That’s my hand! Therefore, that’s my willed action: How body ownership acts upon conscious awareness of willed actions

Published version:

DOI:10.1016/j.cognition.2017.05.035

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That's my hand! Therefore, that's my willed action: how body ownership acts upon conscious awareness of willed actions

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DOI 10.1016/j.cognition.2017.05.035

Abstract

Whether and how body ownership ("this body is mine”) contributes to human conscious experience of voluntary action is still unclear. In order to answer this question, here we incorporated two signatures (i.e., an *ad hoc* questionnaire and the sensory attenuation paradigm) of human’s sense of agency (“this action is due to my own will”) within a well-known experimental manipulation of body ownership (i.e., the rubber hand illusion paradigm). In two different experiments, we showed that the illusory ownership over a fake hand (induced by the rubber hand illusion) triggered also an illusory agency over its movements at both explicit and implicit level. Specifically, when the fake (embodied) hand pressed a button delivering an electrical stimulus to the participant’s body, the movement was misattributed to participant’s will (explicit level) and the stimulus intensity was attenuated (implicit level) exactly as it happened when the own hand actually delivered the stimulus. Our findings suggest that body ownership *per se* entails also motor representations of one’s own movements. Whenever required by the context, this information would act upon agency attribution even prospectively (i.e., prior to action execution).

Keywords: body ownership, sense of agency, rubber hand illusion, sensory attenuation

1. Introduction

When humans perform voluntary actions, they are aware of intending, initiating and controlling their own movements, the so-called “sense of agency” (Jeannerod, 2003). Such experience is thought to rely mainly on signals coming from the motor system. In brief, an internal forward model creates a copy of the current motor commands, which allow predicting the feedbacks that the willed action will produce. The experience of being an agent would be stronger as the match between intended/predicted and actual outcomes of the action gets closer (Blakemore, Wolpert, & Frith, 2002; Haggard & Chambon, 2012; Moore, 2016). In other words, the sense of agency emerges when the consequences of our voluntary actions are strongly consistent with the predictions of such effects made by the motor system. It is worth noticing, however, that any successful achievement of a voluntary action is also underpinned by an embodied and enduring sense that the perceived moving body parts are one’s own, the so-called “body ownership” (Gallagher, 2000). Such experience is known to be rooted on multisensory signals, which constantly reach our body (Costantini & Haggard, 2007; Holmes & Spence, 2005; Petkova et al., 2011; Tsakiris & Haggard, 2005). Indeed, during voluntary actions our own body receives a variety of sensory signals, such as visual, tactile, interoceptive, thermoceptive, nocioceptive and so on. Hence, body ownership would arise from the spatiotemporal integration of all this set of information.

These considerations imply that a coherent and normal conscious awareness of voluntary action (“this willed action is being realized by my own body”) requires not only motor-related signals, leading to the sense of agency, but also body-related signals, which subserve body ownership. Indeed, since human’s actions are achieved mainly through the physical body (Gallese & Sinigaglia, 2010), being aware of one’s own body is a key component of human self-consciousness and the prerequisite for any successful interaction with the environment (Georgieff & Jeannerod, 1998). Despite this, the current neurocognitive models of conscious awareness of willed actions are rooted almost entirely on a variety of internal efferent signals: planning, premotor processing, efference copy signals and sensorimotor predictions (e.g., Haggard, 2005, 2008).

In the present study, we experimentally manipulated the normal experience of body ownership in order to examine its impact on the experience of willed actions. To do so, we combined together the most employed experimental paradigm to alter the physical constraints subserving body ownership, the rubber hand illusion (Armel & Ramachandran, 2003; Botvinick & Cohen, 1998; Burin et al., 2015; Costantini & Haggard, 2007; Costantini et al., 2016; Ehrsson, Holmes, & Passingham, 2005; Ehrsson, Spence, & Passingham, 2004; Longo, Schuur, Kammers, Tsakiris, & Haggard, 2008; Mohan et al., 2012), with two signatures of sense of agency, namely the sensory attenuation paradigm (Bays, Wolpert, & Flanagan, 2005; Blakemore, Wolpert, & Frith, 1998; Stenner et al., 2014; Timm, SanMiguel, Keil, Schroger, & Schonwiesner, 2014; Voss, Ingram, Haggard, & Wolpert, 2006; Voss, Ingram, Wolpert, & Haggard, 2008) and an *ad hoc* questionnaire (Kalckert & Ehrsson, 2012, 2014). The rubber hand illusion allows inducing a temporary feeling of ownership over a fake hand measured through a perceptual mislocalization towards the fake hand and by specific questions aimed at quantifying the experience of owning the rubber hand. The illusion arises when temporally synchronous (but not asynchronous) touches are delivered onto a visible rubber hand and onto the hidden participants' hand. It is worth noticing that the pattern emerges when the rubber hand is placed in a congruent (0°) but not in an incongruent (180°) position with respect the participant's body (i.e., a mere spatiotemporal correlation between tactile and visual stimuli is not sufficient to trigger the illusory effects). It has been argued that the illusion arises because the initial conflict between vision of the rubber hand and tactile and proprioceptive sensation of the own hand is resolved by the embodiment of the rubber hand within the participant's own body representation (Botvinick, 2004; Makin, Holmes, & Ehrsson, 2008). The sensory attenuation paradigm is generally known to be an implicit index of the sense of agency (but see Dewey & Knoblich, 2014; Hughes, Desantis, & Waszak, 2013; Weller, Schwarz, Kunde, & Pfister, 2017) which suggested that they might be independent phenomena). The effect consists in the fact that the intensity of a self-generated stimulus is subjectively perceived as attenuated respect to an identical stimulus generated by others. Sensory attenuation is explained as a decrease of the attentional gain of the sensory consequences of one's own actions. Lastly, the questionnaire on agency quantifies the subjective experience of being an agent by means of explicit questions (e.g., "I felt as if I was causing the movement I saw"). In other words, the implicit measures of the sense of agency are perceptual differences between self- and externally generated action-effects, whereas explicit measures represent direct judgments of causality over the actions (Dewey & Knoblich, 2014; Synofzik, Vosgerau, & Newen, 2008).

In the present study, we investigated both the implicit and the explicit aspects of agency over an embodied fake hand (induced by the rubber hand illusion) that delivered a stimulus to the participant's body by carrying out two experiments.

2. Experiment 1

In the first experiment, we hypothesized that in synchronous, respect to asynchronous condition within the rubber hand illusion (hereinafter RHI) paradigm, participants should subjectively experience agency (explicit level) over the movement of the fake hand and should attenuate the intensity of the stimulus (implicit level) as when the own hand delivers the stimulus.

2.1. Materials and Methods

2.1.1. Participants

Forty right-handed (Oldfield, 1971) healthy participants (twenty-nine female, age range 18-30 years, educational level range 13-21 years) with no previous history of neurological disease gave their written informed consent, approved by the local bioethical committee, to participate in the study.

