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TITOLO DELLA TESI: Owning my body, Moving my body: interaction of body ownership and sense of agency within bodily self-awareness

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General introduction

The fundamental experience of human self-awareness necessarily includes two distinct components: the feeling that one's body belongs to oneself (the so-called body ownership (Gallagher, 2000)) and the feeling that one intends and controls the movements of that body (the so-called sense of agency (Jeannerod, 2009). And while the presence of both these experiences is obvious and often unconscious in everyday life, it remains unclear how they interact and whether they share some common mechanisms that allow constructing the full and coherent self-awareness (Gallagher, 2000; Tsakiris, Schutz-Bosbach, & Gallagher, 2007).

Within cognitive neuroscience, both body ownership and sense of agency can be studied experimentally, for example, in various pathological conditions (e.g., stroke patients with somatoparaphrenia (Gandola et al., 2012; Jenkinson, Haggard, Ferreira, & Fotopoulou, 2013; Vallar & Ronchi, 2009), anosognosia for hemiplegia (Pia et al., 2014; Piedimonte, Garbarini, Pia, Mezzanato, & Berti, 2016), pathological embodiment (Garbarini et al., 2015) and alien limb syndrome (Hassan & Josephs, 2016)). Each of the senses can also be experimentally manipulated in healthy participants, e.g., with the Rubber hand illusion (RHI; Botvinick & Cohen (1998)), in case of body ownership, and Libet's clock paradigm (Haggard, Clark, & Kalogeras, 2002), in case of sense of agency. Their interaction is often studied in some combination of these, or similar, procedures, such as moving RHI (Braun, Thorne, Hildebrandt, & Debener, 2014; Burin, Pyasik, Salatino, & Pia, 2017; Caspar, Cleeremans, & Haggard, 2015; Kalckert & Ehrsson, 2012).

The literature on this topic is abundant, and yet, the existing results are often controversial and do not provide a clear answer to that question. In fact, the existing experimental data support at least two different models – one stating the additive nature of senses of agency and ownership, and the other – their independence (Tsakiris, Longo, & Haggard, 2010). According to the independence model, sense of agency and ownership are entirely different experiences that rely on (Farrer & Frith, 2002; Chlöé Farrer et al., 2008; Lau, Rogers, Haggard, & Passingham, 2004; Schwartz, Assal, Valenza, Seghier, & Vuilleumier, 2005) . In turn, according to the additive model, they are strongly linked to each other; in particular, it has been suggested that agency acts as a strong cue for ownership, hence, agency should include body ownership with the addition of efferent signals related to motor control (Caspar et al., 2015; Garbarini et al., 2015; Garbarini & Pia, 2013; Kalckert & Ehrsson, 2014; Longo & Haggard, 2009; Pia, Garbarini, Fossataro, Burin, & Berti, 2016).

The opposite additive interaction, i.e., the possible contribution of body ownership to the construction of sense of agency, has also been discussed, although in fewer studies (e.g., Kilteni & Ehrsson, 2017; Maselli & Slater, 2013). Interestingly, the independence model is primarily supported by the neuroimaging data, while the additive model is based on behavioral and subjective results. However, there is still no evidence that would strongly prove that only one of these models is correct.

In the first part of my thesis, I will address the problem of the relation between body ownership and sense of agency via the correlation approach. I will first define the concepts of body ownership and sense of agency, as well as various ways of measuring them at both implicit and explicit levels. Then I will present my first study that explores the correlations between implicit and explicit measures of body ownership (measured with the Rubber hand illusion (Botvinick & Cohen, 1998)) and sense of agency (evaluated with the Libet's clock paradigm (Haggard, Clark, & Kalogeras, 2002)) in a large sample of healthy participants (Pyasik, Burin, & Pia, 2018).

In the second part of the thesis, I will discuss how body ownership affects sense of agency. Firstly, I will describe the neural mechanisms of motor intention, which is considered to be a crucial component of the sense of agency, and review the literature that explored the effect of ownership on motor intention and sense of agency. Secondly, I will present two experimental studies on the topic. Having previously shown (Burin et al., 2017) that experimental manipulation of body ownership (RHI) can trigger illusory sense of agency at the behavioral and subjective level, in these two studies, we aim to explore the neural correlates of such illusory agency by means of transcranial magnetic stimulation (TMS; Chapter 2.2, Pyasik et al., 2019) and electroencephalography (EEG; Chapter 2.3).

The third part of the thesis will focus on the opposite interaction between body ownership and sense of agency, i.e., how sense of agency might affect body ownership. I will first describe the two opposing conditions: movement absence and increased amount of movements (motor training). Then I will present an experimental study of body ownership (RHI procedure with static and active conditions) in the natural condition of increased amount of movements, i.e. in a sample of expert pianists (Pyasik, Salatino, & Pia, 2018).

Finally, I will summarize the obtained evidence about the mutual effects of body ownership and sense of agency and discuss these findings in light of the existing theoretical models of body ownership and sense of agency. Specifically, exploring the correlations between implicit and explicit aspects of the two senses would allow clarifying whether they share any common mechanisms at either of the levels (at least, as measured behaviorally and

subjectively). In turn, exploring a possible role of body ownership in the construction of agency, and vice versa, might provide some further insights about their underlying mechanisms. For example, if our results support the additive model, some of the components related to one of the senses might be integrated in the model of the other one.

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Chapter 1. The relation between body ownership and sense of agency: A link at the level of sensory-related signals

1. Introduction

The complex state of self-awareness consists of several crucial components, which include sense of body ownership and sense of agency (Longo, Schüür, Kammers, Tsakiris, & Haggard, 2008). Sense of body ownership refers to experiencing one's body and its parts as belonging to oneself (Gallagher, 2000) and generally requires the integration of afferent information from different modalities. Indeed, when all these signals match (Botvinick, 2004; Ehrsson, 2012; Holmes & Spence, 2005), the conscious experience of the own body arises. On the other hand, sense of agency is the feeling of authorship over one's own actions and of controlling their execution (Jeannerod, 2009). It requires motor intention (Haggard, 2017; Haggard et al., 2002; Moore, 2016) and a subsequent comparison between intended action and its perceived consequences (Sato, 2009; Wegner, Sparrow, & Winerman, 2004). The subjective experience of being the agent of voluntary actions arises when the match between intended and actual outcomes gets closer (Blakemore et al., 2002; Burin et al., 2017a; Desantis et al., 2012; Haggard, 2017; Moore, 2016), that is, when the consequences of our voluntary actions are strongly consistent with the predictions of such effects.

Both body ownership and sense of agency are highly plastic neurocognitive processes, which can be altered within a variety of diseases (e.g., Delorme et al., 2016; Ding et al., 2017; Eshkevari, Rieger, Longo, Haggard, & Treasure, 2012; Finotti & Costantini, 2016; Frith, Blakemore, & Wolpert, 2000; Gandola et al., 2012; Garbarini et al., 2016; Martinaud, Besharati, Jenkinson, & Fotopoulou, 2017; Pia, Garbarini, Burin, Fossataro, & Berti, 2015; Pia, Garbarini, Fossataro, Burin, & Berti, 2016; Piedimonte, Garbarini, Pia, Mezzanato, & Berti, 2016; Vallar & Ronchi, 2009; Wolpe et al., 2014), or by ad-hoc experimental manipulations in healthy participants. In this latter case, the two senses are investigated in their explicit and implicit components. Whereas explicit components use direct subjective judgments about feeling of ownership over the body or being the agent of voluntary action and its consequence, implicit ones rely on indirect judgments about ownership or agency obtained by assessing a correlate of body ownership or a voluntary action (Dewey and Knoblich, 2014; Longo et al., 2008; Moore, 2016). Implicit measures usually involve perceptual judgments – for example, the differences in actual and perceived location of a body part (in case of sense of body ownership) or in actual and subjective timing of actions

and their effects (in case of sense of agency) (Botvinick & Cohen, 1998; Dewey & Knoblich, 2014; Ehrsson, Spence, & Passingham, 2004). In the next sections, we will describe the mechanisms of body ownership and sense of agency and the respective implicit and explicit measures.

1.1 Body ownership

The sense of body ownership is rooted in the afferent signals from the body itself (Tsakiris, Hesse, Boy, Haggard, & Fink, 2007), as well as the coherence between the current incoming sensory signals and a pre-existing internal body representation (Tsakiris & Haggard, 2005). This suggests that the construction of body ownership does not depend solely on the bottom-up processes, i.e., multisensory integration of various afferent signals, but also on the top-down processes, such as the abovementioned pre-existing model of the body. The interaction between these processes modulates the experience of body ownership and provides the distinction between the body and the external world (Tsakiris, 2010). At the neural level, body ownership is supported by the activity of a large network of brain structures, such as premotor areas, the occipito-temporal cortex, the primary/secondary somatosensory areas and the anterior insula (e.g., Henrik Ehrsson et al., 2004; Limanowski, Lutti, & Blankenburg, 2014; Petkova et al., 2011).

As mentioned above, it is possible to manipulate normal body ownership within experimental setups. Possibly the most common experimental paradigm is the rubber hand illusion (RHI) (Botvinick & Cohen, 1998; Costantini & Haggard, 2007; Henrik Ehrsson et al., 2004; Farnè, Pavani, Meneghello, & Ladavas, 2000; Longo, Cardozo, & Haggard, 2008; Tsakiris & Haggard, 2005). During this procedure, a fake hand is placed congruently with the participant's body, while the real hand is hidden from the view. Then, the real and the fake hand are synchronously stroked with paintbrushes, and after about a minute of such synchronous stimulation, the majority of people experience a strong feeling that the fake hand became a part of their own body. This illusory experience of ownership is called embodiment, and it is thought to occur because the initial conflict between the seen touches to the fake hand and the felt touches to the real hand is resolved in favor of vision, which results in the embodiment of the fake hand (Botvinick & Cohen, 1998). The illusory effects are evaluated with two different measures: the first, an implicit behavioral measure called proprioceptive drift, represents the mislocalization of the perceived position of the

participants' hand towards the fake hand (Tsakiris & Haggard, 2005). The second, an explicit measure, is a questionnaire, which reflects the subjective experience of the illusion.

More recently, the RHI paradigm has been adapted for other technologies, resulting in Robot hand illusion (that allows precisely synchronizing participant's movements with the robotic-hand's movements, e.g. (Caspar, De Beir, et al., 2015; Ismail & Shimada, 2016; Romano, Caffa, Hernandez-Arieta, Brugger, & Maravita, 2015; Sato, Kawase, Takano, Spence, & Kansaku, 2018), Virtual hand illusion (that provides higher level of immersiveness, e.g., (Slater, Perez-Marcos, Ehrsson, & Sanchez-Vives, 2009), Full body illusion (expands the RHI to the embodiment of the whole body (e.g., Lenggenhager, Tadi, Metzinger, & Blanke, 2007; Petkova & Ehrsson, 2008) and Virtual body illusion (allows creating a fully immersive experience of owning a virtual body (e.g., Maselli & Slater, 2013). Although these methods provide a more immersive and realistic experience compared to the classic RHI, they are based on similar principles, such as synchronous stimulation and congruence with the own body. Consequently, they typically yield the results similar to the RHI.

