

1998). In two separate experiments, to investigate the body ownership-dependent modulation of tactile (Experiment 1) and visual (Experiment 2) processing, we employed two detection tasks performed before and after the RHI, wherein we administered stimuli slightly above the participants' perceptual threshold level.

The results of both Experiments 1 and 2 demonstrate that the RHI modulated the sense of body ownership. Indeed, we found significantly higher scores in the Synchronous than in the Asynchronous condition of the classical RHI measures (i.e. Embodiment and Disembodiment Questionnaires, proprioceptive drift). Although dummy items that control for general suggestibility were not included in the questionnaires, we show converging evidence using different RHI measures, highlighting that the (dis)embodiment effect was present only in the Synchronous condition. Interestingly, proprioceptive drift resulted almost double in Experiment 2, as compared to Experiment 1. This may be explained by individual differences between the two samples. However, an alternative interpretation could be that in Experiment 1, after each trial of the detection task, proprioception may be recalibrated onto the real hand position due to the tactile stimulation. Conversely, in Experiment 2, visual stimuli delivery should not result in proprioceptive recalibration. Crucially, the results show that, after the RHI, a diametrical effect on tactile and visual accuracy is observed, with a decreased detection of tactile stimuli delivered on the real hand and an increased detection of visual stimuli delivered around the fake hand.

In the tactile domain, a detection decrease following the RHI has already been demonstrated with unilateral threshold

stimuli (Zopf et al., 2011) or employing unilateral above-threshold stimuli (Folegatti et al., 2009), but neither of these studies directly verified whether this effect was circumscribed to the hand subjected to the illusion. In Experiment 1, the results of the main analysis reveal that only when body ownership is modulated (i.e. in the Synchronous condition), tactile detection accuracy is diminished. Interestingly, we found a differential effect between the stimulation of the right and the left hand, revealing that the decrease of somatosensory detection is circumscribed to the hand exposed to the illusion (i.e. the right hand). Importantly, we were able to rule out that this difference was due to the fact that participants could see the left but not the right (“illuded”) hand throughout the task (Tipper et al., 1998, 2001), because no difference between right- and left-hand stimuli detection was found in the baseline task (i.e. TD Pre), in which the RHI stimulation was not applied. Furthermore, our results on bilateral detection are original, since no previous study investigated the effect of the RHI on bilateral stimulations. Crucially, we show that in bilateral trials participants tend to selectively omit the stimulation directed to the hand subjected to the illusion after the induction of the RHI. A similar omissive behaviour has been extensively described in brain-damaged patients with tactile extinction [TE; e.g. see (Chechlacz et al., 2013a, 2013b; Eimer et al., 2002; Fosfataro et al., 2020a, 2020b; Neppi-Modona, 1999; Vallar et al., 1994)], namely a neuropsychological deficit that consists in a failure in detecting contralesional tactile stimuli when simultaneously delivered with competing ipsilesional ones. Since these patients show normal detection of unilateral ipsilesional and contralesional stimuli, revealing spared somatosensory processing in the affected limb, TE has been interpreted as an ipsilesional bias in the orientation of spatial attention (Bisiach & Vallar, 2000; Driver & Vuilleumier, 2001; Heilman et al., 2000; Jacobs et al., 2011). Several works have addressed extinction-like behaviour in healthy participants, either inducing “virtual lesions” employing non-invasive brain stimulation [for a review see (Oliveri & Caltagirone, 2006)], or employing cross-modal (Colavita, 1974; Filbrich et al., 2019; Jacobs et al., 2011; Ronga et al., 2012; Spence et al., 2011) or unimodal (Farnè et al., 2007) detection paradigms. During these experimental manipulations, despite normal detection in unilateral trials, an impaired tactile detection emerged during bilateral stimulations. By contrast, in our study we observe a decrease of tactile detection also in right-hand unilateral trials, suggesting that, here, pseudo-extinction likely occurs as a side effect of the modulation of the right-hand unilateral threshold. Interestingly, the downregulation of somatosensory activity during the RHI has been observed by several studies employing non-invasive brain stimulation techniques either to measure the cortical activity during the RHI (Isayama et al., 2019) or to modulate somatosensory activity to measure the effect on