2.1.2. Experimental Design

The experiment was composed of two parts. In the first part, we aimed at obtaining baseline measures of both body ownership and sense of agency. Hence, we administered both the rubber hand illusion (hereinafter RHI) and the sensory attenuation (hereinafter SA) paradigms. In the second part, we aimed at examining the sense of agency over the embodied fake hand (as a consequence of the RHI). Hence, only those participants showing both the RHI (i.e., drift and questionnaire higher in the synchronous condition) and the SA (stimulus intensity lower in self-generated movements) effects were included in the whole experiment (40 out of 76 assessed participants). In the second part (administered after approximately 10-15 minutes of rest), we combined together the RHI and the SA paradigms within the same setup (hereinafter RHI+ SA) in a between-subjects design (i.e., half of the participants were administered one condition and the other half – another).

2.1.2.1. Rubber Hand Illusion (RHI) paradigm

A summary of the setup and of the procedures is reported in Figure 1a. We employed the vertical version of the RHI (Kalckert & Ehrsson, 2012, 2014). Participants sat in front of a wooden box (40 cm x 30 cm x 20 cm) located on a table. The box included an upper shelf, on which a life-sized model left hand (i.e., a plastic glove filled with flour) was placed, and a lower shelf, on which the participant's left hand (wearing the same glove) was placed. The two hands were vertically (15 cm of separation) and horizontally aligned congruently with respect to the participant's body). A barber sheet covered the space between the fake wrist and the participant's neck (thereby participant's arm was hidden from the view, facilitating the impression that the artificial hand was the participant's own outstretched hand).

As first, participants were blindfolded and asked to indicate the felt position of their own left index finger by pointing their right index finger towards a cardboard placed on the right side of the wooden box (six trials). The position reported on a ruler stickled on the cardboard was referred as pre-proprioceptive judgment (average of the six trials, the SD was ≤ 1.4 for each participant in each condition).

Secondly, participants were reminded to always keep their sight on index finger of the fake hand and, then, they were stimulated on both their own and the fake hand index fingers. In the synchronous (hereinafter *Syn Con*) condition, the two hands were stimulated simultaneously (i.e., visual and tactile stimulus were administered simultaneously within a random interval of approximately 500-1.000 ms), whereas in the asynchronous (hereinafter *Asyn Con*) condition, they were stimulated for two minutes in a temporally incongruent manner (i.e., the visual stimulus preceded tactile ones within a random interval of approximately 500-1.000 ms). It is worth noticing that the experimenter was unaware of the hypothesis under investigation and was trained in advance with the backdrop of metronome beats occurring accordingly to the above-mentioned intervals. After the stimulation, participants were blindfolded and asked to report again (six trials) the position of the finger on the ruler and referred as post-proprioceptive judgment (average of the six trials). The two conditions were counterbalanced between participants.

Thirdly, at the end of each condition, participants had to rate on a -3/+3 Likert scale (+3 strong agreement, 0 neither agreement nor disagreement, -3 strong disagreement) four statements of a questionnaire about their experience of ownership. Two statements (Q1 “I felt as if I was looking at my own hand” and Q2 “I felt as if the fake hand was part of my body”) referred to the actual presence of the illusion (i.e., *Real* questions), two statements (Q3 “It seems as if I had more than one left hand” and Q4 “It appeared as if the fake hand were drifting towards my real hand”) were *Control* questions. These statements were selected from a previous study (Kalckert & Ehrsson, 2014) and were randomly administered.

2.1.2.2. Sensory Attenuation (SA) paradigm

A summary of the set up and of the procedure is reported in Figure 1b. We employed the same previously described wooden box with the fake left hand on the top and the participant’s own left hand below. Two buttons connected to an electrical stimulator (Digitimer DS7A) were placed under both the fake and the participant’s left index finger (Figure 1, right lower part). The stimulator delivered electrical stimuli 2.5 times the subjective threshold (mean = 1.79, SD .46) +4 mA with 300V voltage (i.e. same intensity for each participant throughout all trials). The stimulus was delivered on the lateral digital nerve of the right hand by means of 5-mm-diameter classical bipolar Ag/AgCl surface electrodes. The intensity was chosen according to the results of an experiment in which different intensities were administered and in which none of the subjects reported painful sensations (Burin et al, under review).

As first, participants were told to always keep their sight on the index finger of the fake hand and, then, to wait for a "go" signal. Then, they had to press the button (hereinafter *Self* condition), as soon as possible after a cue (i.e., "press the button now"), or they had to stay still while the index finger of the fake hand (moved by a computer-controlled servomotor) pressed the button (hereinafter *Other* condition). At the end of each trial, participants were asked to rate the perceived intensity of the stimulus delivered to their own right hand on a 0-7 Likert scale (with 0 indicating "absence of stimulation" and 7 indicating "highest intensity").

We administered twenty-four trials within each condition (twenty proper trials and four randomly administered catch trials with no electrical stimulation to avoid habituation and control for phantom sensations). The position of the electrodes along the lateral digital nerve was changed twice (approximately at trial nine and seventeen). The order of the two conditions (i.e., *Self* and *Other*) was counterbalanced between participants. In addition, the order of the RHI and SA paradigms was counterbalanced between participants.

2.1.2.3. Rubber Hand Illusion + Sensory Attenuation (RHI+SA) paradigm

A summary of the setup and of the procedure is reported in Figure 1c. The setup was the same as in the SA paradigm. As first, participants were reminded to stay still and to maintain their sight on the fake index finger. Then, they were stimulated for one minute on both their own and fake hand's index fingers with the same procedures and conditions of the RHI paradigm. However, half of the participants were stimulated synchronously (*Syn Con Group*) and the other half asynchronously (*Syn Inc Group*). Immediately after the stimulation, the index finger of the fake hand (moved by a computer-controlled servomotor) pressed the button. Then, participants had to rate the intensity of the stimulus delivered to the right hand on a 0-7 Likert scale (with 0 indicating "absence of stimulation" and 7 indicating "highest intensity"). The stimulation was administered after each trail. We administered twenty-four trials (twenty proper trials and four randomly administered catch trials with no electrical stimulation to avoid habituation and control for phantom sensations). The position of the electrodes along the lateral digital nerve was changed twice (approximately at trial nine and seventeen).

Secondly, at the end of the condition, participants rated on a -3/+3 Likert scale (+3 strong agreement, 0 neither agreement nor disagreement, -3 strong disagreement) four statements of a questionnaire about their experience of agency. Two statements (Q1 "I felt as if I was controlling the movements of the fake hand" and Q2 "I felt as if I was causing the movement I saw") referred to the actual presence of the illusion (i.e., *Real* questions), two statements (Q3 "It seemed as if the fake hand had a will of its own" and Q4 "I felt as if the fake hand was controlling my movements") were *Control* questions. These statements were selected from a previous study (Kalckert & Ehrsson, 2014) and were administered in random order.

