



# I'm a believer: Illusory self-generated touch elicits sensory attenuation and somatosensory evoked potentials similar to the real self-touch

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## ABSTRACT

Sensory attenuation (i.e., the phenomenon whereby self-produced sensations are perceived as less intense compared to externally occurring ones) is among the neurocognitive processes that help distinguishing ourselves from others. It is thought to be rooted in the motor system (e.g., related to motor intention and prediction), while the role of body awareness, which necessarily accompanies any voluntary movement, in this phenomenon is largely unknown. To fill this gap, here we compared the perceived intensity, somatosensory evoked potentials, and alpha-band desynchronization for self-generated, other-generated, and embodied-fake-hand-generated somatosensory stimuli. We showed that sensory attenuation triggered by the own hand and by the embodied fake hand had the same behavioral and neurophysiological signatures (reduced subjective intensity, reduced of N140 and P200 SEP components and post-stimulus alpha-band desynchronization). Therefore, signals subserving body ownership influenced attenuation of somatosensory stimuli, possibly in a postdictive manner. This indicates that body ownership is crucial for distinguishing the source of the perceived sensations.

## Introduction

Sensations originating from external causes can represent a potential biological threat. Hence, the ability to distinguish them from self-generated sensations has a key role in human evolution. For this reason, our brain produces sensory attenuation, an effect that enables to better predict the sensory consequence of our own actions (see Hughes et al., 2013 for a review).

By definition, sensory attenuation is the fact that the self-generated sensory stimuli are perceived as less intense than identical externally generated ones. This phenomenon is present across a variety of modalities, such as audition (Bass et al., 2008; Sato, 2009; Schafer and Marcus, 1973), vision (Hughes and Waszak, 2011; Schafer and Marcus, 1973; Schwarz et al., 2018) and touch (Blakemore et al., 1999; Blakemore et al., 1998). Interestingly, within the somatosensory domain, the attenuation of stimuli that we actively deliver to our own body, with respect to those coming from the environment, explains why we are unable to tickle ourselves (Blakemore et al., 1998). It is worth emphasizing that sensory attenuation is not only a subjective experi-

ence (Blakemore et al., 1999; Sato, 2009) but also a neural response at the earlier stages of cortical sensory processing (Bass et al., 2008; Blakemore et al., 1998; Schafer and Marcus, 1973). For instance, previous EEG studies have shown a reduction of the N1-P2 components of cortical auditory evoked potentials for the sounds produced by one's voluntary actions, with respect to those generated externally (Bass et al., 2008; Horvath, 2013) or caused by involuntary actions (Timm et al., 2014). Moreover, fMRI evidence pinpointed that parietal operculum and the posterior insula were the key brain structures involved in differentiating self-generated from externally-caused somatosensory stimuli (Limanowski et al., 2019).

Hitherto, sensory attenuation has been thought to arise from the same set of motor signals employed for action planning and execution: motor intentions, planning, premotor processing, efference copy, sensorimotor predictions, etc. (Bays et al., 2006; Bays and Wolpert, 2007; Haggard, 2008). In particular, one influential proposal suggests that it would emerge from the match between intended and actual sensory consequences of a voluntary action (Blakemore et al., 1998; Wolpert and Flanagan, 2001). Specifically, whenever we move intentionally, the brain creates not only the specific motor commands for the action ex-

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education, but also an internal copy of those commands, known as the efference copy. Then, the so-called ‘internal forward model’ employs the efference copy to predict the more likely sensory consequences of the given action. If the willed action is achieved, actual sensory consequences (reafferences) and the predicted ones closely match in spatiotemporal terms. On the contrary, when the action is initiated externally, the consequences lack accompanying predictions and are therefore marked by a larger disparity between expected and perceived outcomes (Blakemore et al., 1998; Limanowski et al., 2018). Hence, by discarding highly anticipated events and enhancing the salience of those more unexpected, sensory attenuation allows disentangling internally- from externally-produced effects (Blakemore et al., 1998; Wolpert and Flanagan, 2001). Since both predictions and efference copies are thought to be necessary for sensory attenuation to occur (Kilteni et al., 2020), sensory attenuation is important for separating our own actions from those with an external origin and, hence, is fundamental to distinguish ourselves from others (Blakemore et al., 1998; Wolpert and Flanagan, 2001). Nonetheless, it is important to underline that some recent works have put into question such interpretation. Indeed, they found that sensorimotor predictions enhance, rather than attenuate, the sensory consequences (Thomas et al., In press; Yon et al., 2018; Yon et al., 2020). Within this framework, attenuation-like effects are thought to arise independently from motor-related signals, being, rather, caused by an increased salience of prediction errors or sensory gating (see Press et al., 2020 for details).

It is worth noting, however, that any complete interpretation of sensory attenuation for somatosensory stimuli should necessarily include also the representations of the body as one’s own (see Pyasik et al., 2019a for a broader discussion). Indeed, distinguishing one’s own caresses from a wasp crawling on one’s arm, for instance, requires the feeling that the forearm unambiguously belongs to oneself, the so-called ‘body ownership’ Gallagher (2000). It is known that body ownership arises from the spatiotemporal integration of the afferent sensory signals that constantly reach our body: visual, tactile, proprioceptive, kinesthetic, and auditory ones. For example, when I caress my forearm, I experience that body part as my own because I see and I feel the touches at the same time and in the same place. In other words, the stronger the spatiotemporal congruency among these signals, the higher the feeling of body ownership. Hitherto, some evidence already supports the view that body-related signals subserving ownership have a key role in motor control. Indeed, being aware of one’s own body allows estimating limb position (Faivre et al., 2017), tuning motor commands (Shibuya et al., 2018) and adjusting errors Nielsen (1963). More in general, we have already mentioned that sensory attenuation have been repeatedly described within the somatosensory domains, that is for body-related action-outcomes (Bays et al., 2005; Blakemore et al., 1998; Kilteni and Ehrsson, 2017). These findings clearly pinpoint that body-related sensory signals, particularly those underpinning the conscious awareness of one’s own body, are crucial for the understanding of sensory attenuation.

Despite the above-mentioned considerations, very little is known about the role of body ownership in sensory attenuation for somatosensory stimuli. To the best of our knowledge, only a few studies addressed this issue, and only at the behavioral level (Burin et al., 2018; Burin et al., 2017c; Kilteni and Ehrsson, 2017; Pyasik et al., 2019b). They combined sensory attenuation measures with an experimental manipulation of body ownership, the rubber hand illusion (hereinafter RHI), which allows inducing an illusory feeling of ownership of a life-sized fake hand (Burin et al., 2017b; Costantini and Haggard, 2007; Farnè et al., 2000; Pyasik et al., 2019c; Tsakiris et al., 2010). These studies showed that somatosensory stimuli delivered by an embodied fake hand were subjectively attenuated similarly to self-initiated ones. Interestingly, in some setups (Burin et al., 2018; Burin et al., 2017c; Pyasik et al., 2019b) any kind of motor-related signal (even predictive) was prevented, thus suggesting that body ownership *per se* can act on sensory attenuation in the absence of motor intentions, feedforward pre-

dictions, etc. It is worth emphasizing that, in general, the link between sensory attenuation and RHI is bidirectional in nature, since the illusory experience can be affected by the attenuation of somatosensory stimuli (Limanowski and Blankenburg, 2015; Zeller et al., 2015). Beyond the scarcity of behavioral evidence, the existing literature has never described electrophysiological signatures of the way body-related signals affect sensory attenuation.