1.2 Sense of agency

The sense of agency is thought to be rooted in the association between a voluntary action and its consequence (Haggard, 2017). Therefore, according to many studies, it arises from signals within the motor system, such as motor intentions, planning, premotor processing, efference copy, sensorimotor predictions etc. (Haggard, 2008). In particular, one of the most influential neurocognitive models of agency focuses on signals related to motor control (Blakemore & Frith, 2003), and puts forward the following explanation. It is known that any willed action starts with a desire or a goal state on which the brain must create the motor commands necessary to trigger and drive the action. Nonetheless, a copy of these to the final goal. Besides the motor commands, the system also creates their efferent copy, which is useful to predict the more likely sensory consequences of the given action (Wolpert, Ghahramani, & Jordan, 1995). It is stated that the subsequent comparison between predicted and actual outcomes is the main source of signals for the construction of the sense of agency is rooted (Blakemore et al., 2002; Haggard, 2005; Haggard & Chambon, 2012; Haggard, 2008; Moore, 2016). Specifically, whenever the actual sensory consequences (reafferences) match the predictions made by the motor system, a feeling of being an agent arises. As for the neural mechanisms of the sense of agency, a number of studies (e.g., Farrer et al., 2003;

Farrer & Frith, 2002; Haggard, 2017; Hassan & Josephs, 2016; Tsakiris, Schutz-Bosbach, & Gallagher, 2007) demonstrated that human sense of agency requires the involvement of the fronto-parietal network including the superior/inferior parietal cortex, the supplementary motor area and the anterior cingulate cortex.

Similarly to body ownership, the sense of agency can be measured with both implicit and explicit measures. The two implicit measures are intentional binding and sensory attenuation of action outcomes; both are based on perceptual differences between self- and externally-generated events and their consequences. More specifically, intentional binding refers to the differences in subjectively perceived and actual timing of actions and their sensory consequences: one's own action and its effect are subjectively perceived as being closer to each other than externally-generated actions and their effects (Haggard et al., 2002; Libet, Gleason, Wright, & Pearl, 1983). Sensory attenuation is a reduction of subjective intensity of self-generated sensory stimuli (Blakemore, Wolpert, & Frith, 1998), for example, a sound or a somatosensory stimulus produced by a person's own button press would be perceived as less intense than an externally-generated stimulus of the same volume/intensity. Although both intentional binding and sensory attenuation focus on the perceptual features of actions and their effects, it has been suggested that they might represent different processes (Dewey & Knoblich, 2014) or have different constraints in terms of temporal and action-specific prediction (Desantis et al., 2012; Hughes, Desantis, & Waszak, 2012). In turn, explicit sense of agency measures refer to participants' judgments about the authorship or attribution of an action or effect, which is rated on a Likert scale (Dewey & Carr, 2013; Dewey & Knoblich, 2014; Sato & Yasuda, 2005).

1.3 The relation between body ownership and sense of agency

While both sense of body ownership and sense of agency are essential for the integral feeling of self-awareness (Gallagher, 2000; Tsakiris, Schutz-Bosbach, & Gallagher, 2007), it is still unclear how and to which extent they are related. Indeed, at least two models have been proposed – one stating the additive nature of senses of agency and ownership, and the other – their independence (Tsakiris et al., 2010). According to the independence model, sense of agency and ownership are separate mechanisms (Farrer & Frith, 2002; Farrer et al., 2008; Lau, Rogers, Haggard, & Passingham, 2004; Schwartz, Assal, Valenza, Seghier, & Vuilleumier, 2005), whereas according to the additive model they are strongly linked to each other (Caspar, Cleeremans, & Haggard, 2015; Garbarini et al., 2015; Garbarini & Pia, 2013;

Kalckert & Ehrsson, 2014; Longo & Haggard, 2009; Pia, Garbarini, Fossataro, Burin, & Berti, 2016). Interestingly, an fMRI study by Tsakiris et al. (2010) reported a dissociation between behavioral and neuroimaging results: subjective reports supported the additive model, while the neuroimaging data showed no shared neural activation for sense of ownership and agency (specifically, the sense of body ownership was related to activation of midline cortical structures, and the sense of agency corresponded with the activation of pre-SMA and Brodmann Area 6). Other previous attempts to investigate the possible interactions between sense of body ownership and sense of agency combined measures of body ownership (rubber-, virtual- or robotic hand illusion) with intentional binding (Braun, Thorne, Hildebrandt, & Debener, 2014; Caspar, Cleeremans, et al., 2015), sensory attenuation (Burin et al., 2017b; Kilteni & Ehrsson, 2017) and/or subjective measures of sense of agency (Dummer, Picot-Annand, Neal, & Moore, 2009; Ismail & Shimada, 2016; Kalckert & Ehrsson, 2012, 2014; Ma & Hommel, 2015; Tsakiris et al., 2010). Typically, such studies varied the position of the fake hand (congruent vs incongruent with respect to participant's point of view), agent (self- vs other-generated movements), kind of movement (active vs passive) (Kalckert & Ehrsson, 2012, 2014; Tsakiris et al., 2010) and movement congruency (congruent vs incongruent with respect to participant's movement) (Caspar et al., 2015). Some studies reported double dissociation between sense of body ownership and sense of agency but the pattern varied depending on experimental conditions. Specifically, both ownership and agency were present only in the condition of synchronous or congruent movements (Braun et al., 2014; Caspar et al., 2015; Kalckert & Ehrsson, 2012, 2014; Tsakiris et al., 2010), whereas incongruent position of the fake hand diminished sense of ownership, but not sense of agency (Braun et al., 2014; Kalckert & Ehrsson, 2012). On the contrary, passive movements of the fake hand decreased sense of agency but did not affect sense of ownership (Kalckert & Ehrsson, 2012; Tsakiris et al., 2010). However, other studies suggested that active movements increased sense of ownership, which supports the idea that agency contributes to sense of body ownership (Dummer et al., 2009; Ma & Hommel, 2015). It is worth noting that none of the abovementioned studies addressed sense of agency *per se*, but rather it is studied in direct relation to sense of body ownership over an embodied hand and over an embodied movement. Specifically, Kalckert and Ehrsson (2012) suggest distinguishing between external agency (controlling an object or a tool) and body agency (controlling own arm), and claim that body agency might "contribute an additional component over and above the basic agency experienced when controlling an external object". This is supported by their findings that stronger sense of agency was observed in the

condition of active movements of the congruently-positioned fake hand (i.e., in the condition where sense of body ownership was present), and additionally, subjective ratings of ownership and agency were correlated also only in the active congruent condition.

Considering the just-mentioned somewhat controversial categories of findings, here we aimed at further investigating how, and to which extent, sense of agency and body ownership depend on similar or different mechanisms. In order to evaluate sense of agency independently from experimental modulations of body ownership, and vice versa, we measured the two senses in separate experimental settings and in all their implicit and explicit aspects. Then, we examined the intra-individual correlations among these measures. Specifically, we analyzed the correlations between the indexes of body ownership within the RHI paradigm (i.e., proprioceptive shift and subjective experience of ownership) and the indexes of sense of agency within the Libet's clock paradigm (intentional binding, attenuation of the intensity of action outcomes, subjective experience of authorship). This method prevents defining whether one sense contributes to the experience of other (as in some of the studies described above (Dummer et al., 2009; Ma & Hommel, 2015; Tsakiris et al., 2010)) but the pattern of correlations between several indexes of the two phenomena measured independently allows seeing whether or not the two senses share at least some properties. Significant correlations between any indexes of the two senses would point to the existence of possible common underlying mechanisms. However, due to the controversial nature of previous findings, we did not hypothesize any specific pattern of correlations.

2. Material and methods

2.1 Participants

Eighty-three right-handed (Oldfield, 1971) healthy volunteers (52 females and 31 males, age range – 19-36 years, mean age 23.5, SD 3.51) were recruited in May 2017. They gave written informed consent to participate in the study approved by the Local Bioethical committee of the University of Turin.

Sample size was determined using *a priori* power analysis. The power analysis was conducted in G-POWER using an alpha of .05, a power of .80, and a medium effect size (ρ = .3) for a two-tailed test. The required sample size was determined to be eighty-two.

2.2. Experimental design

Sense of body ownership and sense of agency were measured in separate experimental settings (RHI for ownership and Libet's clock paradigm for agency; see below for details) in a within-subject design. Both paradigms were administered in a single session with their order being counterbalanced between participants.

2.3 Sense of body ownership

Sense of body ownership was assessed with the classical RHI procedure (Botvinick, 2004; Botvinick & Cohen, 1998). In all participants, we administered the RHI only for the right (dominant) hand because the participants used only this hand to perform the sense of agency tasks. Additionally, it is known that the vividness of the RHI does not depend on the hand laterality (Adamo et al., 2012; Smit et al., 2017; Ocklenburg et al., 2011).

2.3.1. Setting

Participants were seated in front of a table on which a wooden box (60*40*20 cm) was placed. The box was divided in two equal parts by a vertical panel with one of them being open to the view from the top. A wooden panel of the same size (60*40 cm) was used to cover the top of the box during the experiment. The box was placed in front of the participants' chest and their right hand was placed in the closed part of the box in a relaxed position with palm facing down and fingers pointing forward. A prosthetic hand, male or female according to participants' gender, was placed in the other part of the box, aligned with participants' shoulder. Participants' shoulder and both fake and real forearms were covered with a cloth. The setting of the RHI procedure is presented in Figure 1.

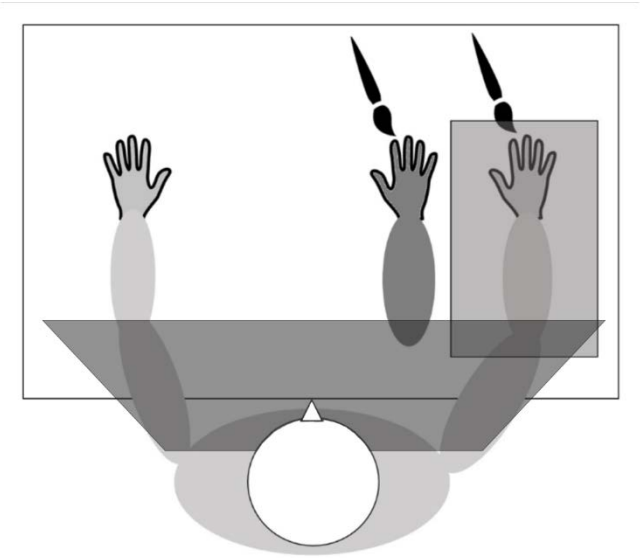


Figure 1. Rubber hand illusion setting (participant's right hand is aligned with the rubber hand and hidden from participant's view; synchronous paintbrush touches are applied to participant's hidden hand and the rubber hand; participant's shoulder and forearm and fake hand's forearm are covered with a cloth).