2.1.3 Statistical analysis

In the RHI paradigm, pre-proprioceptive judgments were subtracted from post-proprioceptive judgments (i.e., proprioceptive drift, see (Tsakiris & Haggard, 2005)) and ratings on *Real* and *Control* questions on ownership were averaged. In the RHI + SA paradigm, ratings on *Real* and *Control* questions on agency were averaged. Since at least one set of data for each required analysis (i.e., proprioceptive drift, ownership questionnaire, perceived intensity and agency questionnaire) failed to meet the criteria for normality of distribution on a Shapiro-Wilk test, we ran Friedman Tests, Wilcoxon signed-rank tests or Wilcoxon Mann-Whitney tests. The size of the effect was estimated using Cohen's *d*.

2.2 Results

2.2.1 Rubber Hand Illusion (RHI) paradigm

As regards the drift, a Wilcoxon signed-rank test with stimulation condition (*Syn Con*, *Asyn Con*) resulted to be significant (Z = 2.87, $p = .004$, $d = .38$) with higher values in the *Syn Con* (mean = 1.96, SE = .48) respect to the *Asyn Con* (mean = -.05, SE = .39) condition (see Figure 2a). It is worth noticing that, within each stimulation condition, participants subsequently assigned to a different condition in the RHI + SA paradigm (i.e., *Syn Con Group*, *Asyn Inc Group*) did not differ ($p > .05$) from each other (Wilcoxon Mann-Whitney tests). These results demonstrate that participants displayed the RHI effects in terms of proprioceptive drift and that such pattern was the same for participants subsequently assigned to a different stimulation condition in the RHI + SA paradigm.

With respect to the ownership rating, a Friedman Test with stimulation condition (*Syn Con*, *Asyn Con*) and questions (*Real*, *Control*) yielded significant results ($\chi 2 = 50.68$, df = 2, $p < .001$). Post hoc Wilcoxon signed-rank tests showed that rating given to *Real* questions in the *Syn Con* (mean = .59, SE = .33) condition was positive and significantly ($p < .016$ Bonferroni corrected) higher respect to all the other ratings (*Syn Con Control*: mean = -.38, SE = .32; *Asyn Con Real*: mean = -1.88, SE = .24; *Asyn Con Control*: mean = -2.11, SE = .2; see figure 2b). It is worth noticing that within each stimulation and question conditions, participants subsequently assigned to a different condition in the RHI + SA paradigm (i.e., *Syn Con Group*, *Asyn Inc Group*) did not differ ($p > .05$) from each other (Wilcoxon Mann-Whitney tests). These results show that participants displayed the RHI effects also in terms of ownership questionnaire and that such pattern was the same for participants subsequently assigned to a different stimulation condition in the RHI + SA paradigm.

2.2.2 Sensory Attenuation (SA) paradigm

As regards perceived intensity, a Wilcoxon signed-rank test with kind of stimulation (*Self*, *Other*) resulted to be significant (Z = 3.28, p = .001, d = .57) with lower values in *Self* (mean = 4.11, SE = .24) respect to *Other* (mean = 4.86, SE = .18) condition (see Figure 2c). It is worth noticing that within each stimulation condition, participants subsequently assigned to a different condition in the RHI + SA paradigm (i.e., *Syn Con Group*, *Asyn Inc Group*) did not differ (p > .05) from each other (Wilcoxon Mann-Whitney tests). These results show that participants displayed SA effects and that such pattern was the same for participants subsequently assigned to a different stimulation condition in the RHI + SA paradigm.

2.2.3 Rubber Hand Illusion + Sensory Attenuation (RHI + SA) paradigm

With respect to the perceived intensity, a Wilcoxon Mann-Whitney test with group (*Syn Con Group*, *Asyn Con Group*) resulted to be significant (z = -2.55, p = .009, d = 1.3) with lower intensity in the *Syn Con Group* (mean = 3.33, SE = .32) respect to the *Asyn Con Group* (mean = 4.61, SE = .27) group (see Figure 3a). It is worth noticing that within each group, Friedman Tests comparing intensities with those in the SA paradigm resulted to be significant (p < .002). Post hoc Wilcoxon signed-rank tests showed that in the *Syn Con Group*, the perceived intensity in the RHI + SA paradigm (mean = 3.33, SE = .32) was significantly (p <.025 Bonferroni corrected) lower than the one in the *Other* condition of the SA paradigm (mean = 4.94, SE = .24, d = 1.2) but did not differ (p >.025 Bonferroni corrected) from the intensity in the *Self* condition of this paradigm (mean = 4.18, SE = .41). On the contrary, in the *Asyn Con Group* the perceived intensity in the RHI + SA paradigm (mean = 4.61, SE = .27) did not differ (p >.025 Bonferroni corrected) from the *Other* condition in the SA paradigm (mean = 4.78, SE .29) but was significantly (p <.025 Bonferroni corrected, d = .51) higher than the one in the *Self* condition of the same paradigm (4.04, SE = .27). These results show that participants stimulated synchronously, but not those stimulated asynchronously, displayed SA attenuation effects exactly as it happened in the SA paradigm.

With respect to agency rating, a Friedman Test on questions (*Real*, *Control*) and group (*Syn Con Group*, *Asyn Con Group*) was significant ($\chi 2 = 50.68$, df = 3, $p < .001$). Post hoc Wilcoxon signed-rank tests (i.e., one for each group) showed that in the *Syn Con Group* rating for *Real* questions (mean = .12, SE=.45) was positive and significantly higher ($p < .045$ $d = 1.22$) than rating in *Control* questions (mean = -.87, SE = .41). On the contrary, in the *Asyn Con Group* rating for *Real* questions (mean = -1.7, SE= .39) did not differ from rating for *Control* questions (mean = -1.5, SE = .33 $d = .72$). Post hoc Mann-Whitney t tests (i.e., one for each question) showed that for *Real* questions, rating in the *Syn Con Group* (mean = .12, SE=.45) was significantly higher than rating of control group (mean = -1.7, SE= .39, $d = .91$). On the contrary, for *Control* questions, rating in *Syn Con Group* (mean = -.87, SE = .41) did not differ from rating of the *Asyn Con Group* (mean = -1.5, SE = .33); see Figure 3b. These results show that participants stimulated synchronously, but not those stimulated asynchronously, experience agency in the questionnaire.

2.3 Discussion

Here we showed that within the RHI + SA paradigm, the synchronous, but not the asynchronous group, experienced agency over the movement of the fake finger at both explicit (questionnaire) and implicit (sensory attenuation) level. Specifically, in the former group the movement of the fake embodied finger was subjectively misattributed to the participant's own will and the stimulus intensity delivered by that finger was attenuated (exactly as it happened when the own finger delivered the stimulus in the sensory attenuation paradigm). On the contrary, in the asynchronous group, the movement of the fake embodied finger was not misattributed to the participant's own will and the stimulus intensity delivered by that finger was not attenuated (and, indeed, was treated as when it was the other hand that delivered the stimulus in the sensory attenuation paradigm).