Analysis of event-related brain potentials (ERPs) is well-suited for the investigation of sensory attenuation in response to somatosensory peripheral nerve stimulation induced by self-initiated movement (i.e., sensory gating; Macerollo et al., 2016; Papakostopoulos et al., 1975). Overall, previous studies have demonstrated that the amplitude of the evoked somatosensory cortical activity is attenuated during self-initiated movement. The same result (attenuation of ERP amplitudes) was found during the suppression of self-generated movement consequences across different sensory modalities (Horvath, 2013; Hughes and Waszak, 2011). Moreover, in the time-frequency domain, cortical oscillations are likely to play a role in somatosensory gating during functional movement. Central brain low-frequency oscillations (mainly within the alpha frequency band, i.e., 8–12 Hz) react to contralateral movement and sensory stimuli (Chatrian et al., 1959). Changes in cortical oscillations can be investigated by computing the event-related (de)synchronization (ERD/S; Pfurtscheller and Aranibar, 1977). In a given frequency band, ERD indexes capture the attenuation of the oscillation amplitude, whereas ERS corresponds to an increase in amplitude following the event (e.g., sensory stimulation). It is well established that somatosensory stimulation during passive sitting induces an immediate and transient ERS of oscillations in the somatosensory cortices across the 10–75 Hz frequency bands, generally followed by an ERD of the somatosensory cortical oscillations, mainly detectable throughout the alpha band that usually extends from about 150 to 600 ms (Gaetz and Cheyne, 2003; Kurz et al., 2018a; Wiesman et al., 2017). Moreover and crucially for our study, these frequency-specific somatosensory cortical oscillations are modulated by haptic movement (Kurz et al., 2018b). Compared with the active movement condition, the low-frequency oscillation decrease was significantly stronger in the right precentral somatosensory area during the passive condition. The relation between oscillatory responses and sensory attenuation during active movement was further confirmed by Gehringer and colleagues (Gehringer et al., 2019b). The authors found that the strength of somatosensory low-frequency ERD responses was significantly lower when participants performed ankle movements compared with passive no-movement condition.

In order to explore the role of body ownership in sensory attenuation, here, we combined a body-ownership manipulation (the RHI paradigm) with a procedure for measuring the sensory attenuation. We compared subjective intensity ratings, somatosensory evoked potentials (hereinafter, SEPs), and the post-stimulus neural oscillatory activity for self-generated somatosensory stimuli, other-generated stimuli and stimuli generated by a fake hand that was embodied in the RHI. Furthermore, in accordance with previous studies of our group (Burin et al., 2018; Burin et al., 2017c; Pyasik et al., 2019b), we included another condition where the stimuli were generated only by a fake hand that, however, was not embodied. Therefore, the first two conditions allowed obtaining the baseline sensory attenuation indices (comparison between self- and other-generated stimuli) and the second two focused on the possible sensory attenuation modulations driven purely by body ownership (since these two conditions did not involve any motor-related signals).

We predicted that the behavioral sensory attenuation (i.e., the reduction of the perceived stimulus intensity) induced by self-generated and embodied hand-generated stimuli should be paired with reduced SEP amplitudes, affecting both N140 and P200 SEP components, in accordance with previous EEG studies on auditory and visual ERPs, showing an sensory attenuation-driven modulation on the whole vertex potential (Horvath, 2013; Hughes and Waszak, 2011). Moreover, coherently with previous studies (Gehringer et al., 2019b; Kurz et al., 2018a) we

expected to observe a decrease in alpha ERD following self-generated and embodied hand-generated electrical stimulation.

## Materials and methods

### Participants

Fourteen healthy right-handed (Oldfield, 1971) participants (9 females, age range – 20–34 years) signed a written informed consent for participating in the study. All experimental procedures were approved by the Bioethical Committee of the University of Turin and carried out in accordance with the ethical standards of the 2013 Declaration of Helsinki.

Sample size was determined using a priori power analysis conducted in G-POWER with alpha level and effect size from a previous behavioral study (Burin et al., 2017c) and a power of 0.80 (two-tailed test). The required sample size was determined to be twelve.

### Experimental design

The study was composed of two sessions in a within-subject design. In the first part, participants were administered the RHI paradigm and the sensory attenuation paradigm (see Supplementary Materials). Since we aimed at investigating the sensory attenuation of stimuli produced by an embodied fake hand, all participants with both sensory attenuation and embodiment of the fake hand were selected for the second part of the study (see details about the screening procedure in the Supplementary Materials). The screening included 42 participants; 34 (82%) had the RHI effects and 25 (60%) had the sensory attenuation effect. 18 participants had both effects and were selected for the second part of the study, with 4 dropping out before the second part. In the main experiment (administered approximately one week after the first one), we combined the RHI paradigm and the Sensory Attenuation paradigm in a single setup. Then, we compared the subjective intensity, the SEPs and alpha ERD for self-produced stimuli and the stimuli generated by the embodied or the non-embodied fake hand.

### Main experiment

The experiment included four conditions (the setup and procedure are summarized in Fig. 1). The first two conditions served as sensory attenuation baseline (i.e., included the comparison between self- and other-generated stimuli, *Self* and *Other\_Allo* conditions, respectively). The other two conditions were related to the sensory attenuation of the stimuli produced by an embodied fake hand (*Other\_Ego\_RHI* and *Other\_Allo\_RHI* conditions, depending on the position of the fake hand – egocentric or allocentric with respect to participant's body; see details below). Each condition was presented in two consecutive blocks of 12 trials (10 trials and 2 randomly presented catch trials without electrical stimulation) with a total of 24 trials per condition. The structure of a single trial was identical throughout the conditions, except for the presence of visuotactile stimulation (see Fig. 1B-D for trial timeline), and the order of the conditions was counterbalanced across participants.

Throughout the experiment, non-painful somatosensory electrical stimuli were delivered to participant's right hand by an electrical stimulator (Digitimer DS7A) by means of bipolar Ag/AgCl surface electrodes placed on the hand dorsum; the electrodes were positioned in shape of an isosceles triangle with approximately 10 mm sides. The stimulation intensity was set at 2.5 times the subjective threshold + 4 mA with 300 V voltage. It was chosen according to the results of a previous study that compared different intensities and types of stimuli in a similar sensory attenuation paradigm (Burin et al., 2017a). The subjective threshold for somatosensory stimuli was identified with an ascending-descending-ascending staircase method and was set at an intensity at which the participant reported feeling a stimulus in 50% of trials (5 out of 10).