2.3.2. Procedure

After presenting the instructions, the experimenter covered the top of the box with a panel to hide the rubber hand from the view. Then, the experimenter placed a soft ruler on the top of the box and asked the participants to indicate the position of their index finger by a corresponding number on the ruler for six trials (pre-proprioceptive judgment). In order to avoid numbers repetition, the ruler was randomly repositioned before each trial. The experimenter recorded the difference (in cm) between the actual position of participants' index finger and the number they indicated. After the pre-proprioceptive judgment measurement, the experimenter opened the top of the box and asked the participants to always look at the index finger of the rubber hand during the upcoming stimulation phase. Then, for 2 minutes the experimenter stroke both the participants' index finger and the fake index finger with two brushes, either synchronously (participants' index finger and the fake finger were stroked simultaneously) or asynchronously (the strokes of the participants' finger and the fake finger were temporally incongruent, i.e., visual stimulation preceded the tactile within the interval of 500-1000 ms). Immediately after each type of stimulation, the experimenter covered the top of the box with a panel again, placed the soft ruler on top of it and repeated the proprioceptive judgment measurement for six trials (post-proprioceptive judgment). After each type of stimulation, participants were asked to fill out a questionnaire

consisting of six statements presented in a randomized order (see Table 1). Statements 1-3 (Q1-Q3) addressed various aspects of the subjective feeling of the illusion (feeling of ownership of the rubber hand, perceived location of touches), while questions 4-6 (Q4-Q6) served as control for task compliance and suggestibility effects (Kalckert & Ehrsson, 2014). The participants had to rate how strongly they agree with each statement on a seven-point Likert scale from -3 ("completely disagree") to +3 ("completely agree") with 0 meaning neither agreement, nor disagreement. The order of conditions (synchronous and asynchronous) was counterbalanced between subjects.

Table 1. Statements included in the rubber hand illusion questionnaire for measuring subjective experience of the illusion.

Real statements	Q1. It felt as if I was feeling the stroking touch in the location where I saw the rubber hand touched Q2. It seemed as though the touch I felt was caused by the paintbrush touching the rubber hand Q3. I felt as if the rubber hand were my hand
Control statements	Q4. It felt as if my hand were drifting towards the left/right (towards the rubber hand) Q5. It seemed as if the touch I was feeling came from somewhere between my own hand and the rubber hand Q6. It felt as if my hand was turning 'rubbery'

2.4 Sense of agency

In order to assess sense of agency we used the Libet's method which measures the subjective timing of events (Libet et al., 1983). The task was modified to include different sense of agency measures – implicit (intentional binding and attenuation of auditory outcomes) and explicit – in each trial, so that the sense of agency over the same event would be evaluated in different aspects. Typically, intentional binding paradigm within the Libet's method implies measuring the timing of both an action and its sensory consequence, because intentional binding is the subjectively perceived temporal attraction of the intended action

and its outcome (e.g., (P Haggard et al., 2002)). However, since here the other two measures of agency, which were included in each trial, were related only to the sensory consequence, in the intentional binding paradigm we also focused only on the timing of the consequence (i.e., its anticipation), but not on the timing of the action.

2.4.1. Setting

Participants were seated in front of a computer with their right (dominant) hand placed on a button of a response box. They were asked to put on the earphones and adjust the computer sound volume to a comfortable level; after that, the volume remained the same throughout the experiment. Participants were instructed that the experiment includes two tasks ("Action" and "Observation") with several blocks of trials. In both tasks (conditions), in the middle of the computer screen, participants saw a clock face with the numbers marking the time (0-5-10, etc.) and a rotating handle (each complete handle rotation lasted for 2520 ms). Each condition included four blocks of 20 trials, which were presented in ABBA order, starting from Action condition, twice. Before the beginning of the testing phase, the participants had a short training session for each condition (10 trials each). Stimuli presentation and response logging was conducted with E-prime V1.0 (Psychology Software Tools, Inc). The setting of the Libet's clock paradigm is presented in Figure 2.

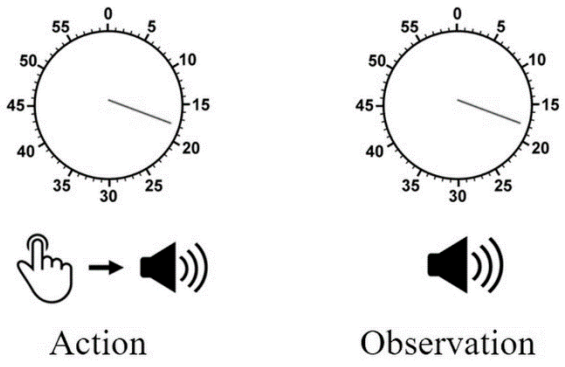


Figure 2. Libet's clock paradigm setting for Action and Observation conditions

2.4.2. Procedure

In the first condition ("Action"), participants were instructed to press the button on the response box with the index finger of their right hand at any moment of their own choice. There were only two limitations – they had to wait at least one complete rotation of the handle before pressing the button and they had to press the button at any moment they choose

without selecting any specific number on the clock beforehand. 250 ms after the button press the participants heard a tone (1000 Hz) through the earphones. After the tone presentation, the clock handle kept rotating for 1000 ms, then the clock disappeared from the screen and the participants had to indicate the timing of the tone by naming a number on the clock (intentional binding measurement). After that, they were asked to judge the tone intensity on a seven-point Likert scale where 0 meant absence of the tone and 7 meant highest intensity possible (sensory attenuation measurement). They were also asked to rate how strongly they agree with the statement: "My button press caused the tone", on the same seven-point scale where 0 meant "completely disagree" and 7 – "completely agree" (explicit sense of agency measurement). In each trial, the intentional binding question was always presented first in order to avoid interference, while the order of the other two questions (sensory attenuation and the explicit question) was randomized for each participant.

In the second condition ("Observation"), the setting was the same as in the first one but the subjects were instructed that they just had to look at the rotating handle and, at some point, they would hear a tone (same as in Action condition). The timing of the tone was based on the data from previously performed Action condition. For each participant, we calculated mean time and standard deviation of the participant's button presses. In Observation condition, the timing of the tone was random within the interval of the calculated mean ± 2SDs. Participants were asked to judge the same three aspects of the sense of agency, namely the timing of the tone, the tone intensity and to answer the same question about the explicit feeling of agency (How strongly do you agree with the statement: "My button press caused the tone"?). In this condition, with the absence of a button press, the explicit question served as a control for participants' compliance with the instructions and the experimental procedure. The order of questions in each trial was balanced the same way as in Action condition.

2.5 Statistical analysis

Statistical analysis was performed in GraphPad Prism 7.0 for Windows (GraphPad Software, La Jolla California USA, www.graphpad.com).

All variables were tested for possible outliers with ROUT method (Motulsky & Brown, 2006) adapted for detecting outliers in a stack of values. Participants that presented the values marked as outliers in at least one of the analyzed variables were excluded from further

analysis (a total of six participants were removed, with the final sample resulting to be seventy-seven).

2.5.1 Sense of body ownership

Preliminary analysis (paired sample t-test) compared pre-stimulation proprioceptive judgments. Then, pre-stimulation values were subtracted from the post stimulation values and referred to as the proprioceptive drift (Tsakiris & Haggard, 2005). Positive values represented a mislocalization of the perceived location of the participants' hand towards the rubber hand. Subjective experience of the illusion was measured as the difference between individual real (Q1-Q3) and control (Q4-Q6) statements in synchronous condition and the difference between individual statements in synchronous and asynchronous conditions. As an overall score, it was represented by the averaged ratings in real (Q1-Q3) and control (Q4-Q5) statements in synchronous and asynchronous condition, which resulted in a scale from -6 to +6 (in accordance with previous studies, e.g. Abdulkarim & Ehrsson (2016), Kalckert & Ehrsson (2014)). Positive values represented the subjective feeling of the illusion.

All values were tested for normality of distribution by Shapiro-Wilk test. Accordingly, the difference in proprioceptive drift between conditions (synchronous vs asynchronous) was evaluated by Wilcoxon signed rank test. The differences in the subjective ratings between conditions (individual statements and real-control statements in synchronous vs asynchronous condition) were examined with Wilcoxon signed rank test.

2.5.2 Sense of agency

As first, we calculated the differences between subjective and objective timing of the tone in each condition, and compared those difference between Action and Observation condition. Intentional binding (anticipation of action outcomes) implies that this difference is greater in Action condition compared to Observation. Sensory attenuation and explicit sense of agency were represented by the differences in the subjective ratings between conditions. Sensory attenuation effect implies that the intensity of the tone in Action condition is rated lower than in Observation condition. Higher ratings of the explicit question represent stronger feeling of agency.

All values were tested for normality of distribution by Shapiro-Wilk test. Accordingly, differences in intentional binding and intensity ratings between Action and Observation conditions were evaluated by paired sample t-test; ratings of the explicit question between conditions were analyzed by Wilcoxon signed rank test.

2.5.3 Correlations

Proprioceptive drift of asynchronous condition was subtracted from proprioceptive drift of synchronous condition in order to obtain a relative synchrony-specific measure of the changed perceived location of the hand. This measure was referred to as proprioceptive shift (Abdulkarim & Ehrsson, 2016). Positive values represented a higher mislocalization of the perceived location of the participants' hand towards the rubber hand in the synchronous condition. Subjective experience of ownership was represented by subjective shift (difference between mean subjective ratings in real and control statements in asynchronous condition subtracted from the same difference in synchronous condition) (Grynberg & Pollatos, 2015). Intentional binding, sensory attenuation and explicit ratings of agency were calculated as the differences between responses in Action and Observation conditions.

Since some variables were not normally distributed (Shapiro-Wilk test, $p < .05$), we calculated Spearman's rank order correlations with significance level set at $p < .05$ between different measures of sense of body ownership (proprioceptive and subjective shift) and sense of agency (intentional binding, sensory attenuation and explicit sense of agency). Bonferroni corrections were conducted for 10 performed comparisons.

3. Results

Firstly, we analyzed the data for each measure of sense of ownership and agency separately in order to establish whether our sample displayed all of the effects, and then calculated the correlations between these measures.