It is worth noticing that, despite the fact that participants, randomly assigned to a different stimulation condition in the RHI + SA paradigm, did not differ in any baselines measures of body ownership (known to have high long-term intra-individual stability (Bekrater-Bodmann, Foell, Diers, & Flor, 2012)), within subjects designs are always preferable. Most importantly, as also pinpointed by anonymous reviewers, comparing synchronous against asynchronous stimulation does not allow to separate the general effects of synchrony from specific effects of ownership. Indeed, this is possible, for instance, with a condition in which synchronous stroking does not lead to ownership. Hence, in order to overcome these two problems, we ran a second experiment in which subjects were tested in all conditions (i.e., a full within-subjects design) and in which we added a condition with synchronous stimulation but incongruent rubber hand position (i.e., 180° rotated with respect the participant's body).

3 Experiment 2

In the second experiment, we hypothesized that in synchronous, respect to both asynchronous and synchronous incongruent conditions within the RHI paradigm, participants should subjectively experience agency (explicit level) over the movement of the fake hand and should attenuate the intensity of the stimulus (implicit level) as when the own hand delivers the stimulus.

3.2 Materials and methods

3.2.1 Participant*s*

Twenty right-handed (Oldfield, 1971) healthy participants (twelve female, age range 18-30 years, educational level range 13-21 years) with no previous history of neurological disease gave their written informed consent, approved by the local bioethical committee, to participate in the study.

3.2.2 Experimental Design

The experiment included the same two parts as the Experiment 1, that is RHI and SA paradigms, as well as the RHI+ SA paradigm. Only participants displaying both the RHI (i.e., drift and questionnaire higher in the synchronous condition) and the SA (stimulus intensity lower in *Self* condition) effects (20 out of 42) participated in the whole study.

3.2.2.1 Rubber Hand Illusion (RHI) paradigm

Setup and procedures were the same as those in Experiment 1, except for the fact that we added another condition where the fake hand was placed also in an incongruent position (180 degrees rotated) with respect to the participant's body (hereinafter *Syn Inc* condition) and, in this condition, participants' and fake fingers were stimulated synchronously (see Figure 4a).

3.2.2.2 Sensory Attenuation (SA) paradigm

Setup and procedures were the same as those in Experiment 1 (see Figure 4b).

3.2.2.3 Rubber Hand Illusion + Sensory Attenuation (RHI+SA) paradigm

Setup and procedures were the same as those in Experiment 1, except for the fact that we added another condition where the fake hand was placed also in an incongruent position (180 degrees rotated) with respect to the participant's body (hereinafter *Syn Inc* condition) and, in this condition, participants' and fake fingers were stimulated synchronously (see Figure 4c).

3.3 Results

As in Experiment 1, pre-proprioceptive judgments were subtracted from post-proprioceptive judgments (i.e., proprioceptive drift, see Tsakiris & Haggard, 2005) and ownership ratings on *Real* and *Control* questions were averaged (RHI paradigm), whereas agency ratings on *Real* and *Control* questions were averaged (RHI + SA paradigm). Analyses were performed by means of Wilcoxon signed-rank test or Friedman Test (at least one data set was not normally distributed), multiple comparisons were Bonferroni corrected and effect sizes were indicated with Cohen's *d*.

3.3.1 Rubber Hand Illusion (RHI) paradigm

As regards proprioceptive drift, a Friedman Test with stimulation condition (*Syn Con*, *Asyn Con, Syn Inc*) resulted to be significant ($\chi 2 = 11.7$, df = 2, $p = .002$). Post hoc Wilcoxon signed-rank tests showed that proprioceptive drift in *Syn Con* condition (mean = 2.42, SE = .48) was significantly higher (Z = 3.06, $p <.025$ with Bonferroni correction, $d = 1.22$) with respect to both *Asyn Con* (mean = -.01, SE = .43) and (Z = 3.25, $p <.025$ with Bonferroni correction, $d = 1.18$) *Syn Inc* (mean = -.11, SE = .48) conditions, whereas *Sync Inc* and *Asyn Inc* did not differ from each other ($p >.025$ with Bonferroni correction); see figure 5a. These results show that participants displayed the classical RHI effects in terms of proprioceptive drift.

As regards ownership rating, a Friedman Test with stimulation condition (*Syn Con*, *Asyn Con, Syn Inc*) and question (*Real*, *Control*) as within-subjects factor resulted to be significant ($\chi 2 = 50.9$, df = 5, n = 20, $p < .001$). Post hoc Wilcoxon signed-rank tests showed that ownership rating given to *Real* questions in *Syn Con* condition (mean = -.08, SE = .47) was significantly higher with respect to all the other ratings, that is *Syn Con Control* (mean -.5, SE= .47; Z = 2.7, $p <.01$ with Bonferroni correction, $d = 0.65$), *Asyn Con Real* (mean = -1.26, SE=.38; Z = 3.62, $p <.01$ with Bonferroni correction, $d = 1.07$), *Asyn Con Control* (mean = -2.31, SE = .23; Z = 3.62, $p <.01$ with Bonferroni correction, $d = 1.73$), *Syn Inc Real* (mean = -2.25, SE = .26; Z = 3.55, $p <.01$ with Bonferroni correction, $d = 1.68$) and *Syn Inc Control* (mean = -2.56, SE = .2; Z = 3.74, $p <.01$ with Bonferroni correction, $d = 1.85$); see Figure 5b. These results show that participants displayed the classical RHI effects also in terms of ownership questionnaire.

3.3.2 Sensory Attenuation (SA) paradigm

As regards perceived intensity, Wilcoxon signed-rank test on stimulation (*Self*, *Other*) as within-subjects factor was performed. Results showed that perceived intensity was significantly (Z = 3.25, $p <.025$ with Bonferroni correction, $d = 1.11$) lower in *Self* (mean = 3.7, SE = .24) respect to

Other (mean = 4.66, SE = .2)) condition (see Figure 5c). These results show that participants displayed SA effect.