The stimulation intensity was the same for each participant in all conditions. In order to avoid habituation and control for phantom sensations (i.e., false detection of the somatosensory stimuli), the position of the active electrode was changed approximately every seven trials in each block of each condition. The position of the active electrode was changed by changing the electrode configuration on the stimulator and not on the participant's hand, which left the participant unaware of the changes.

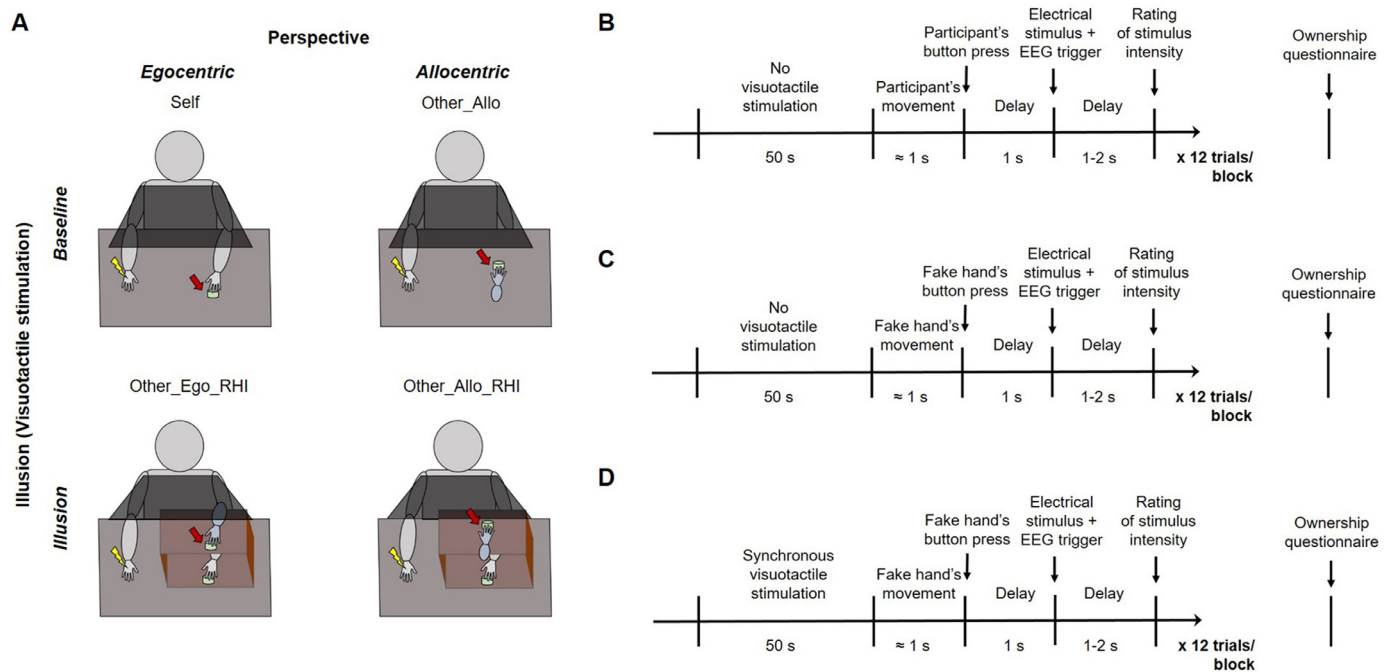
In *Self* and *Other\_Allo* conditions, participants were seated in front of a table. A button was connected to the electrical stimulator and placed on the tabletop approximately in line with the participant's left shoulder. Participants were wearing a plastic glove on their left hand, in order to create a similarity between the participant's hand and the fake hand (an identical plastic glove filled with flour). Participant's shoulders and arms were covered with a barber sheet.

In *Self* condition (see Fig. 1A and 1B), participants put their left hand on the button and their right hand in a comfortable position on the table. They were instructed to maintain their gaze on their left hand. Each trial was preceded by a 50 s interval that was included in order to make the trial structure identical in all conditions (the 50 s interval contained synchronous visuotactile stimulation in *Other\_Ego\_RHI* and *Other\_Allo\_RHI* conditions; see details below). After the intertrial interval, the participants were asked to press the button with their left index finger upon the "go" signal from the co-experimenter (i.e., instructions to "Press the button now"). The button press produced the somatosensory electrical stimulus that was delivered to the participant's right hand after a 1000 ms delay. This delay was introduced in order to avoid movement-related artifacts during the EEG recording, and it has been shown not to affect sensory attenuation (Burin et al., 2017c; Lange, 2011; Pyasik et al., 2018). At the end of each trial, participants were asked to rate the intensity of the stimulus on a 0–7 Likert scale where 0 indicated absence of stimulation and 7 – highest intensity imaginable.

In *Other\_Allo* condition (see Fig. 1A and 1C), the button press was executed by the fake left hand. The fake hand was placed on the button in the allocentric position (i.e., rotated 180° with respect to the participant's body). The participant's left hand was hidden from the view (placed under the table). As in the *Self* condition, each trial was preceded by the 50 s interval, and the participants were asked to maintain their gaze on the fake hand. After the interval, the participants were instructed that the fake hand would press the button, and the fake hand pressed the button with its index finger. The movement was executed by a computer-controlled servomotor (SG90 mini servomotor, operating speed - 0.12 s/60°). The servomotor was placed at the base of the fake-hand's index finger, which was made out of plaster and inserted in the rubber glove; the delay between the trigger of the motor and the beginning of the finger movement was < 50 ms and the total movement of the finger lasted 2000 ms. The button press produced the somatosensory electrical stimulus to the participant's right hand after the delay of 1000 ms. Participants rated the stimuli intensity on the 0–7 Likert scale, as in the *Self*-condition.

In *Other\_Ego\_RHI* and *Other\_Allo\_RHI* conditions, a vertical RHI setting Kalckert and Ehrsson (2014) was introduced. A wooden box (40 × 30 × 20 cm; length x width x height) that consisted of a lower and an upper shelf with open front and back was placed on the table in front of the participants. Participant's left hand was placed on the lower shelf, and the fake left hand was placed on the upper shelf. The button was placed under the fake-hand's index finger, and an identical button was put under the participant's index finger.