3.1 Sense of body ownership

Pre-stimulation proprioceptive judgments did not differ significantly between conditions ($t = -.14$; $df = 76$; $p = .89$): synchronous condition mean = 2.44 cm, SD = 3.06, asynchronous condition mean = 2.48 cm, SD = 3.65). Proprioceptive drift was significantly higher ($n = 77$; $Z = 4.39$; $p < .0001$; $d = .83$) in synchronous condition (median = 1.25; IQR = 2.40) than in asynchronous (median = .00; IQR = 1.58).

As for the ownership questionnaire, only the ratings of the real statements (Q1-Q3) in synchronous condition were positive (Q1: median = 3.00; IQR = 1.00; Q2: median = 2.00; IQR = 2.00; Q3: median = 1.00; IQR = 2.50), and they were significantly higher than the corresponding control statements in synchronous condition (Q1 vs Q4: $n = 77$; $Z = 6.51$; $p < .0001$; $d = 2.05$; Q2 vs Q5: $n = 77$; $Z = 6.17$; $p < .0001$; $d = 1.67$; Q3 vs Q6: $n = 77$; $Z = 5.37$;

p < .0001; d = .86). Furthermore, the ratings of all statements in synchronous condition were significantly higher than the corresponding ratings in the asynchronous condition (Q1: n = 77; Z = 6.30; p< .0001; d = 2.02; Q2: n = 77; Z = 6.09; p < .0001; d = 2.60; Q3: n = 77; Z = 6.45; p < .0001; d = 2.30; Q4: n = 77; Z = 4.84; p < .0001; d = 1.15; Q5: n = 77; Z = 2.83; p = .005; d = 0.45; Q6: n = 77; Z = 4.86; p < .0001; d = 1.09). Overall subjective ratings (Real-Control) were significantly higher in synchronous condition (n = 77; Z = 6.63; p = < .0001; d = 1.30; synchronous condition − median = 2; IQR = 2.33, asynchronous − median = 0; IQR = 1).

Overall, our sample displayed higher proprioceptive drift and explicit sense of ownership ratings in synchronous condition (see Figure 3).

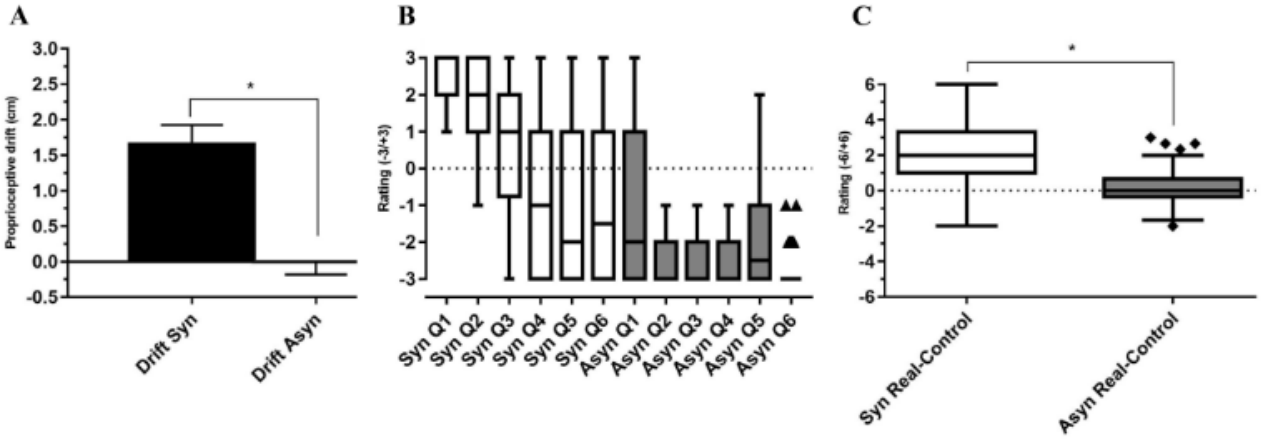


Figure 3. Proprioceptive drift in synchronous and asynchronous conditions (error bars represent standard errors of means; A) and subjective ratings (ratings in individual statements in synchronous and asynchronous conditions (-3/+3; B) and difference between averaged scores in real and control statements in synchronous and asynchronous conditions (-6/+6; C)). For B and C, the box represents the first and the third quartile with the line in the middle of the box representing the median, and the bottom and top whiskers represent the first quartile minus 1.5*IQR and the third quartile plus 1.5*IQR). * p < .05.

3.2 Sense of agency

Intentional binding was significantly stronger (t = -11.78; df = 76; p < .0001; d = -1.18) in Action (mean = -140.96 ms, SD = 109.76) than in Observation (mean = -39.56 ms, SD = 51.51) condition. The tone intensity was rated significantly lower (t = -2.14; df = 76; p = .04; d = -.11) in Action (4.21, SD = 1.20) compared to Observation (mean = 4.34, SD = 1.20) condition. Explicit rating was significantly higher in Action condition (n = 77; Z = 7.22; p <

.0001; d = 8.95; Action condition – median = 6.33; IQR = 1.34; Observation − median = 0; IQR = 0).

These results show that our sample displayed the typical intentional binding and sensory attenuation effect. Additionally, participants subjectively experienced agency of the consequence of their button presses in Action condition (see Figure 4).

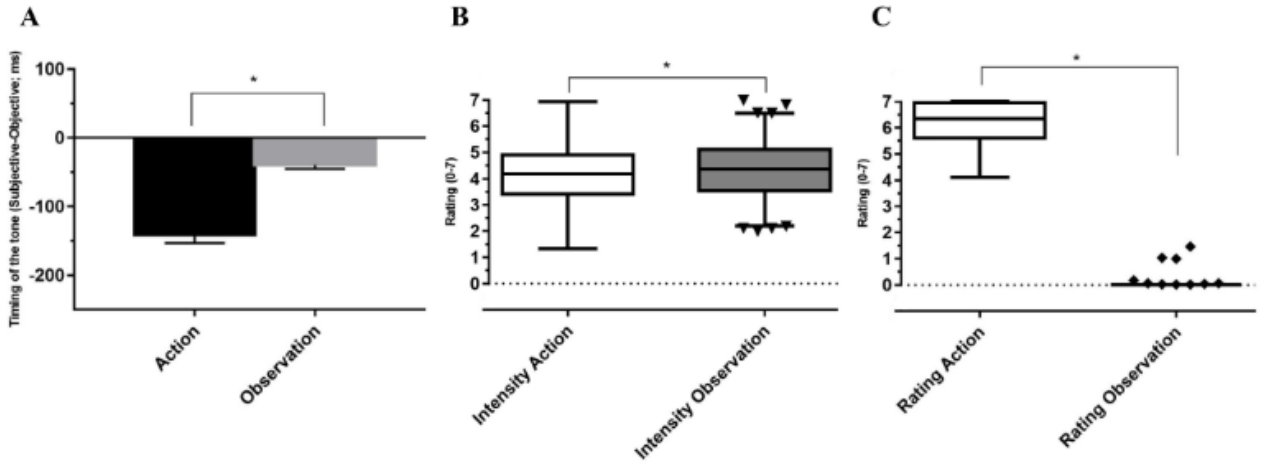


Figure 4. Intentional binding (subjective timing of the tone; error bars represent standard errors of means; A), sensory attenuation (intensity of the tone (0-7); B) and explicit rating of agency (0-7; C) in Action and Observation conditions. For B and C, the box represents the first and the third quartile with the line in the middle of the box representing the median, and the bottom and top whiskers represent the first quartile minus 1.5*IQR and the third quartile plus 1.5*IQR. (* $p < .05$).

3.3 Correlations

As regards the correlations within each sense, body ownership measures (proprioceptive and subjective shift) were not correlated ($\rho = .23$; $n = 77$; $p = .04$ (not significant with Bonferroni correction). With respect to the sense of agency, intentional binding was positively correlated with the explicit sense of agency ($\rho = .36$; $n = 77$; $p = .002$; $d = .77$; see figure 5A) but sensory attenuation did not correlate with either intentional binding ($\rho = -.16$; $n = 77$; $p = .17$), or explicit sense of agency ($\rho = -.07$; $n = 77$; $p = .56$).

As regards the correlations between the two senses, a significant positive correlation was found between proprioceptive shift and sensory attenuation ($\rho = .34$; $n = 77$; $p = .003$, $d = .72$; see Figure 5B). Proprioceptive shift did not correlate either with the other implicit measure of agency ($\rho = .12$; $n = 77$; $p = .29$) or the explicit one ($\rho = .09$; $n = 77$; $p = .45$). Subjective shift did not correlate significantly with any sense of agency measures (intentional

binding: ρ = -.18; n = 77; p = .10; sensory attenuation: ρ = .15; n = 77; p = .20; subjective ratings of agency: ρ = .14; n = 77; p = .26).

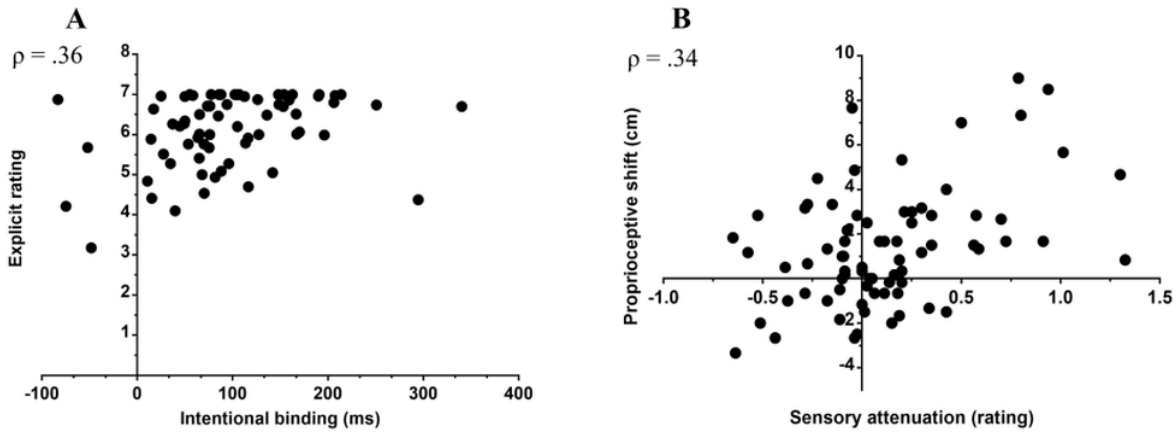


Figure 5. Correlation between intentional binding and explicit rating of agency (A), and between proprioceptive shift and sensory attenuation (B); $p < .005$ with Bonferroni correction.