3.3.3 Rubber Hand Illusion + Sensory Attenuation (RHI + SA) paradigm

As regards perceived intensity, a Friedman Test with stimulation condition (*Syn Con*, *Asyn Con, Syn Inc*) as within-subjects factor resulted to be significant ($\chi2$ = 15.7, df = 5, p < .001). Post hoc Wilcoxon signed-rank tests showed that the intensity in *Syn Con* (mean = 3.57, SE = .23) was significantly lower (Z = 2.65, *p* <.025 with Bonferroni correction, *d* = 1.68) with respect to both *Asyn Con* (4.39, SE = .16) and (Z = 3.25, *p* <.025 with Bonferroni correction, *d* = .89) and *Syn Inc* (mean = 4.62, SE = .26), whereas *Sync Inc* and *Asyn Inc* did not differ from each other (*p* >.025 with Bonferroni correction); see figure 6a. It is worth noticing that, within each stimulation condition, Friedman Tests comparing intensities with those in the SA paradigm resulted to be significant (*p* = .001). Post hoc Wilcoxon signed-rank tests showed that in *Syn Con* (mean = 3.57, SE = .23), intensity was significantly (*p* <.025 Bonferroni corrected, *d* = 1.2) lower than in *Other* (mean = 4.66, SE = .2) but did not differ (*p* >.025 Bonferroni corrected) from *Self* (mean = 3.7, SE = .24). On the contrary, in *Asyn Con* (4.39, SE = .16), intensity did not differ (*p* >.025 Bonferroni corrected) from *Other* (mean = 4.66, SE = .2) but was significantly (*p* <.025 Bonferroni corrected, *d* = 1.3) higher than the one in the *Self* (mean = 3.7, SE = .24). Similarly, in *Syn Inc* (mean = 4.62, SE = .26), intensity did not differ (*p* >.025 Bonferroni corrected) from *Other* (mean = 4.66, SE = .2) but was significantly (*p* <.025 Bonferroni corrected, *d* = 1.1) higher than the one in the *Self* (mean = 3.7, SE = .24). These results show that participants displayed SA effects when stimulated synchronously (but not asynchronously or synchronously with incongruent rubber hand posture) exactly as it happened in the SA paradigm.

As regards agency ratings, a Friedman Test with condition (*Syn Con*, *Asyn Con, Syn Inc*) and question (*real*, *control*) as within-subjects factor resulted to be significant ($\chi2$ = 15.7, df = 2, n = 20, p < .001). Post hoc Wilcoxon signed-rank tests showed that agency rating given to *Real* questions in the *Syn Con* condition (mean = .38, SE = .47) was significantly higher respect to all the other ratings, that is *Syn Con Control* (mean = -1.64, SE = .34; Z = 3.27, p <.01 with Bonferroni correction, d = 1.08), *Asyn Con Real* (mean = -1.7, SE = .36; Z = 2.73, p <.01 with Bonferroni correction, d = 1.09), *Asyn Con Control* (mean = -2.08, SE = .24; Z = 3.08, p <.01 with Bonferroni correction, d = 1.44), *Syn Inc Real* (mean = -2.25, SE = .25; Z = 3.6, p <.01 with Bonferroni correction, d = 1.53) and *Syn Inc Control* (mean = -2.59, SE = .16; Z = 3.64, p <.01 with Bonferroni correction, d = 1.87) conditions (see figure 6b). These results show that participants displayed an illusory sense of agency when stimulated synchronously but not asynchronously or synchronously with incongruent rubber hand posture

4 Discussion

In the present study, we aimed at examining a debated issue within human sciences, namely which is the specific role of body ownership in the subjective experience of voluntary actions. Indeed, despite it is an obvious consideration that not only motor-related signals but also body-related ones are necessary to give rise to a full and coherent experience of willed actions, whether and how this happens is still highly unclear.

As first, in order to obtain baseline measures of both body ownership and sense of agency, we administered the rubber hand illusion and the sensory attenuation paradigms. As regards the rubber hand illusion, participants experienced feeling of ownership over the fake hand at both implicit (proprioceptive drift) and explicit (questionnaire) levels with synchronous (but not asynchronous) stimulation (Experiment 1), and with congruent but not incongruent position of the fake hand (Experiment 2). These results replicate previous literature (Armel & Ramachandran, 2003; Botvinick & Cohen, 1998; Burin et al., 2015; Costantini & Haggard, 2007; Costantini et al., 2016; Ehrsson et al., 2005; Ehrsson et al., 2004; Longo et al., 2008; Mohan et al., 2012) and confirm that a key component of human body ownership is multisensory integration (Costantini & Haggard, 2007; Holmes & Spence, 2005; Petkova et al., 2011; Tsakiris & Haggard, 2005). In respect to the sensory attenuation paradigm, participants experienced the intensity of self-generated stimuli delivered to their hand as attenuated respect to intensity of other-generated stimuli (Experiment 1 and 2). These data confirm several previous studies (Bays et al., 2005; Blakemore et al., 1998; Stenner et al., 2014; Timm et al., 2014; Voss et al., 2006; Voss et al., 2008) and are in line with the idea that sensory attenuation, by means of enhancing the ability to disentangle self-produced from externally-generated actions, is a key component of our ability to the experience of authorship over voluntary actions (Blakemore et al., 2002).

Secondly, in order to answer the main question (i.e., which is the role of body ownership on the sense of agency), we incorporated the two above-mentioned paradigms within the same setting (RHI + SA paradigm). This paradigm was administered only to participants showing both RHI and SA affects. In other words, the whole sample was composed by participants displaying baseline measures of both body ownership and sense of agency. It is worth noticing that body ownership measures (i.e., drift and questionnaire) were no more recorded in the RHI + SA paradigm. However, since high intra-individual long-term stability of the rubber hand illusion effects is well-known (e.g., (Haans, Kaiser, Bouwhuis, & Ijsselsteijn, 2012)), it is very unlikely to hypothesize a different pattern in a quite short time delay (i.e., the resting phase of about 15 minutes between the first and the second part of each experiment). In this paradigm, we showed that after synchronous, but not asynchronous, stimulation (Experiment 1), and with congruent, but not incongruent, position of the fake hand (Experiment 2), participants experienced also agency over the movement of the fake finger at both explicit (questionnaire) and implicit (sensory attenuation) level. Specifically, in the condition of synchronous stimulation and congruent position of the fake hand, the movement of the fake embodied finger was subjectively misattributed to the participant's own will and the stimulus intensity delivered by that finger was attenuated (exactly as it happened when the own finger delivered the stimulus in the sensory attenuation paradigm). On the contrary, in case of asynchronous stimulation and synchronous stimulation with incongruent position of the fake hand, the movement of the fake embodied finger was not misattributed to the participant's own will and the stimulus intensity delivered by that finger was not attenuated (and, indeed, it was treated as when it was the other hand, which delivered the stimulus in the sensory attenuation paradigm).