In *Other\_Ego\_RHI* condition (see Fig. 1A and 1D), the fake hand was placed in the egocentric position with respect to participant's body and was aligned with the participant's left hand and shoulder. The barber sheet covered the space between the wrist of the fake hand and the participant's neck, therefore facilitating the impression that the fake hand was the participant's own hand. Participants were instructed to maintain their gaze on the fake hand. At the beginning of each trial, synchronous visuotactile stimulation was delivered to the participant's and



**Fig. 1.** Main experiment, setup and procedure: A – experimental setup in the four experimental conditions, arranged according to the  $2 \times 2$  within-participant design with factors Illusion (Baseline, Illusion), i.e., absence or presence of the synchronous visuotactile stimulation, and Perspective (Egocentric, Allocentric), i.e., the position of the hand with respect to the participant's body; B – trial timeline in the *Self* condition (participant presses the button with the left hand, which triggers the somatosensory electrical stimulus to the right hand); C – trial timeline in the *Other\_Allo* condition (non-embodied fake hand presses the button, which triggers the somatosensory electrical stimulus to participant's right hand); D – trial timeline in the *Other\_Ego\_RHI* and *Other\_Allo\_RHI* condition (embodied/non-embodied fake hand presses the button after 50 s of synchronous visuotactile stimulation; the button press triggers the somatosensory electrical stimulus to participant's right hand).

fake-hand's index finger by the strokes of paintbrushes administered by the co-experimenter (the strokes were administered synchronously at approximately 1 Hz frequency). The stimulation phase lasted 50 s. Immediately after, the participants were told that the fake hand would press the button and the fake hand pressed the button with its index finger (as in the *Other\_Allo* condition), delivering the somatosensory electrical stimulus to the participant's right hand (after the 1000 ms delay). The participants rated the intensity of the stimulus on the 0–7 Likert scale.

In *Other\_Allo\_RHI* condition (see Fig. 1A and 1D), the setup was the same as in the *Other\_Ego\_RHI* condition, but the fake hand was rotated 180°. The barber sheet covered the space between the participant's neck and the upper shelf of the box. The instructions and the structure of the trials were the same as in *Other\_Ego\_RHI* condition, i.e., after 50 s of synchronous visuotactile stimulation, the fake hand pressed the button to deliver the somatosensory stimulus to the participant's right hand, and the participants rated the stimulus intensity on the 0–7 scale.

Furthermore, in order to evaluate the embodiment of the fake hand and compare it with ownership of one's own hand, we included a questionnaire on the sense of body ownership at the end of each block of each condition. It consisted of a statement that described the experience of owning the hand that performed the button press (an illusion statement; “It felt as if I was looking at my own hand”) and a control statement (“It seemed as if I had more than one left hand”). The statements were selected from the RHI questionnaire by Kalckert and Ehrsson (2014) and adapted to be appropriate for all experimental conditions, i.e., not only for the conditions with embodied/non-embodied fake hand (as in the typical RHI questionnaire) but also for the condition with participant's own hand. The participants were asked to rate their agreement or disagreement with each statement using a -3/+3 Likert scale (-3 represented complete disagreement, 0 neither disagreement nor agreement, and +3 complete agreement).

During the entire experiment, the EEG was recorded using 32 Ag-AgCl electrodes placed on the scalp according to the International 10–20 system and referenced to the nose. Electrode impedances were kept below 5 k $\Omega$ . The electro-oculogram (EOG) was recorded from two surface electrodes, one placed over the right lower eyelid and the other placed lateral to the outer canthus of the right eye. Signals were amplified and digitized at a sampling rate of 1.024 Hz (HandyEEG – SystemPlus Evolution, Micromed, Treviso, Italy).

### Statistical analysis

As regards the RHI paradigm, we compared the proprioceptive drift between Egocentric and Allocentric conditions. The questionnaire scores were compared between the conditions and between illusion and control statements within each condition. In the sensory attenuation paradigm, we compared the ratings of self- and other-generated stimuli. See Supplementary Materials for details.

### Main experiment

#### Behavioral data

All variables were tested for the normality of distribution using Shapiro-Wilk test; when at least one variable in each analysis violated the criteria for normality ( $p < .05$ ), nonparametric analyses were performed. Effect sizes were estimated using  $\eta_p^2$  or Pearson's correlation coefficient  $r$  (for nonparametric tests).

Intensity ratings of somatosensory electrical stimuli were analyzed using a  $2 \times 2$  repeated-measures ANOVA with Illusion (Baseline, Illusion), i.e., absence or presence of the synchronous visuotactile stimulation, and Perspective (Egocentric, Allocentric), i.e., the position of the hand with respect to the participant's body, as within-subject factors. Within the Illusion factor, the Baseline conditions are *Self* and *Other*,

and the Illusion conditions are the two RHI conditions, *Other\_Ego\_RHI* and *Other\_Allo\_RHI*. In the factor Perspective, the conditions with Egocentric perspective are *Self* and *Other\_Ego\_RHI*, and those with Allocentric perspective are *Other\_Allo* and *Other\_Allo\_RHI*.

In the ownership questionnaire, Wilcoxon signed-rank test was used to compare the ratings in illusion statement with the ratings in control statement within each condition, and the ratings in illusion statement between the four conditions (in the latter case, the p values were Bonferroni-corrected for 6 comparisons, i.e. alpha level for statistical significance set at  $p = .008$ ).

#### Electrophysiological data

SEPs were pre-processed and analyzed using Letswave v.6 (<http://www.nocions.org/letswave>; (Mouraux and Iannetti, 2008)). We segmented continuous EEG data into epochs using a time window ranging from 0.5 s before somatosensory stimulation to 1 s after stimulation (total epoch duration: 1.5 s). Data were then band-pass filtered (1–30 Hz) using a fast Fourier transform filter and baseline corrected using the interval from -0.5 to 0 s as reference. Artifacts selectively due to eye blinks or eye movements were subtracted using a validated method based on an Independent Component Analysis (Jung et al., 2000). Furthermore, for each single subject, epochs belonging to the same experimental condition were averaged time-locked to the onset of the stimulus, thus yielding four different average waveforms (*Self*, *Other\_Allo*, *Other\_Ego\_RHI* and *Other\_Allo\_RHI*).

#### EEG analyses in the time domain

To explore the presence of sensory attenuation across conditions, we performed one point-by-point, repeated-measures  $2 \times 2$  ANOVA on SEPs, with two within-subject factors: Illusion (Baseline, Illusion) and Perspective (Egocentric, Allocentric). It is worth of noting that point-by-point analyses represent a statistical approach common in EEG studies (Harris et al., 2018; Novembre et al., 2018; Ronga et al., 2013), directed to highlight possible differences between conditions across the whole epoch time-course, without any a-priori assumption. One statistical comparison for each time point composing a waveform is performed. In order to correct for multiple comparisons, cluster-based permutation testing approach (1000 random permutations) is employed to each point-by-point analysis Maris and Oostenveld (2007). The presented clusters of significance represent the result of the point-by-point analyses, corrected by permutation testing. For a similar statistical approach, please refer to (Bruno et al., 2019; Sarasso et al., 2020; Sarasso et al., 2019).