4. Discussion

In the present study, we aimed at further exploring the relation between sense of body ownership and sense of agency. As first, we administered in our sample both the RHI and the Libet's clock paradigms. Body ownership measures included proprioceptive shift toward the rubber hand and the subjective experience of owning that hand within the RHI paradigm. Sense of agency measures consisted in anticipation of the intended consequences (intentional binding), suppression of the intensity of the intended consequences (sensory attenuation) and subjective experience of authorship within the Libet's clock paradigm. Then, we examined the correlations between implicit and explicit measures of these two senses.

As regards body ownership and sense of agency measures, we found the following results. Firstly, synchronous, but not asynchronous, stimulation within the RHI paradigm induced the feeling of ownership over the rubber hand. This was demonstrated by both higher proprioceptive drift and higher ratings of the subjective statements about the feeling of ownership. These data replicate the typical pattern of the RHI (Armel & Ramachandran, 2003; Botvinick & Cohen, 1998; Burin et al., 2015; Costantini et al., 2016; Costantini & Haggard, 2007; Ehrsson et al., 2005; Ehrsson et al., 2004; Longo et al., 2008; Mohan et al., 2012). Moreover, we revealed no correlations between explicit and implicit measures of the RHI. This corresponds with previous suggestions and findings that explicit and implicit measures of body ownership might reflect different aspects (Caspar et al., 2015; Finotti & Costantini, 2016; Kallai et al., 2015; Rohde et al., 2011). However, other studies do report

such correlations (Botvinick & Cohen, 1998; Longo, Schüür, Kammers, Tsakiris, & Haggard, 2008). These controversial findings might suggest that implicit (perceived location of the body part) and explicit (subjective experience of ownership) aspects of body ownership might rely on (partially) different underlying mechanisms; however, a full and coherent experience of body ownership requires both of those components (Dempsey-Jones & Kritikos, 2014; Longo et al., 2008). Secondly, within the intentional binding paradigm, we found stronger intentional binding in the Action condition (where the participants estimated the timing of an event that was the consequence of their own action) in comparison with the Observation condition. This also corresponds with the typical pattern of the intentional binding – subjective timing of the consequences of one's own actions anticipates its actual timing (Haggard et al., 2002; Libet et al., 1983). Furthermore, sensory attenuation was significant for the same stimuli, i.e. stimuli intensity in Action condition was rated lower than in Observation condition (Blakemore, Frith, & Wolpert, 1999; A. Sato, 2008; Weiss, Herwig, & Schütz-Bosbach, 2011). Subjective ratings of the explicit sense of agency were significantly higher in Action condition than in Observation condition (i.e., the subjects considered the event to be the consequence of their action and experienced agency over it). We found a positive correlation between intentional binding and the explicit sense of agency, i.e., stronger intentional binding was related to stronger feeling of authorship over the consequence of one's action. However, the other implicit measure of agency (sensory attenuation) did not correlate with other agency measures. Such pattern might be explained by some possible differences with respect to the underlying mechanisms of the two implicit measures of agency. Specifically, it has been suggested (Desantis et al., 2012) that intentional binding might rely solely on temporal control over the timing of the event (i.e., the ability to control the onset of the action consequence), rather than on motor prediction. In turn, sensory (in this case, auditory) attenuation is more related to the sensory consequence *per se*, because it is driven by motor identity prediction, i.e., the action consequence is attenuated when its sensory characteristics are predictable (Baess et al., 2008; Hughes et al., 2012). The absence of correlation between the two implicit measures of agency is consistent with previous studies (Dewey & Knoblich, 2014; Hughes et al., 2012; Synofzik et al., 2008). On the other hand, the positive correlation between intentional binding and the explicit measure of agency differs from previous studies that reported no correlations between those agency measures (Dewey & Knoblich, 2014; Ebert & Wegner, 2010; Saito et al., 2015). This might be explained by the fact that in the abovementioned studies, intentional binding and explicit

sense of agency were measured in separate experimental blocks, while in the present study, we measured all aspects of agency over the same event in each single trial.

With respect to the correlation between ownership and agency measures, our results showed that the implicit measure of body ownership (proprioceptive shift) was positively correlated with one of the implicit measures of sense of agency (sensory attenuation). In other words, the greater was the mislocalization increase in the synchronous respect to the asynchronous condition, the greater was the perceived intensity decrease in self-generated, respect to externally-generated, stimuli. On the contrary, the subjective experience of ownership did not correlate with any sense of agency measures. Such specific pattern of relationship between ownership and agency might be explained as follows. Firstly, it is known that proprioceptive shift emerges because visual information is given a higher weighting to influence the final percept. Therefore, the initial conflict between vision of the rubber hand and tactile and proprioceptive sensation of the own hand is resolved by shifting the perceived location of the own hand toward the rubber hand (Botvinick, 2004; Makin, Holmes, & Ehrsson, 2008). However, the mislocalization occurs when conflicting stimuli are congruent in spatiotemporal terms, that is when they are delivered at the same time and to the same body part (Aimola Davies & White, 2013; Burin, Pyasik, Salatino, & Pia, 2017; Tsakiris & Haggard, 2005). It is worth noticing that the illusory effects do not necessary disappear completely with a certain degree of asynchrony, which might be related to individual differences in the sensitivity to asynchrony (Costantini et al., 2016; Ismail & Shimada, 2016; Shimada, Fukuda, & Hiraki, 2009). Put in other words, proprioceptive shift can be thought as an index of spatiotemporal congruency among incoming signals (Botvinick & Cohen, 1998; Rohde et al., 2011). This, in turn, indicates that, within low-level mechanisms of integrating the variety of incoming sensory signals, such feature is necessary in order to give rise to the sense of body ownership. Secondly, sensory attenuation is known to rely on the match between predicted and actual consequences of willed actions (Bays, Flanagan, & Wolpert, 2006; Blakemore et al., 1999). More specifically, when we move voluntarily, our brain processes not only centrally generated motor commands but also visual, tactile and kinesthetic predictions they produce (efference copy) (Haggard et al., 2002; Haggard & Clark, 2003), as well as actual visual, tactile and kinesthetic signals. Hence, the sensory attenuation effect would arise when predicted and actual outcomes match in both spatial and temporal terms. Consistently, it has been demonstrated that sensory attenuation effect decreases with an increased temporal delay between one's own action and its effect (Blakemore et al., 1999; Shanks, 1989; Weller, Schwarz, Kunde, & Pfister, 2017) or with

increased spatial incongruence (Blakemore et al., 1999). These data demonstrate that spatiotemporal proximity between an intended action and its consequence (i.e., causes and effects) is a key prerequisite for the feeling of agency (Blakemore et al., 1999, 2002; Pacherie, 2008). It is necessary to point out that our experimental design implied a delay of 250 ms between the action (button press) and its effect (sound), which was necessary for measuring intentional binding. Whether such delay might affect the sensory attenuation (including attenuation of auditory outcomes) is debated, since some literature showed that sensory attenuation effect disappeared with a delay as short as 200 ms (Bays, Wolpert, & Flanagan, 2005; Blakemore et al., 1999), while other studies showed that it was still present with delays up to 1000 ms (Burin et al., 2018a; Lange, 2011; Van Elk, Salomon, Kannape, & Blanke, 2014). Additionally, in our study, the participants were asked to provide subjective ratings of the stimuli intensity (as in the study by Burin et al. (Burin et al., 2018b) with somatosensory stimulation), while other studies typically used psychophysics measurements, such as force matching task (e.g., Bays et al., 2005; Blakemore et al., 1999; Kilteni & Ehrsson, 2017), which might partially explain the different sensivity of the effect to the increased temporal delay. Considering these controversial findings, we believe that the 250 ms delay in our study might have presented a certain limitation (for example, the sensory attenuation effect in our sample might have been stronger without this delay), but it was not enough to disrupt the effect (which was indeed shown to be significant).

It is worth noticing, that we did not find a similar correlation between proprioceptive shift and intentional binding. We might speculate on a possible interpretation, namely, that intentional binding and sensory attenuation might be rooted on at least some partially different processes (as described above). If sensory attenuation is rooted more on motor prediction of the identity of the sensory consequence, and intentional binding relies more on temporal control over the timing of the event (Desantis et al., 2012; Hughes et al., 2012), then intentional binding might be less related to the sensory consequence *per se* compared to sensory attenuation. Considering that proprioceptive shift relies on the integration of sensory information (as described above), such difference in the mechanisms of the two implicit measures of agency (concerning the role of the sensory feedback) might explain the present pattern of correlations.

As mentioned above, we did not find any correlations between explicit aspects of the two senses. It is worth noting that they both require more than mere spatiotemporal integration among inputs (i.e., tactile and visual stimuli in case of the RHI and predicted/actual outcomes in case of the explicit sense of agency). It is possible to

hypothesize that, at the level of some additional high-level processes, sense of ownership and agency do not share any common features. With respect to body ownership, for instance, it is known that subjective experience of the body as own emerges after different multisensory integration processes and it depends on the activation of different brain areas: while resolving the multisensory conflict is related to the activity of the PPC (Ehrsson et al., 2005; Makin et al., 2008), subjective experience of body ownership is subserved by the activity of the right posterior insula (Tsakiris et al., 2007; Tsakiris et al., 2007). As regards the subjective experience of agency, it is known that further additional mechanisms, such as the will to move and a combination of predictive and inferential processes (Dewey & Knoblich, 2014), are necessary. It is worth noting that some studies did report correlations between explicit ownership and agency measures (Kalckert & Ehrsson, 2012, 2014), however, those correlations were present only in a specific situation when the measures addressed a single phenomenon, i.e., a movement of an embodied fake hand. In this case, it was body agency, rather than external agency, and the former might be rooted on additional mechanisms related to the body (Kalckert & Ehrsson, 2012). When the fake hand was not embodied (i.e., external agency), such correlation between explicit measures of ownership and agency was not present, which corresponds with our results.

However, it is necessary to point out that, in our study, there was hardly any ambiguity about the participants' agency in either Action or Observation condition, which might be an alternative explanation for the lack of correlations with the explicit ownership measure (similar limitation is discussed in the study by Dewey and Knoblich (2014)). Considering that we aimed at testing the sense of agency over the same event in each trial, it seemed impossible to vary the degree of uncertainty of action outcomes without affecting other agency measures in an unpredictable way or overcomplicating the task for the participants.