Most of the existing literature interested in studying the impact of body ownership on agency typically measured it with respect to actual participant's movements (e.g., Kalckert & Ehrsson, 2012, 2014). This is due to the fact that the subjective experience of being an agent is thought to be rooted almost entirely on the match between predicted and actual action outcomes (Blakemore et al., 2002; Haggard, 2005, 2008; Haggard & Chambon, 2012; Moore, 2016). Among such literature, only a few studies examined body ownership in absence of participants' voluntary movements. For instance, a new form of stroke-induced disorder of body ownership in which hemiplegic patients treat and care someone else's hand as their own hand has been reported recently (Fossataro, Gindri, Mezzanato, Pia, & Garbarini, 2016; Pia, Garbarini, Fossataro, Burin, & Berti, 2016; Pia, Garbarini, Fossataro, Fornia, & Berti, 2013). Crucially, when these patients are requested to execute an action (which they cannot perform due to severe motor impairments) and the alien hand achieves such action, patients misattribute such action to their own will (Garbarini et al., 2015; Garbarini et al., 2013). In other words, if the intended outcomes match the actual outcomes of the action achieved by the embodied hand, an illusory sense of agency over the movements of that hand arises. Similarly, it has been demonstrated that when a life-sized embodied virtual avatar moved synchronously with real body movements, participants falsely attributed to themselves the words uttered by the avatar (Banakou & Slater, 2014). In other words, if participants' motor behavior is synchronized online with the one of the avatar, an illusory agency over the movements achieved by the avatar (only) arises. Additionally, it has been reported that when the embodied avatar walks for a certain period of time while the participant is completely still, an illusory feeling of walking arises (Kokkinara, Kilteni, Blom, & Slater, 2016), demonstrating that, if the embodied avatar achieves a highly automated/rhythmic action, an illusion of agency over its movements can arise.

Despite all of the above-mentioned studies did suggest that body ownership has a role in the emergence of our conscious experience of voluntary actions, they always entailed, in one way or another, efferent signals within their experimental paradigms: actual motor intentions (Garbarini et al., 2015; Garbarini et al., 2013), actual (although task-unrelated) movements (Banakou & Slater, 2014) and primed (Kokkinara et al., 2016) movements (it is worth noting that walking is a highly trained behavior which might trigger in advance an intention to move). Moreover, the only study which excluded any efferent signals (Braun, Thorne, Hildebrandt, & Debener, 2014) reported conflicting findings: some double dissociations and some associations between ownership and agency. Consequently, the available literature does not allow obtaining clear-cut evidence on the role of body ownership *per se* on the subjective awareness of voluntary actions. On the contrary, in our setup, any kind of actual or even possible efferent signal was eliminated. Indeed, participants neither performed nor intended any action and, nonetheless, employing a quick unpredictable (i.e., one-shot) movement achieved by the fake finger, allowed us to prevent even priming an efferent signal. Additionally, we employed both explicit (i.e., questionnaire) and implicit (i.e., sensory suppression) measures. Beyond the fact this can provide an in-depth picture of sense of agency, it is important to emphasize that most of the existing literature shows that a necessary condition in order to observe sensory attenuation is the presence of internal-related signals related to the preparation of a voluntary action (Timm et al., 2014; Voss et al., 2006; Voss et al., 2008). It is worth noting, however, that some studies suggested that these two phenomena might be independent (Dewey & Knoblich, 2014; Hughes et al., 2013; Weller et al., 2017). As mentioned above, most of the existing literature explains the sense of agency within the different levels of motor hierarchy (e.g., (Haggard, 2005, 2008)). However, at present it is not clear whether and to which extent afferent signals also contribute to the emergence of sense of agency (Chambon, Sidarus, & Haggard, 2014). Indeed, it has been demonstrated that sense of agency is modulated by external cues as, for instance, prior beliefs (Desantis, Roussel, & Waszak, 2011) or outcome values (Moretto, Walsh, & Haggard, 2011). Hence, agency might rely on the optimal integrations of different kinds of signals, which are weighted according to the given context and to actual availability (Moore & Fletcher, 2012; Synofzik et al., 2008). Consistently, here we suggest that signals giving rise to body ownership are among those external cues. This idea can be integrated within the present neurocognitive model of human body ownership (Maselli & Slater, 2013; Tsakiris, 2010). Indeed, the model states that body ownership over an external object arises whenever bottom-up incoming signals are congruent in terms of postural, structural and anatomical properties with top-down preexisting internal representations of the body. We suggest that such process would include also movement properties as, for instance, structural constraints, anatomical modifications, postural adjustments and sensory predictions (see (Pia et al., 2016) for a more extended discussion). Interestingly, this seems to be consistent with the fact that during the rubber hand illusion (i.e., when we experience also the disembodiment of our own hand), smaller motor evoked potentials in primary motor cortex are reported (Della Gatta et al., 2016; Schutz-Bosbach, Mancini, Aglioti, & Haggard, 2006), as if representing motor properties of the fake hand would be mirrored in a decrease of motor excitability of the own hand. Summarizing, we suggest that any representation of the body as one's own (even in static conditions), would entail also motor representation of its movements. This, in turn, would allow (if required) to act upon agency attribution in a pure prospective way (Chambon & Haggard, 2012; Wenke, Fleming, & Haggard, 2010), that is, in absence of any representation of the actual action outcomes. Put in simple words, owning the body would lead to the inference "since this is my body part, any action would be intended by me".

To conclude, further studies should provide further behavioral and, most importantly, anatomo-physiological evidence of the role of body ownership in conscious awareness of willed actions. We believe that this would help to clarify whether and how both internal and external inferential processes are integrated within the neurocognitive models of conscious awareness of voluntary action.

Figures Legend

Figure 1. Procedures/setup of Experiment 1. Rubber hand illusion (Figure 1a), sensory attenuation (Figure1b) and rubber hand illusion + sensory attenuation (Figure 1c).

Figure 2. Results (means and SE) of Experiment 1. Rubber hand Illusion (Figure 2a) and sensory attenuation (Figure 2b). * = significant.

Figure 3. Results (means and SE) of Experiment 1. Rubber hand Illusion + sensory attenuation (Figure 3a and 3b). * = significant.

Figure 4. Procedures/setup of Experiment 2. Rubber hand illusion (Figure 4a), sensory attenuation (Figure4b) and rubber hand illusion + sensory attenuation (Figure 4c).

Figure 5. Results (means and SE) of Experiment 2. Rubber hand Illusion (Figure 5a) and sensory attenuation (Figure 5b). * = significant.

Figure 6. Results (means and SE) of Experiment 2. Rubber hand Illusion + sensory attenuation (Figure 6a and 6b). * = significant.

Acknowledgements

This work was supported by a 2014-2016 Torino University Grant (ex 60%) to L.P. and by Talenti della Società Civile 2015 (Fondazione Goria, Fondazione CRT, Fondazione Molo) scholarship to D.B.