#### EEG analyses in the time-frequency domain

Time-frequency decomposition for the alpha frequency band (8-12 Hz) was calculated for each single pre-processed trial of each subject, using a Short-term Fourier transform (STFT) with a Hanning window width of 0.25 s. STFT was applied to the time window between -500 ms before stimulus onset (used as a reference interval to perform baseline correction – see below) until 600 ms post stimulus onset, where previous literature highlighted the sensory attenuation effects (Gaetz and Cheyne, 2003; Kurz et al., 2018a; Wiesman et al., 2017). The present decomposition allows to visualize a power value in each time point (relative to stimulus onset) and in each frequency. We then applied a baseline correction, using the interval -500 ms; -100 ms as reference. Therefore, STFT estimates were displayed as an event-related percentage (ER%) change in oscillation amplitude relative to a baseline. STFT files were then averaged according to their experimental condition, thus, to obtain four spectrograms for each subject (*Self*, *Other*, *Other\_Ego\_RHI* and *Other\_Allo\_RHI*). ER% changes constituted the input of subsequent analyses. To test for the presence of significant modulations in ERD values we performed one point-by-point, repeated-measures  $2 \times 2$  ANOVA on SEPs, with two within-subject factors: Illusion (Baseline, Illusion) and Perspective (Egocentric, Allocentric). In order to correct for multiple

comparisons, cluster-based permutation testing approach (1000 random permutations) was employed.

## Results

As regards the RHI paradigm and the sensory attenuation paradigm, the selected participants presented significant RHI (embodying the fake hand in the Egocentric condition but not in the Allocentric, which was represented by proprioceptive drift towards the fake hand and positive ownership ratings in the questionnaire only in the Egocentric condition) and sensory attenuation (rating the self-produced stimuli as significantly less intense than the externally-generated ones); for detailed results, see Supplementary figure 1 in the Supplementary Materials.

#### Main experiment

##### Intensity ratings

The ANOVA on the stimuli intensity ratings showed a significant main effect of Perspective [ $F(1,13) = 14.85$ ;  $p = .002$ ;  $\eta_p^2 = .53$ ], with higher ratings for Allocentric (mean  $\pm$  SEM =  $3.04 \pm .24$ ) compared to Egocentric (mean  $\pm$  SEM =  $2.46 \pm .22$ ) perspective. Neither the Illusion  $\times$  Perspective interaction [ $F(1,13) = .05$ ;  $p = .83$ ;  $\eta_p^2 = .004$ ], nor the Illusion factor [ $F(1,13) < .001$ ;  $p = .99$ ;  $\eta_p^2 < .001$ ] were significant (see Fig. 2A). These results suggest that, when the movement was performed by a hand located in Egocentric perspective (i.e., *Self* and *Other\_Ego\_RHI* conditions), the intensity of the stimuli was attenuated in comparison with the stimuli produced by a hand in Allocentric perspective (*Other\_Allo* and *Other\_Allo\_RHI* conditions), regardless of the presence/absence of the visuotactile stimulation.

The ratings in all catch trials were always 0, and therefore, were not included in the analysis.

##### Ownership questionnaire

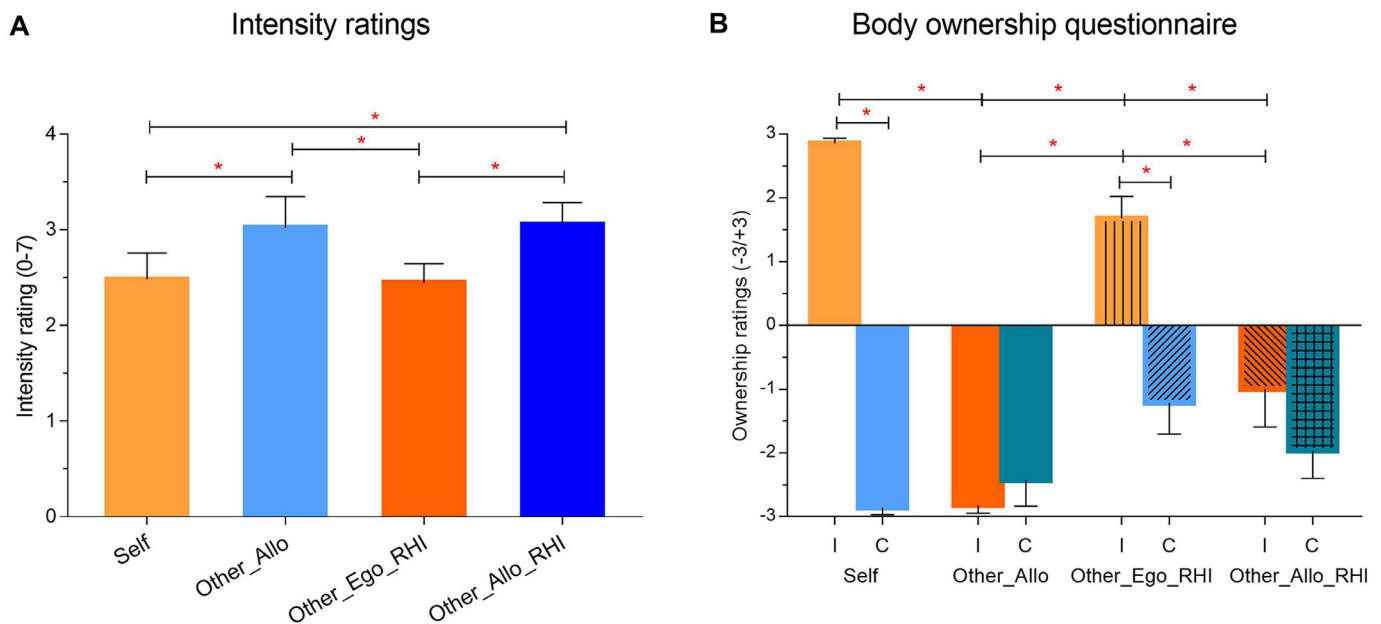
Wilcoxon signed-rank test showed that the ratings in the illusion statement were significantly higher than in the control statement in *Self* ( $n = 14$ ;  $Z = 3.30$ ;  $p < .001$ ;  $r = .99$ ; Illusion: mean  $\pm$  SD =  $2.86 \pm .31$ ; Control: mean  $\pm$  SD =  $-2.86 \pm .41$ ) and *Other\_Ego\_RHI* ( $n = 14$ ;  $Z = 3.20$ ;  $p = .001$ ;  $r = .68$ ; Illusion: mean  $\pm$  SD =  $1.69 \pm 1.23$ ; Control: mean  $\pm$  SD =  $-1.21 \pm 1.82$ ) conditions, but not in *Other\_Allo* ( $n = 14$ ;  $Z = .80$ ;  $p = .42$ ; Illusion: mean  $\pm$  SD =  $-2.82 \pm .46$ ; Control: mean  $\pm$  SD =  $-2.43 \pm 1.51$ ) and *Other\_Allo\_RHI* ( $n = 14$ ;  $Z = 1.61$ ;  $p = .11$ ; Illusion: mean  $\pm$  SD =  $-1.00 \pm 2.21$ ; Control: mean  $\pm$  SD =  $-1.96 \pm 1.61$ ) conditions.