the RHI (Hornburger et al., 2019). In addition, a number of studies have investigated the neural bases of the RHI capitalising on neuroimaging techniques (Bekrater-Bodmann et al., 2014; Brozzoli et al., 2012; Ehrsson et al., 2004, 2005; Guterstam et al., 2019; Limanowski & Blankenburg, 2015, 2016). Interestingly, Limanowski and Blankenburg (2016) found, during the RHI, lower touch-related activity in S1 and a significant activity increase in the lateral occipital complex (LOC) and the secondary somatosensory cortex (S2). These researchers also investigated the connectivity patterns involved in the embodiment of an artificial limb, by measuring psycho-physiological interactions (PPIs) on fMRI data (Limanowski & Blankenburg, 2015), showing that the functional connectivity between fronto-parietal areas (including IPS and ventral PMC) and visual areas (including LOC) is increased when the embodiment of the fake hand emerges. It is noteworthy that both these results and those of Zeller et al. (2016) revealed a decrease in S1 activity and an increase in the connectivity between visual and multimodal cortices.

Despite the converging evidence on the effects of the RHI on the somatosensory system, the modulations induced in the visual system seem to be less investigated in literature, and previous findings are controversial. A behavioural study by Longo and colleagues showed that the RHI enhances the perceived physical similarity between the real and the fake hands (Longo et al., 2009), demonstrating a detriment of visual processing after the RHI. On the other hand, Van Der Hoort et al., (2017) indicate that the saliency of the visual input is somehow enhanced by the embodiment of a virtual hand. They addressed whether the embodiment of a virtual hand affects visual awareness in a binocular rivalry paradigm. The authors manipulated the sense of body ownership by applying visuo-tactile stimulation onto the participants’ real hand while observing two rival images: a hand and a mask image that randomly alternated at 10 Hz. The authors found that the amount of time wherein participants were able to see the hand image despite the presence of the mask increased only when the participants’ body ownership was manipulated. According to this latter study, the Experiment 2 results show that participants’ performance in a visual detection task is significantly improved after the modulation of body ownership (i.e. VD Post of the Synchronous condition). To our knowledge, our study is the first to test the visual system modulation during the RHI, measuring the perceptual threshold as a behavioural correlate of visual processing. This novel finding indicates that the embodiment of a dummy hand influences the perceptual processes in the tactile and visual domains in diametrical directions.

Within the framework of the predictive coding theory, the RHI has been explained as the consequence of the central nervous system’s (CNS) attempt to minimise prediction errors, by modulating the ‘weight’ attributed to each source of sensory information according to their reliability,

estimated on the bases of current sensory experiences and of evolutionary priors associated with each sensory domain (Ernst & Bühlhoff, 2004; Friston, 2011; Limanowski & Blankenburg, 2013). During the RHI, somatosensory inputs coming from the participant's own hand (i.e. "my hand is being stroked") are incongruent with visual inputs coming from the fake hand (i.e. "the rubber hand is being stroked"). This multisensory conflict likely generates an "error signal", which is resolved by the brain to restore a coherent representation of one's own body. It has been proposed that the neural mechanism through which the CNS settles the multisensory conflict relies on the contribution of two simultaneous processes: (1) the weight attributed to somatosensory inputs is downregulated, as physiologically reflected by the reduction of somatosensory activity; (2) the weight attributed to visual inputs is increased, via the upregulation of the forward connectivity from visual to multimodal areas (Limanowski & Blankenburg, 2016; Zeller et al., 2016). Why should our brain rely more on visual rather than somatosensory inputs when they are incongruent? According to the predictive coding account, from time to time, the CNS explains away conflicting proprioceptive and visual information by estimating the precision of each modality and thus adjusting the weight attributed to each sensory input to minimise estimation errors (Ronga et al., 2017; van Beers et al., 1999; van Beers et al., 2002). In other words, the CNS determines the signal-to-noise ratio of each input, according to current experience (e.g. evaluating the congruency between different sources of information) and to acquired knowledge (e.g. some aprioristic factors, such as the generally higher amount of noise present in proprioceptive as compared to visual information). As an example, it has been demonstrated that, when there is a small visuo-proprioceptive disparity (e.g., $\leq 10^\circ$), the CNS tends to rely on visual input, which is considered less noisy, and therefore, more precise in the exact determination of locations in space (Ernst & Banks, 2002). Whereas, under a condition of large disparity (e.g., $> 20^\circ$), namely when the incongruency cannot be attributed to the lower signal-to-noise ratio of proprioceptive information, proprioception overcomes the visual input (Fang et al., 2019; Fossataro, et al., 2020a, 2020b). In line with these results, it is well known that in the classical RHI setting, when the fake hand is in an anatomically plausible position (i.e. a small disparity is present), vision of the fake hand largely dominates over proprioception so that the tactile sensation is remapped onto the fake hand and the illusion arises. Conversely, when the fake hand is in an anatomically implausible position relative to the participants' posture (i.e. a large disparity is present), proprioception can overcome vision preventing subjects to experience the illusion [e.g. see (Fang et al., 2019; Ide, 2013; Kalckert & Ehrsson, 2014; Kalckert et al., 2019)]. Therefore, provided the discrepancy is within reasonable limits,