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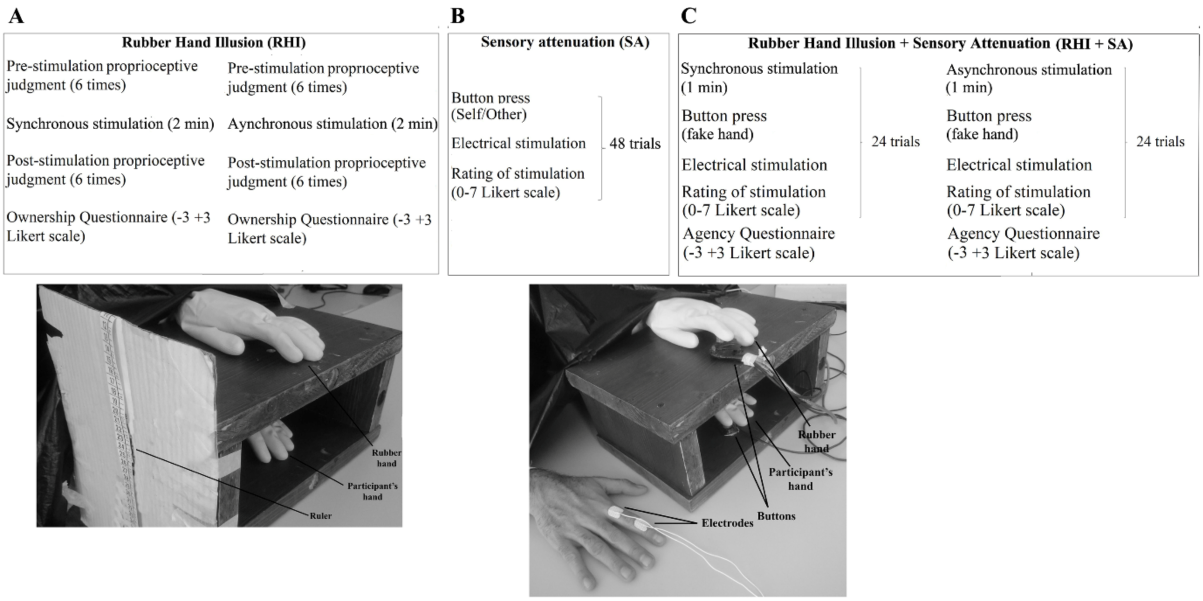
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Post-stimulation proprioceptive judgment (6 times)
Ownership Questionnaire (-3 +3 Likert scale)
Ownership Questionnaire (-3 +3 Likert scale)
B
Sensory attenuation (SA)
Button press (Self/Other)
Electrical stimulation
Rating of stimulation (0-7 Likert scale)
48 trials
C
Rubber Hand Illusion + Sensory Attenuation (RHI + SA)
Synchronous stimulation (1 min)
Button press (fake hand)
Electrical stimulation
Rating of stimulation (0-7 Likert scale)
24 trials
Agency Questionnaire (-3 +3 Likert scale)
Asynchronous stimulation (1 min)
Button press (fake hand)
Electrical stimulation
Rating of stimulation (0-7 Likert scale)
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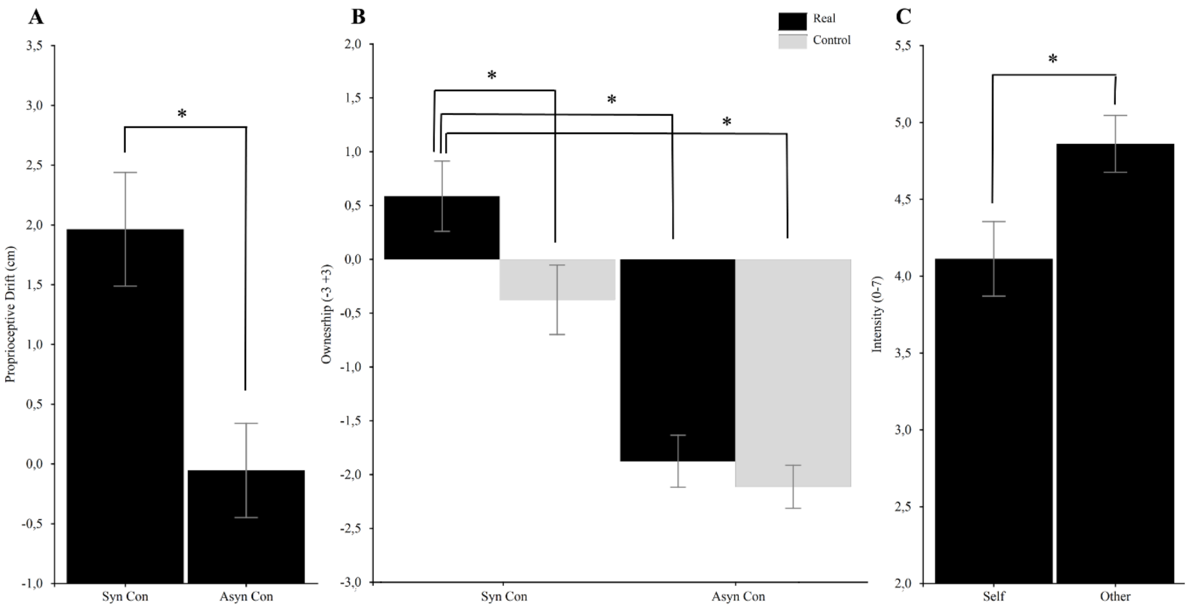
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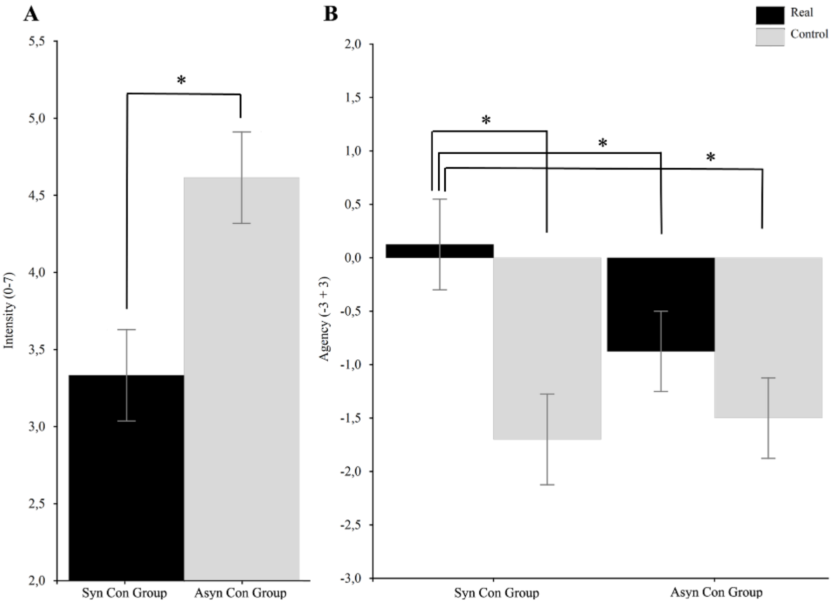
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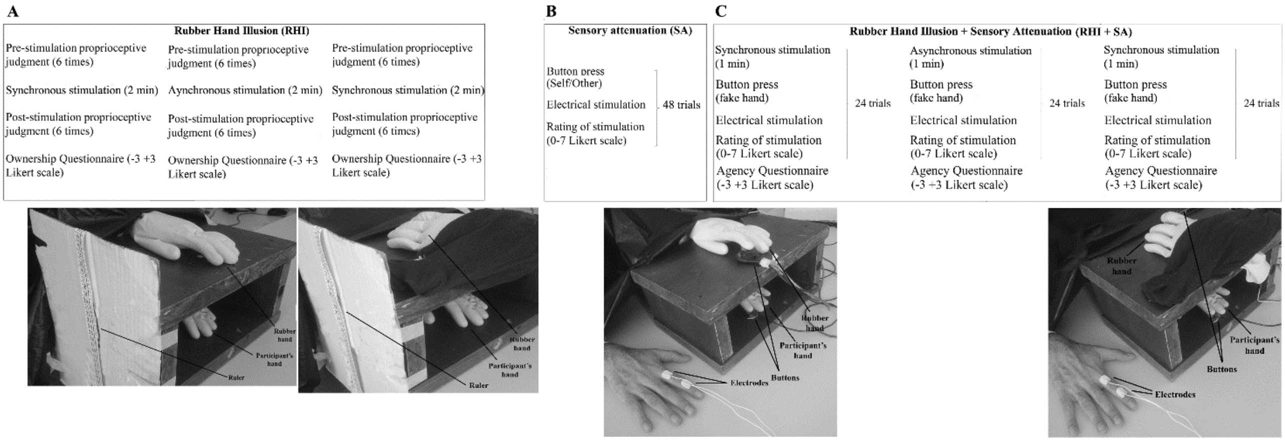