The comparison of the ratings in the illusion statement between conditions showed that the ratings in *Self* condition were significantly higher than in all other conditions: *Other\_Allo* ( $n = 14$ ;  $Z = 3.30$ ;  $p < .001$ ;  $r = .99$ ), *Other\_Ego\_RHI* ( $n = 14$ ;  $Z = 2.67$ ;  $p = .008$ ;  $r = .53$ ) and *Other\_Allo\_RHI* ( $n = 14$ ;  $Z = 3.30$ ;  $p < .001$ ;  $r = .77$ ). Similarly, the ratings in *Other\_Ego\_RHI* condition were significantly higher than in *Other\_Allo* ( $n = 14$ ;  $Z = 3.30$ ;  $p < .001$ ;  $r = .92$ ) and *Other\_Allo\_RHI* ( $n = 14$ ;  $Z = 3.11$ ;  $p = .002$ ;  $r = .59$ ). Finally, the ratings in *Other\_Allo* and *Other\_Allo\_RHI* conditions were not significantly different ( $n = 14$ ;  $Z = 2.52$ ;  $p = .01$  (not significant with Bonferroni correction for 6 comparisons; alpha level set at  $p = .008$ ). See Fig. 2B.

These results suggest that ownership of participant's own hand was the strongest (with ratings in the illusion statement being close the maximum) but in *Other\_Ego\_RHI* condition the fake hand was also embodied (as indicated by rather high subjective ratings), unlike the two conditions with the allocentric perspective.

##### SEPs (EEG analyses in the time domain)

The  $2 \times 2$  point-by-point ANOVA revealed a main effect of Perspective over frontal, central and parietal channels, with overall larger amplitude in response to allocentric as compared to egocentric condition. At Cz, Perspective was a significant source of variance within two different time intervals: 84–166 ms ( $F(1,13) = 33.01$ ,  $p < 0.001$ ), coinciding with the latency of the N140 wave; 194–281 ms ( $F(1,13) = 25.10$ ,



**Fig. 2.** Main experiment, ratings of somatosensory stimuli intensity and questionnaire responses: A – Intensity ratings in the four experimental conditions (0–7 Likert scale); B – Ratings in illusion (I) and control (C) statements of the ownership questionnaire in the four experimental conditions (-3/+3 Likert scale). Error bars represent standard errors of means; \* - significant differences.

$p < 0.001$ ), coinciding with the latency of the P200 wave (Fig. 3A). Crucially, we did not find a significant effect of Illusion, nor any significant interaction Perspective  $\times$  Illusion (see Fig. 3B-C).

#### Neural oscillatory activity (EEG analyses in the time-frequency domain)

The  $2 \times 2$  point-by-point ANOVA exploring possible modulations of ERD values (within the alpha frequency band) across conditions revealed a main effect of Perspective over frontotemporal, central and parietal channels, with overall greater ERD values in response to allocentric as compared to egocentric condition (see Fig. 3D-E). At Cz, Perspective was a significant source of variance within one time interval: 466–600 ms ( $F_{1,15} = 11.52, p < 0.001$ ). We did not find a significant effect of Illusion, or any significant interaction Perspective  $\times$  Illusion (see Fig. 3E), thus fully paralleling the results in the time domain.

#### Discussion

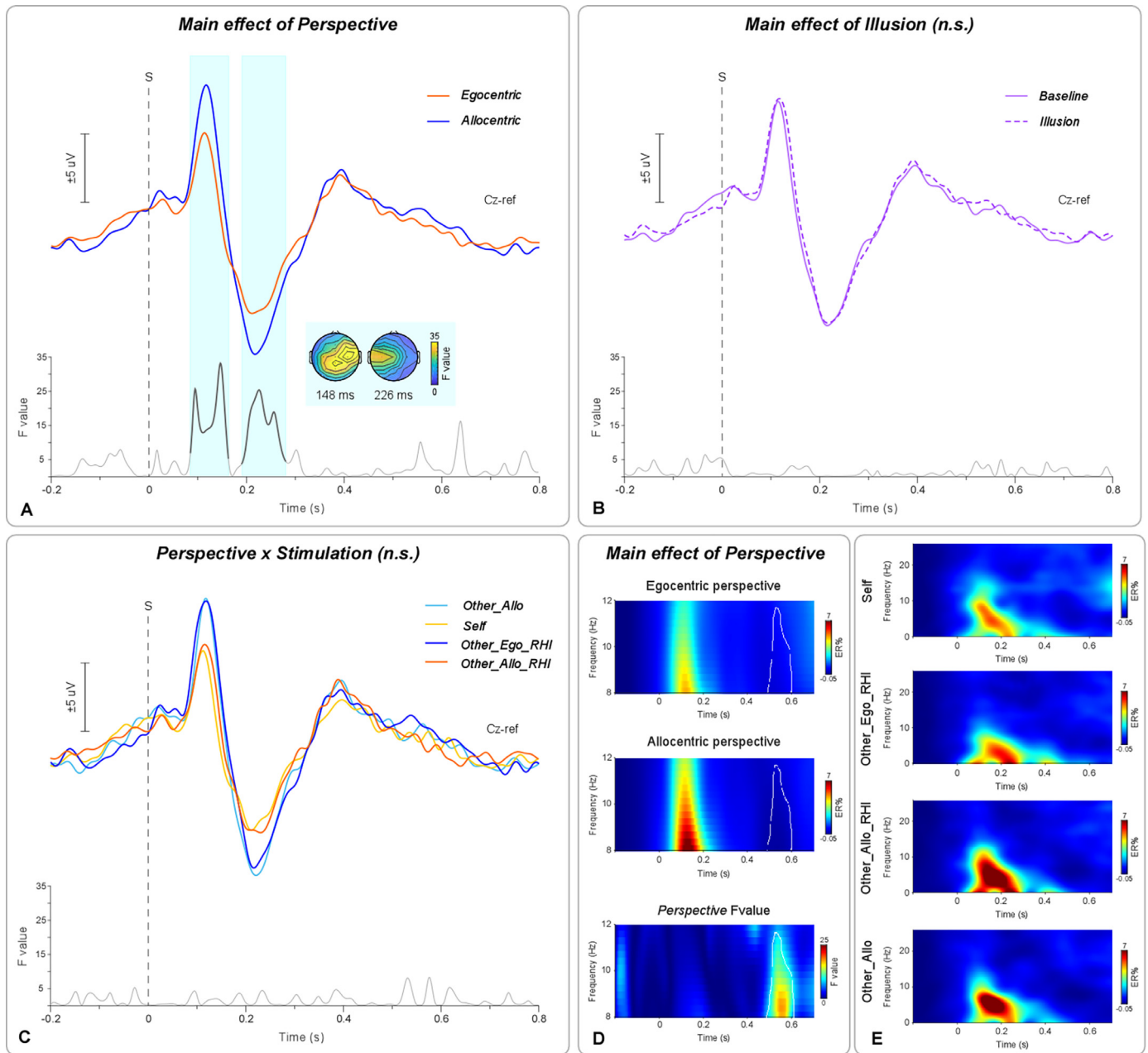
In the present study, we investigated behavioral and neurophysiological mechanisms of sensory attenuation for somatosensory stimuli triggered by body-related afferent signals subserving body ownership in comparison with sensory attenuation triggered by motor-related signals. Specifically, in a sample of healthy participants with both embodiment of the fake hand in the RHI paradigm and attenuation of self-produced somatosensory stimuli in the sensory attenuation paradigm, we confronted subjective intensity ratings, SEPs and alpha ERD, for somatosensory electrical stimuli triggered by the participant's hand, a non-embodied fake hand, or an embodied fake hand. In a  $2 \times 2$  design, we manipulated the spatial perspective of the hand (egocentric or allocentric) and the presence of synchronous visuotactile stimulation (absent in the baseline conditions and present in the RHI conditions). The main comparison of interest was between the two conditions where body ownership was expected to be equally present, but the sense of agency was different: the condition where participants performed the movement themselves, thus there was also the real sense of agency, and the condition where the embodied fake hand performed the movement, i.e., there was possibly a consequent illusory sense of agency.