5. Conclusions

Taken together, our findings seem to suggest that spatiotemporal constraints in integrating sensory-related signals are common to both body ownership and sense of agency. In other words, an optimal integration among sensory-related signals might be a prerequisite for a full and coherent experience of both the body and the movement as being one's own, distinct from those of the others. Indeed, it has been shown that spatial and temporal constraints of body ownership and sense of agency demonstrate that the two senses mostly

overlap in both temporal and spatial terms (as demonstrated by the study of mirror illusion (Tajima, Mizuno, Kume, & Yoshida, 2015)). However, the sense of agency presented a slightly wider range, which corresponds with the findings of Ismail and Shimada (2016) that demonstrated strongest experience of ownership and agency when the temporal discrepancy did not exceed 200 ms, while with a larger temporal asynchrony (290-490 ms) sense of ownership disappeared and sense of agency remained present, although being weaker. Finally, neither ownership, nor agency were observed with temporal discrepancy over 590 ms. However, to our knowledge, only one study so far (Costantini et al., 2016) explored how individual differences in temporal resolution of multisensory integration affect the RHI susceptibility. The authors found that the individuals with wider temporal binding window were more susceptible to the RHI in the condition of asynchronous stimulation. Further studies should address this aspect within the sense of agency, as well as the individual differences in spatial constraints of both processes. In turn, the explicit components of both sense of ownership and agency might rely on additional processes with respect to the implicit ones (as suggested by Holmes, Snijders, & Spence (2006) and Longo et al. (2008) regarding body ownership and by Braun et al. (2014), Dewey & Knoblich (2014), Ebert & Wegner (2010) regarding sense of agency). This corresponds with the idea of partial double dissociation between sense of body ownership and sense of agency (Braun et al., 2014; Caspar et al., 2015; Kalckert & Ehrsson, 2012, 2014).

Despite these findings, whether and how such interplay would contribute to creating a unitary state of bodily self-awareness is still an open question. On this line, one possibility might be to further explore the temporal scales of neural activity, which correspond to the frequency of cortical oscillations (Kiebel et al., 2008), in relation to multisensory integration in senses of ownership and agency. According to Kiebel et al. (2008), the frequency of neural oscillations corresponds to different time scales of environment representation. In line with this hypothesis, Costantini et al. (2016) described different time scales involved in the RHI, with the lowest level representing the comparison between the sensory input, and the highest corresponding to the comparison of the visual form (fake hand) with the existing model of the body. A similar temporal structure of the sense of agency might include the comparison between the efferent copy and the perceived sensory feedback, as the lower level, and the postdictive inference of causality, as the higher level. Therefore, the integration, common for sense of ownership and agency, might correspond with the same lower-level fast fluctuations of neural activity.

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Chapter 2. Shared neurocognitive mechanisms of attenuating self-touch and illusory self-touch: Does body ownership affect sense of agency?

1. Introduction

In the previous chapter, I presented the data on the correlations between the sense of body ownership and the sense of agency, which suggested the existence of possible common mechanisms underlying the two senses. However, correlation does not allow establishing causal relations, and therefore, in the next chapters, I would explore how manipulating one of the senses affects the other one. In particular, this chapter addresses the role of body ownership in the construction of agency at both behavioral and neural level.

It is known that a successful achievement of goal-directed actions is subserved by a perceived causality of the self, i.e., the feeling of intending and controlling that action in order to influence the external events. Such experience, known as 'sense of agency' (Jeannerod, 2003), is assumed to depend on signals coming from the motor system (i.e., efferent signals). Specifically, whenever we intend to achieve a willed action, the brain constructs not only a specific motor program but also predictions of the sensory consequences of the given movement. Then, predicted and actual action outcomes are compared and the result of such comparison is fundamental not only for any online motor adjustment but also for triggering sense of agency. Specifically, the stronger is the match between predicted and actual consequences, the stronger is the experience of being the agent (Haggard & Chambon, 2012; Moore, 2016).

It is worth emphasizing, however, that humans move essentially through their own body (Gallese & Sinigaglia, 2010). Hence, the body and its physical properties are crucial for interacting with the external environment (Georgieff & Jeannerod, 1998). Therefore, a full and coherent experience of being an agent is also rooted on an enduring sense that the moving body belongs to oneself. The feeling of owning one's own body, known as 'body ownership' (Gallagher, 2000), is thought to be rooted on the integration of signals coming from the sensory systems. Specifically, the stronger is the spatiotemporal correspondence among the variety of incoming signals that constantly reach the body (e.g., visual, tactile, proprioceptive, interoceptive, etc.), the higher is the feeling of own (Botvinick, 2004; Ehrsson, 2012; Holmes & Spence, 2005).

Although these considerations clearly pinpoint that body ownership must be integrated within any neurocognitive model of human's experience of willed actions, existing theories are rooted almost entirely on a variety of internal efferent signals: planning, premotor processing, efference copy, sensorimotor predictions and so on (Haggard, 2017; Moore, 2016). Additionally, the very few available attempts to claim that body-related signals per se can trigger sense of agency have provided only behavioral evidence. For instance, it has been reported that the embodiment of someone else's arm due to brain damage (Pia, Garbarini, Fossataro, Burin, & Berti, 2016) entails also sense of agency over its actions (Fossataro, Gindri, Mezzanato, Pia, & Garbarini, 2016; Garbarini et al., 2013; Garbarini, Rabuffetti, Piedimonte, Solito, & Berti, 2015). The same happens with an 'embodied' real-sized fake hand (Burin et al., 2018; Burin, Pyasik, Salatino, & Pia, 2017; Kilteni & Ehrsson, 2017) or a virtual avatar (Banakou & Slater, 2014; Kokkinara, Kilteni, Blom, & Slater, 2016).

In the present chapter, we reasoned that if afferent signals towards the body could induce a sense of agency as the efferent signals towards the external world did, then both these "kinds" of sense of agency would depend, at least in part, on the activation of the same brain structures. In order to test this hypothesis, we performed a TMS and an EEG experiment with similar setup that combined an experimental manipulation of body ownership with different measures of sense of agency. Specifically, we used the RHI paradigm to create a temporary sense of ownership of a fake hand by applying synchronous tactile stimulation to the participant's own (hidden) hand and the fake hand (Botvinick & Cohen, 1998). Then, we used sensory attenuation (SA) paradigm to measure agency. As described in the previous chapter, SA refers to the fact that self-produced stimuli (i.e., stimuli related to the execution of a voluntary action) are perceived as less intense in comparison with externally-generated stimuli (i.e., stimuli completely unrelated one's own action) of the same intensity (Blakemore, Wolpert, & Frith, 1998, 2002; Burin, Battaglini, et al., 2017). SA is thought to arise when the sensory consequence of a voluntary action matches the consequence predicted by an internal forward model, and therefore, is considered to reflect the sense of agency (Blakemore, Frith, & Wolpert, 1999; Borhani, Beck, & Haggard, 2017; Burin, Pyasik, et al., 2017).

In both experiments, we combined the RHI and the SA paradigms in order to measure the SA of the stimuli produced by an embodied fake hand, and compared it with the SA of the self-generated stimuli and stimuli produced by a non-embodied fake hand (the condition that represented externally-generated stimuli). Then, in the TMS experiment we attempted to disrupt the SA of the stimuli generated by one's own movements and embodied fake hand's

movements using single-pulse TMS over a brain area known to sub-serve the intention-programming system (i.e., the Supplementary Motor Area (SMA) (Carlsen, Eagles, & MacKinnon, 2015; Cunnington, Windischberger, Deecke, & Moser, 2002). We predicted that feeling of ownership of the fake hand would trigger the attenuation of sensory consequences of its movements that would be comparable to attenuation of self-generated sensory stimuli, and that TMS over the SMA would similarly disrupt the SA in both conditions. Secondly, in the EEG experiment, we used a similar setup combined with EEG recording, and compared somatosensory evoked potentials (SEPs) and subjective intensity ratings of self-generated somatosensory stimuli, other-generated stimuli and stimuli generated by an embodied fake hand. We predicted to observe a reduced subjective intensity paired with reduced amplitudes of N140 and P200 SEPs components for both self-generated and embodied hand-generated stimuli. In the next sections of this chapter, I will describe those two experiments in detail.

2. Single-pulse TMS study

2.1 Methods

2.1.1 Participants

Sixteen right-handed (Oldfield, 1971) healthy participants (fourteen females, age range 20-37 years) with no previous history of neurological disease, gave written informed consent to participate in the study approved by the Bioethical Committee of the University of Turin. The study was carried out in accordance with relevant guidelines and regulations for the protection of human participants. All participants were screened against inclusion/exclusion criteria for a safety use of TMS (Rossi, Hallett, Rossini, Pascual-Leone, & Safety of TMS Consensus Group, 2009).

2.1.2 Procedure

The experiment consisted of two parts in a within-subject design.

Firstly, we obtained baseline measures of sense of body ownership using the RHI paradigm, and sense of agency using the SA paradigm.

Secondly, since we also aimed at measuring sense of agency over the movements of an embodied fake hand, we merged the RHI and SA paradigms in a single setup (hereinafter RHI+SA). It included the SA measurement and, in addition, the measurement of subjective ownership of the fake hand as well as subjective agency over its movements (by means of ad

hoc questionnaires). For the RHI+SA paradigm, participants were required to have both baseline effects (i.e. RHI and SA). The initial testing included 47 participants; 34 participants (81%) had the RHI effect and 27 participants (64%) had the SA effect. 20 participants displayed both effects, and therefore, were selected for the second part of the experiment (4 dropped out before the second part).

Furthermore, in the SA and RHI+SA paradigms, we used single-pulse TMS to disrupt the activity of the SMA, and examined how it affected the attenuation of somatosensory stimuli produced by either one's own movement or by the movement of the embodied fake hand.

As a control condition for the TMS, in a different group of ten participants, we administered the SA paradigm with the TMS applied over the vertex, a control site that should not be expected to induce any specific effects (Heinen et al., 2011; Ricci et al., 2012) (see Control experiment).

2.1.3 Rubber Hand Illusion (RHI) paradigm

The baseline measure of body ownership was obtained in the RHI procedure with the vertical setting (Kalckert & Ehrsson, 2012, 2014).

Participants sat in front of a wooden box (40 cm x 30 cm x 20 cm) positioned on a table top. A life-sized model left hand (i.e., a plastic glove filled with flour) was placed on the upper shelf of the box, and the participant's left hand, wearing an identical plastic glove, was placed on the lower shelf of the box. The hands were aligned vertically (20 cm apart) and positioned congruently with respect to the participant's shoulder. The space between participant's shoulder and the fake wrist was covered by a cloth, which also covered participant's real hand, creating the impression that the fake hand was the participant's outstretched hand.

Firstly, participants, being blindfolded, were asked to indicate the perceived position of their left index finger by pointing their right index finger toward a vertical cardboard attached to the right side of the box (for six trials). The position marked on the ruler that was glued to the cardboard was averaged for six trials and referred to as pre-stimulation proprioceptive judgment. Then, the participants were instructed to always maintain their gaze on the index finger of the fake hand and remain still, while a trained experimenter delivered touches of a paintbrush to both participant's and fake-hand's index finger for two minutes. There were two experimental conditions that varied according to the type of stimulation: the touches were either synchronous or asynchronous (i.e. the touches to the fake and the real

hand were temporally asynchronous within a random interval of approximately 500-1000 ms). Immediately after the stimulation phase, the participants were again blindfolded and asked to indicate the perceived position of their left index finger on the same cardboard (six trials, the average was referred to as post-stimulation proprioceptive judgment).