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Aynchronous stimulation (2 min)
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Ownership Questionnaire (-3 +3 Likert scale)
Pre-stimulation proprioceptive judgment (6 times)
Synchronous stimulation (2 min)
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Rating of stimulation (0-7 Likert scale)
48 trials
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Rubber Hand Illusion + Sensory Attenuation (RHI + SA)
Synchronous stimulation (1 min)
Button press (fake hand)
Electrical stimulation
Rating of stimulation (0-7 Likert scale)
24 trials
Agency Questionnaire (-3 +3 Likert scale)
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Synchronous stimulation (1 min)
Button press (fake hand)
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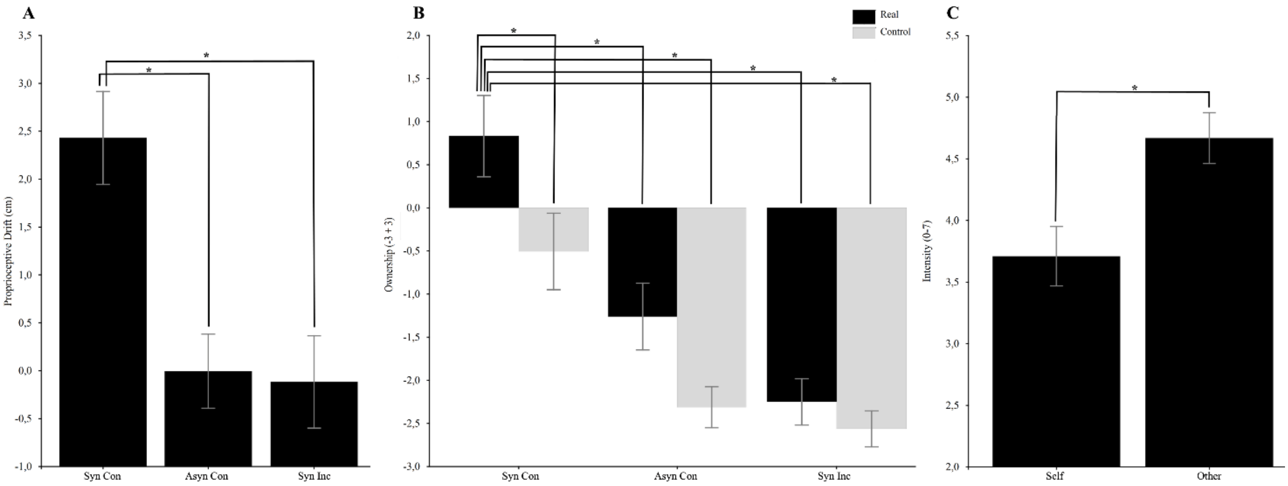
Rubber hand
Participant's hand
Buttons
Electrodes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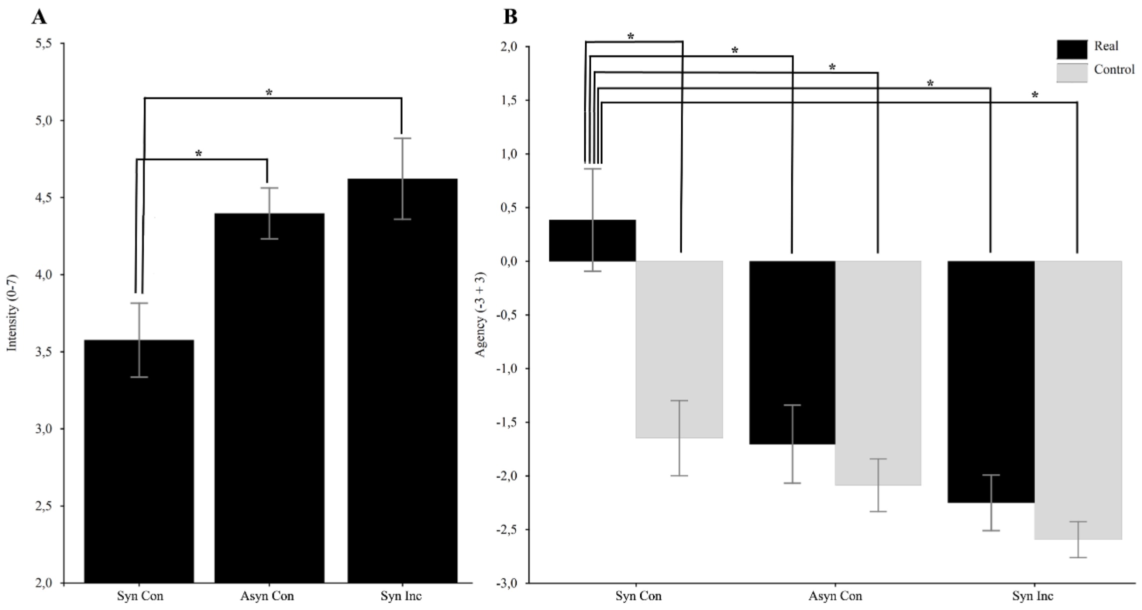
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Syn Inc