At the behavioral level, we found comparable subjective attenuation of the intensity of self-produced somatosensory stimuli and stimuli generated by the embodied fake hand. These results are strongly in line with

previous behavioral evidence (Burin et al., 2018; Burin et al., 2017c; Pyasik et al., 2019b).

With respect to the neurophysiological data, firstly, we found reduced N140 and P200 SEP components for self-produced somatosensory stimuli in comparison with the externally generated ones. These data are consistent with previous physiological data within the auditory domain. Indeed, previous studies reported attenuation of the N1-P2 complex of auditory evoked potentials (AEPs) for self-produced sounds, in particular, following intended actions, but not the non-intended ones (Bass et al., 2008; Horvath, 2013; Timm et al., 2013). Crucially, the reduction of N1-P2 complex has been linked to predictive processes, such as the match between expected and actual sensory outcomes within the comparator model (Timm et al., 2013). Hence, it is possible that the reduction of N140 and P200 components of the SEPs was accounted for by a very similar mechanism, which would attenuate the correctly predicted sensory outcomes (Palmer et al., 2016). The second relevant result is an almost identical SEPs reduction for the self-generated stimuli and stimuli produced by the embodied fake hand (but not by the non-embodied fake hand), which also corresponds with the behavioral data.

Moreover, and coherently with previous studies evidencing a correlation between SEPs and ERD (Brickwedde et al., 2020; Nierhaus et al., 2015), the attenuation of SEPs during the *Self* and *Other\_Ego\_RHI* conditions was paralleled by reduced ERD in the alpha frequency band. In general, oscillations in low frequency bands are linked to excitability changes in neural populations (Jensen and Mazaheri, 2010; Thut et al., 2012), and therefore are likely candidates for selective gain control of incoming sensory information (Cao et al., 2017; Friston, 2019). Alpha ERD has been found to be related to sensory detectability and discriminability (Hanslmayr et al., 2007; Romei et al., 2010) and is commonly acknowledged as an index of the release of the inhibition of cortical excitability, which is fundamental to suppress activity in task-irrelevant neural populations (Haegens et al., 2011b; Jensen and Mazaheri, 2010). Such inhibitory function of oscillatory activity might underlie sensory attenuation, i.e., the top-down filtering or gating of afferent information during movement (Cheng et al., 2015; Gehringer et al., 2019a) and the suppression of consequences of self-generated actions (Abbasi and Gross, 2020). More specifically, somatosensory-related alpha attenua-



**Fig. 3.** Main experiment, SEPs and ER% analyses: Panels A-B-C – point-by-point ANOVA results for Perspective (A), Illusion (B) and Perspective x Illusion (C), waveforms (top panels) and point-by-point F-values (bottom panels). Note that significant time intervals are highlighted in blue. Scalp maps represent the distribution of the F-values across the scalp. Panels D-E – time-frequency results; point-by-point ANOVA results for Perspective (D) within the alpha frequency band, the bottom panel represents point-by-point F-values; time-frequency decomposition for each experimental condition (E). Note that significant time intervals are marked in white and that alpha ERD is significantly greater for the Alloentric as compared to the Egocentric perspective.

tion (Fukuda et al., 2010) reflects the excitability of the thalamocortical somatosensory system (Haegens et al., 2011a) and might constitute an efficient mechanism to weigh somatosensory inputs (i.e., movement feedback gain control) during movement control (Lebar et al., 2017). Therefore, the presence of a similar alpha ERD decrease in the *Self* and *Other\_Ego\_RHI* conditions, as compared to *Other\_Allo* and *Other\_Allo\_RHI* conditions (i.e., main effect of Perspective, see Figure 3D-E), might be considered as supporting evidence of comparable sensory attenuation mechanisms for self-initiated actions and those produced by an embodied fake hand. Apparently, provided that body ownership toward the acting effector is present, sensory attenuation may be observed, both at a behavioral and at an electrophysiological level.

It is necessary to point out that as a control condition for the embodiment we used alloentric position of the fake hand with synchronous visuotactile stimulation (e.g., Kalkert and Ehrsson, 2012, 2014) but not another classical condition within the RHI paradigm (i.e., the egocentric position with asynchronous visuotactile stimulation). In principle, this does not allow dissociating ownership and visual perspective (i.e., first- vs. third-person perspective). However, given that we have previously shown (Burin et al., 2017c) that, at the behavioral level, those two control conditions were fully comparable (i.e., they were equally ineffective at inducing either embodiment, or sensory attenuation), our findings are more likely explained by ownership rather than just observation of a hand from a first-person perspective. Moreover, in our study, the delay between the participant's/fake-hand's button press and the so-