At the end of each condition, participants were asked to rate their agreement with six statements about their experience of body ownership on a scale from -3 (representing complete disagreement) to +3 (complete agreement). The questionnaire included three real statements that described the actual illusory experience and three control statements (see Appendix 1); they were selected from a previous study (Botvinick & Cohen, 1998) and administered in randomized order.

The order of stimulation conditions (synchronous, asynchronous) was counterbalanced between participants.

2.1.4 Sensory attenuation (SA) paradigm

In order to obtain the baseline measure of SA, we compared the subjective judgments of the intensity of somatosensory electrical stimuli, which were delivered to the participant's right hand either by the participant's own button press (executed with their left hand) or by a button press performed by a non-embodied fake hand. Single-pulse TMS over the SMA was used to interfere with the sensory attenuation effect.

Setup and procedure are summarized in Fig. 6A and 6B. Here, the participants sat in front of the wooden box (same as in the RHI paradigm), with the fake hand placed on the upper shelf of the box and the participant's hand placed on the lower shelf. Additionally, they were facing a computer screen, while the TMS coil was placed on the scalp over their SMA.

TMS pulses were administered through a MagstimRapid2 stimulator (Magstim, Whitlan, Dyfed, Wales, UK) connected to a 70-mm figure-of-eight coil positioned over the Supplementary Motor Area–proper (SMA). The SMA was localized at 3.3 cm anterior to Cz, according to the 10-20% system (Arai et al., 2011). Before the experimental sessions, the coil was positioned over the left motor hotspot to determine the individual resting motor threshold (rMT), that was determined as the lowest stimulus intensity that induced at least three visible muscle twitches out of six consecutive TMS pulses (Rossi et al., 2009). Mean rMT was 56.9 (SD=7.40) (ranging from 42% to 69%) of maximum stimulator intensity.

During the experimental session, the stimulation intensity was set at 100% of the rMT, as in the previous study by Haggard & Whitford (2004). Within the experimental blocks, some trials contained "effective" TMS pulses, while others included "ineffective"

TMS pulses (see details below). During the effective TMS trials, the coil center was placed over the SMA. In the ineffective TMS trials, the coil was positioned perpendicularly to the scalp over the SMA. Such position of the coil allows obtaining an ineffective stimulation while producing cutaneous and acoustic sensation similar to the effective TMS.

Two buttons were connected to an electrical stimulator (Digitimer DS7A); one was placed under the fake hand's index finger, and the other one - under participant's left index finger. The stimulator delivered electrical stimuli (2.5 subjective threshold + 4 mA with 300V voltage) to the lateral digital nerve of the right hand by means of 5-mm-diameter classical bipolar Ag/AgCl surface electrodes. The stimulation intensity was chosen according to the results of a preliminary experiment that tested the effect of different intensities (Burin, Battaglini, et al., 2017).

The participants were instructed to maintain their gaze on a grey fixation cross on the computer screen for the inter-trial interval (which varied between 9 and 12 s) and wait for instructions. Then, the fixation cross was replaced with written instructions (presented for 3 s) to either press a button upon the subsequent cue ("When you see the red cross on the screen, press the button as fast as possible", i.e., *Self* condition; see Fig. 6B), or to look down at the index finger of the fake hand as it pressed the button ("Look at the index finger of the fake hand", i.e. *Other* condition; see Fig. 6B). In the latter condition, the movement of the fake hand was executed by a computer-controlled servomotor that was installed inside the fake hand at the base of the index finger. In half of the trials of *Self* condition, a single TMS pulse was delivered over the SMA (100% of rMT) 10 ms before the cue to move (i.e., *Self+TMS* condition; see Fig. 6A). The timing of the TMS pulse was chosen according to a previous study (Haggard & Whitford, 2004). In order to control for unspecific effects of TMS, single TMS pulses were also included in the remaining half of the trials in *Self* condition and in the *Other* condition (where it was delivered 10 ms before the onset of fake-hand's movement), but in these cases, the TMS pulses were ineffective (i.e., the coil was positioned perpendicularly to the scalp over the SMA). In each trial, the button press produced the somatosensory electrical stimulus to the participant's right index finger, and the participants were required to rate the perceived intensity of the stimulus on a 0-7 Likert scale (0 indicating absence of stimulation, 7 – highest intensity).

The conditions were administered in a single block with randomized order of trials; each condition included twenty trials and four catch trials (i.e. without electrical stimulation), i.e. seventy-two trials in total. The position of the electrodes along the later digital nerve was changed every 7-10 trials.

2.1.5 Rubber hand illusion + Sensory attenuation (RHI+SA) paradigm

Here, the RHI and SA paradigms were combined in order to measure sensory attenuation of the stimuli produced by an embodied fake hand, the subjective feeling of ownership of the fake hand and agency over its movements. As in the SA paradigm, we used single-pulse TMS to interfere with the SMA activity.

Setup and procedure are summarized in Fig. 6C and 6D. The RHI setting was the same as in the SA condition (however, here participants were not looking at the computer screen), with the TMS coil placed over the SMA.

The participants were asked to always maintain their gaze on the index finger of the fake hand. Then, in each trial, the experimenter synchronously stroked participant's and fake-hand's index finger with paintbrushes (as in the RHI paradigm) for one minute. Immediately after that, the fake-hand's index finger moved to press the button that delivered a somatosensory electrical stimulus to the participant's right index finger. Then, the participants were asked to rate the intensity of the electrical stimulus on the 0-7 Likert scale (the physical intensity of the stimuli was the same as in the SA paradigm). In each trial, a TMS pulse was delivered over the SMA 10 ms before the onset of the fake-hand's movement. Its intensity was set at 100% of the rMT, and the TMS pulses were either effective (*Embodiment+TMS* condition; Fig. 6C), or ineffective (*Embodiment* condition; Fig. 6C), which was achieved with the same procedure as in the SA paradigm.

Each condition included twenty trials and two catch trials, with both conditions being presented in a single block with randomized order of trials (total of forty-two trials). The position of the electrodes along the later digital nerve was changed every 7-10 trials.

Furthermore, each condition included a questionnaire on the subjective experience of agency. It was administered after one of the trials of *Embodiment* condition and one of the trials of *Embodiment+TMS* condition (the trials were selected pseudo-randomly from the middle of the experimental block). The questionnaire included two *real* statements describing actual illusory experience of agency and two *control* statements; they were selected from a previous study (Kalckert & Ehrsson, 2014) and administered in randomized order (see Appendix 1). The participants had to rate their agreement with these statements on the scale from -3 (complete disagreement) to +3 (complete agreement).

Additionally, to control for the possible effect of TMS on the embodiment of the fake hand that was induced by the synchronous stimulation in each trial, two ownership questionnaires were included as separate trials administered pseudo-randomly around the

middle of the experimental block (see Fig. 6D). In these trials, for one minute, the participants experienced synchronous tactile stimulation with the paintbrushes; immediately after, a TMS pulse was delivered over the SMA, and then the questionnaire was administered. The TMS pulse was either effective (*Embodiment+TMS* condition), or ineffective (*Embodiment* condition). The questionnaire consisted of the same six statements as in the RHI paradigm, and the participants rated their agreement with the statements on the same -3 to +3 scale.

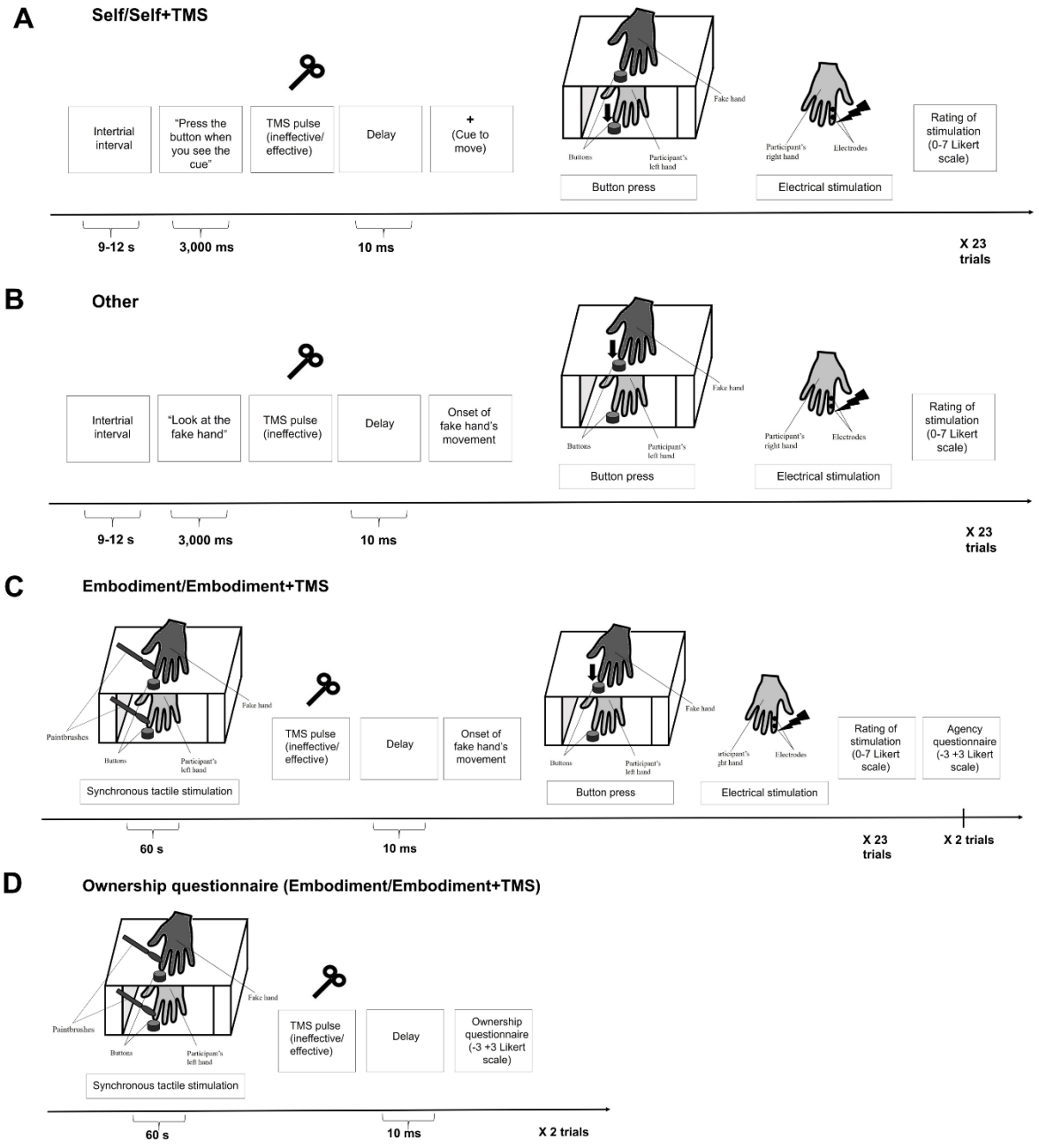


Figure 6. Experimental setup: timeline and procedure of a single trial in SA (**A** and **B**) and RHI+SA (**C** and **D**) paradigms.