during the RHI visual inputs seem to overcome somatosensory inputs, because the visual system can compute a less noisy (i.e. more reliable) estimation of one's own hand. As a supporting evidence, Ronga et al. (2017) showed that when the brain judges visual input as more noisy than proprioception (as it happens for a special kind of prismatic adaptation performed through eye-movements, precluding the view of the own body), a proprioception capture of vision is observed (i.e. the conflict between vision and proprioception is resolved in favour of proprioception). If visual dominance occurs in the context of the RHI because the variance associated with visual estimation is lower than that associated with proprioceptive estimation (Ernst & Banks, 2002), one should observe that, when visual input is rendered noisier, somatosensory inputs overcome visual inputs. Future studies could test this interpretation by experimentally making visual input noisier, hence, overturning the balance between visual and proprioceptive input's noisiness.

One final issue should be discussed, that is the role of attentional processes in the RHI. In both Experiments, the participant's focus of attention was directed towards the target modality, because the task required to detect tactile or visual stimuli. Hence, the effect highlighted here cannot be explained by low-level attentional factors such as the simple presence of a fake hand in the visual scene, otherwise between-condition differences would not be observed. Nevertheless, it is possible that embodiment-dependent modulations (i.e. modulations that are present only after the synchronous RHI) may be mediated by attention. Attentional factors likely play a major role in the modulation of visual and tactile inputs when an incongruency between multiple sensory inputs occurs (Limanowski & Friston, 2019, 2020; Talsma et al., 2010). According to the maximum-likelihood estimation model, somatosensory and visual inputs are integrated by weighting each single modality relative to its estimated precision, to obtain the most reliable multisensory prediction (Ernst & Banks, 2002; Ernst & Bühlhoff, 2004). Given that attention has been associated with top-down modulation of sensory precision estimate (Limanowski & Friston, 2019, 2020), it is very likely that attentional shifts towards the fake hand contribute to mediate the influence of embodiment on sensory processing. However, further research is needed to isolate the specific contribution of attention in such processes.

Despite the evidence that we provide, some limitations of the study need to be addressed. First, the detection tasks employed for the tactile (Experiment 1) and visual (Experiment 2) modalities show methodological differences; hence, no direct comparison could be made between their results. Second, given the impossibility of applying the Signal Detection Theory (Stanislaw, 1999) to the present data, we cannot dissociate detection changes from other changes, i.e.

response bias. Further studies are needed to address this specific issue.

Conclusion

To sum up, the present study describes a body ownership-dependent diametrical modulation of tactile and visual perceptual thresholds following the RHI, with decreased tactile and increased visual detection performances. Under normal circumstances, visual and somatosensory inputs provide congruent information to higher-order integrative cortices that implement them in a unitary and coherent representation of one's own body. Employing experimental procedures, such as the RHI, aimed to generate a multi-sensory mismatch, can shed light on the neural mechanism through which our brain plastically adapts to uncertainty by attributing differential weights to each source of sensory information, according to its expected and prior reliability values. Here, we provide original behavioural evidence that, during the RHI, the alteration of the sense of body ownership relies both on the attenuation of somatosensory inputs coming from one's own hand and on the enhancement of visual perception around the fake hand. The diametrical pattern of our results strongly supports the view that, during the RHI, the weight attributed to somatosensory information is decreased while that of visual information is increased, in line with the EEG and fMRI findings discussed above. Taken together, the two experiments described here confirm and expand on previous knowledge about the RHI effect in the somatosensory system and provide the very first behavioural evidence of a modulation of the visual system as a consequence of the alteration of the sense of body ownership, in line with the predictive coding framework.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00426-021-01608-0>.

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Availability of data and material Datasets have been made publicly available as *Supplementary Material*.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All the procedures performed in studies involving human participants were in accordance with the ethical standards of the Ethical Committee of the University of Turin (prot. n°122571) and with the 1964 Helsinki Declaration and its later amendments.

Informed consent Informed consent was obtained from all the individual participants included in the study.

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