matosensory stimulus was 1000 ms, while some of the previous literature reported a significant reduction of attenuation with delays higher than 250 ms (Bays et al., 2005; Blakemore et al., 1999). However, those studies employed very different paradigms (i.e., direct self-touch delivered by one hand onto the other and no subjective rating of the stimulus intensity), while both behavioral (Burin et al., 2018; Pyasik et al., 2018) and neurophysiological Lange (2011) studies that included subjective ratings demonstrated sensory attenuation with delays up to 1000 ms. Similarly, the action performed by either the participant or by rubber hand occurred also with a spatial separation from the subsequent tactile event, while previous studies employing self-touch reported that such kind of separation reduced the sensory attenuation (Bays et al., 2005; Kilteni and Ehrsson, 2017). However, we have already reported the same behavioral results with an identical procedure (Burin et al., 2018; Burin et al., 2017c; Pyasik et al., 2019b) and such procedure is very similar to those demonstrating auditory attenuation (i.e., participant's button press produces a distal consequence). Another potential confounding factor worth of being discussed is that ownership of the embodied fake hand is thought to persist during the movements of that hand, despite the participant's hand is still. It is known that under such a condition of sensorimotor incongruencies, illusory ownership can decrease, or even break (Kokkinara and Slater, 2014). However, it is also known that illusory ownership of a moving rubber can occur in absence of any participant's hand movements (Tieri et al., 2015) and the illusory experience can be present also during very complex movements while participants are still (e.g., a walking avatar (Kokkinara et al., 2016; Tambone et al., In press). In other words, whenever the illusion is strong, incongruent cues could remain unprocessed, at least to some extent (see Maselli and Slater (2013) for a deeper discussion). One more potential limitation that is necessary to acknowledge is related to the differences of the setup in *Other\_Allo* and *Other\_Allo\_RHI* conditions. In particular, the location of the real hand was different in those conditions: in *Other\_Allo*, it was placed under the table, while in *Other\_Allo\_RHI*, it was on the lower shelf of the RHI box, and therefore, less vertically separated from the fake hand. This potentially makes those conditions not fully comparable as the same level of the Perspective factor. However, neither of the conditions were designed to evoke any level of embodiment, and they, indeed, did not (the analyses showed completely comparable intensity ratings, SEP amplitudes and absence of subjective ownership). Hence, we believe that it did not affect the results.

Taken together, our results provide the first neurophysiological evidence that sensory attenuation for somatosensory stimuli can be triggered not only by motor-related signals but also by the signals that constantly reach the body and maintain the bodily self-consciousness. A key remaining question is: how could this be integrated within the current neurocognitive model of sensory attenuation for tactile stimuli? It is known, within the motor control theories of willed action, that the forward model predicts the most likely bodily state consequences of a given movement. Whenever predicted and actual action outcomes closely match each other, sensory attenuation arises (Blakemore et al., 1998; Wolpert and Miall, 1996). This, in turn, means that action preparation is a necessary condition for sensory attenuation to occur (i.e., for the ability to distinguish self-generated from other-generated actions). However, in line with other studies (Burin et al., 2018; Burin et al., 2017c; Pyasik et al., 2019b), here there was no forward model (because any preparation to act was prevented) and, therefore, no comparisons were possible. It is worth emphasizing that the motor control theories of voluntary action include a second mechanism, the so called 'inverse model' (Blakemore et al., 1998; Wolpert and Miall, 1996) that acts in the opposite direction and selects the motor commands necessary for the specific desired bodily state. Here, we propose that (mis)representing the movement as belonging to oneself might be embedded within one's sensorimotor system, as one's own desired bodily state. This, in turn, would feed the inverse model and activate the neural circuits to achieve the specific changes in bodily states. Consequently,

attenuation of the sensory consequences of that specific act would be activated (see (Banakou and Slater, 2014; Pyasik et al., 2019a; Tambone et al., In press) for a discussion). Our proposal is consistent with previous TMS data showing that disrupting the activity of one brain structure known to subserve sensory attenuation (i.e., the Supplementary Motor Area) eliminated sensory attenuation for both one's own movements and the movements of an embodied fake hand (Pyasik et al., 2019b). It is also in line with another study that demonstrated enhanced neural activation (mu-rhythm desynchronization) within the motor system during observation of the fake-hand's movement (Shibuya et al., 2018).

It is worth noticing that the present findings, paired with those previously published by our group, strongly support the idea that sensory attenuation for somatosensory stimuli is induced by the same neurocognitive processes that occur during real action execution. In other words, our interpretation is specifically framed within classical motor control theories. As we have observed in the introduction, there is an alternative, namely that sensory attenuation would be based on a mere cancellation of predictable events (and thus not primarily motor-related). Hence, further studies are needed to support our conclusion. Another more theoretical question that is still open is the evolutionary meaning of a mechanism that employs not only motor-related signals, but also those subserving body ownership, in order to distinguish our actions from those coming from the environment. Obviously, during actual actions, that information would simply provide additional signals to the efferent ones. Nevertheless, here we have demonstrated that body ownership acted *per se* upon motor functioning (i.e., in absence of any kind of efferent signals). As for the natural conditions that mimic our setup, a recent study in stroke patients demonstrated that an immersive virtual reality training, in which patients experienced illusory ownership over the body of a walking avatar, improved a variety of their motor deficits (Tambone et al., In press). We put forward the idea that the possible advantage of such mechanism might be to guarantee the access to the motor system even when forward mechanisms are highly deteriorated, as in stroke patients. Within this framework, motor control mechanism should be conceived as highly flexible in nature, being able to weigh all the given sources of information (efferent and afferent signals) according to the specificity of the context and the actual availability of signals. It is worth emphasizing that such interpretation clearly needs further evidence to be strengthened.

To summarize, we showed that the sensory attenuation triggered by body ownership and the sensory attenuation triggered by motor-related signals had similar behavioral and neurophysiological correlates (in form of the reduction of perceived intensity, N140 and P2 SEPs components and alpha ERD). This finding further confirms that body ownership has a role *per se* in sensory attenuation, to the extent of being able to activate those internal motor signals that subserve willed actions, possibly, in a retrospective way. Broadly speaking, this suggests that both body ownership and body-related signals must be included in any model of sensory attenuation.

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## Credit author statement

M. Pyasik: Conceptualization, Data curation, Methodology, Software, Formal analysis, Investigation, Writing - original draft, Visualization. D. Burin: Data curation, Software, Formal analysis, Investigation. I. Ronga: Methodology, Writing - original draft. P. Sarasso: Methodology, Writing - original draft. A. Salatino: Data curation, Writing - review & editing. F. Garbarini: Data curation, Writing - review & editing. R. Ricci: Data curation, Writing - review & editing. L. Pia: Conceptual-



ization, Methodology, Writing – review & editing, Supervision, Project administration, Funding acquisition.

## Data and code availability statement

The data that support the findings of this study are available on request from the corresponding author (LP) and are not publicly available due to the conditions of our ethics approval. Access can be granted only to named individuals in accordance with ethical procedures governing the reuse of sensitive data. There are no further conditions for granting access on request.

## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2021.117727.

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