2.1.6 Statistical analysis

When at least one variable in each analysis violated the criteria of normal distribution (Shapiro-Wilk test), nonparametric tests were used, and when multiple comparisons were present, the *p* values were Bonferroni corrected. The effect size was estimated using d_z for parametric tests and *r* for nonparametric tests.

In the RHI paradigm, pre-proprioceptive judgments were subtracted from post-proprioceptive judgments and referred to as proprioceptive drift (Tsakiris & Haggard, 2005), and the ratings of *Real* and *Control* statements were averaged. Then, proprioceptive drift and the subjective ratings were compared between *Synchronous* and *Asynchronous* condition.

In the SA paradigm, stimuli intensity ratings were compared between *Self, Other* and *Self+TMS* conditions.

In the RHI+SA paradigm, stimuli intensity ratings were firstly compared between *Embodiment* and baseline SA conditions (*Self* and *Other*), and then, between *Embodiment* and *Embodiment+TMS* conditions. Ratings on *Real* and *Control* statements were averaged both in ownership and in agency questionnaires. Then, they were compared between *Embodiment* and *Embodiment+TMS* conditions.

2.2 Results

2.2.1 Rubber hand illusion (RHI) paradigm

According to a paired sample t test, proprioceptive drift in *Synchronous* condition (mean=3.13±3.00) was significantly higher than in *Asynchronous* condition (mean=-1.30±2.23; t=4.32, df=15, p<.001, d_z=1.64) (see Fig. 7A). As regards the ownership questionnaire, Wilcoxon signed-rank test showed the ratings in *Real* statements in *Synchronous* condition (mean=2.00±1.05) were significantly higher than the ratings in *Real* statements in *Asynchronous* condition (mean=-1.02±1.78; Z=3.21, p=.001, r=.57), and *Control* statements in both *Synchronous* (mean=-.08±1.95; Z=2.56, p=.005, r=.44) and *Asynchronous* (mean=-1.33±1.66; Z=3.21, p=.001, r=.57) conditions. The ratings in *Real* statements in *Asynchronous* condition were not significantly different from the ratings in *Control* statements in both *Synchronous* (Z=1.47, p=.14) and *Asynchronous* (Z=.31, p=.75) conditions (see Fig. 7B). These results show that our sample displayed typical RHI effects in terms of both proprioceptive drift and subjective experience of ownership.

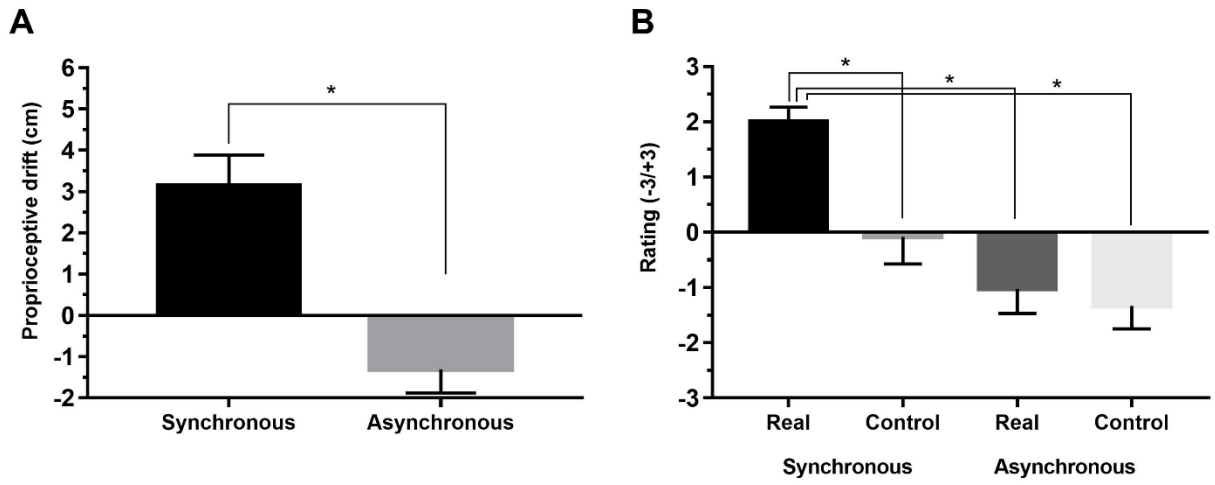


Figure 7. Results of RHI paradigm: **A** – mean proprioceptive drift in *Synchronous* and *Asynchronous* condition; **B** – mean ratings in *Real* and *Control* statements of the ownership questionnaire in *Synchronous* and *Asynchronous* condition). Error bars represent standard error of means; * = significant.

2.2.2 Sensory attenuation (SA) paradigm

Friedman's test for condition (*Self, Other, Self+TMS*) resulted to be significant ($\chi 2$ = 22.32, df=2, n=16, p<.001). Post-hoc Wilcoxon signed-rank test showed that the ratings in *Self* condition (mean=3.87±1.49) were significantly lower than in *Other* (mean=4.60±1.39; Z=3.52, *p*<.001, *r*=-.62) and in *Self+TMS* (mean=4.36±1.55; Z=3.15, *p*=.002, *r*=-.55), while the ratings in *Self+TMS* were not significantly different from *Other* (Z=1.91, *p*=.06); see Fig. 8A. These results show that participants displayed typical SA effect, and TMS over the SMA disrupted this effect.

2.2.3 Rubber hand illusion + Sensory attenuation (RHI+SA) paradigm

With respect to the perceived intensity of the somatosensory electrical stimulus delivered to the participant's right hand, a Friedman's test comparing intensities in the *Embodiment* condition with those in the SA paradigm (*Self, Other*) resulted to be significant ($\chi 2$ = 18.32, df=2, n=16, p<.001). Post hoc Wilcoxon signed-rank tests showed that in *Embodiment* (mean=3.62±1.60) condition, the perceived intensity was significantly lower than in *Other* condition (Z=2.90, *p*=.004, *r*=-.51) and did not differ from *Self* condition

(Z=.93, *p*=.11). This result shows that when the embodied fake hand produces somatosensory electrical stimuli, its intensity is attenuated as the intensity of self-produced stimuli.

Furthermore, when the TMS was applied over the SMA before the onset of the fake-hand's movement, according to a paired sample t test, stimuli intensity ratings were significantly lower in *Embodiment* condition compared to *Embodiment+TMS* condition (mean=3.81±1.63; *t*=-2.49, df=15, *p*=.025, d_z=.12); see Fig. 8B. Therefore, TMS over the SMA decreased sensory attenuation of the stimuli produced by the embodied fake hand, similarly to the condition of self-generated stimulation.

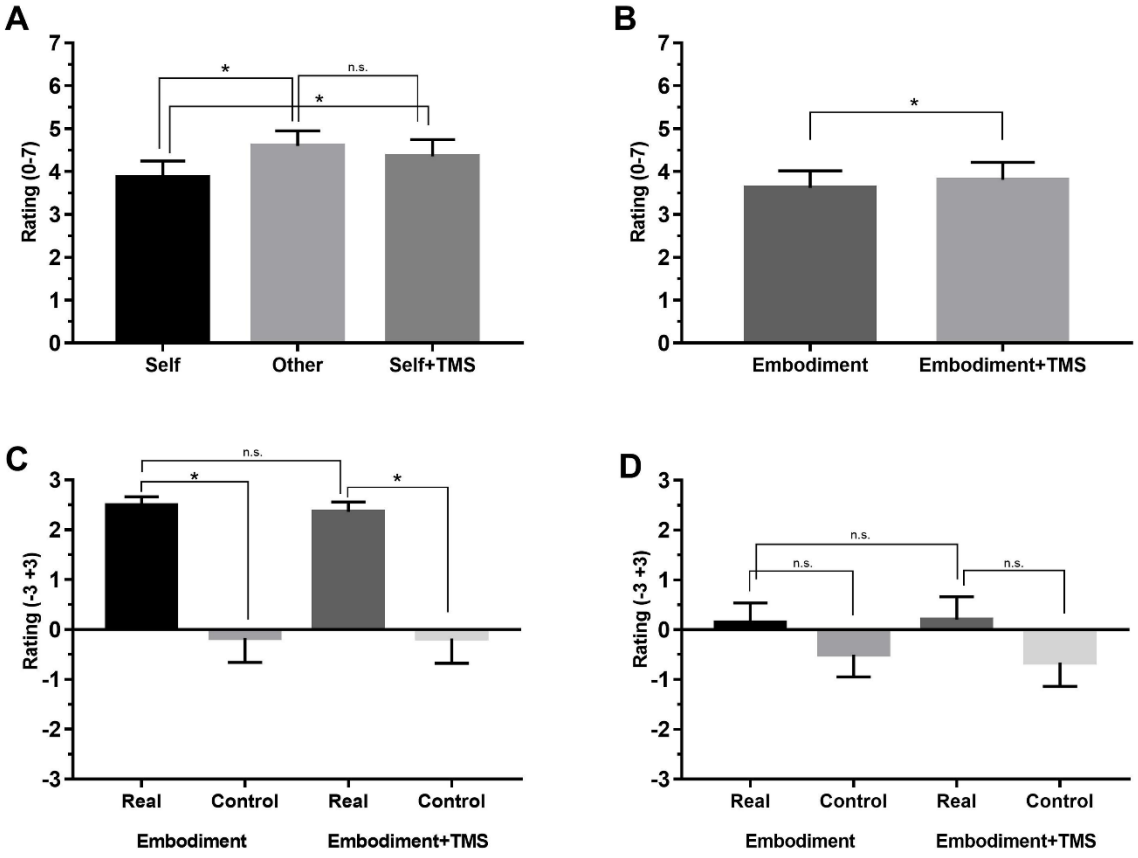


Figure 8. Results of SA and RHI+SA paradigm (mean ratings of the somatosensory electrical stimuli intensity): **A** – mean intensity ratings in *Self*, *Other* and *Self+TMS* conditions; **B** – mean intensity ratings in *Embodiment* condition compared to *Embodiment+TMS* condition; **C** – mean ratings in *Real* and *Control* statements of the ownership questionnaire in *Embodiment* and *Embodiment+TMS* condition; **D** – mean ratings in *Real* and *Control* statements of the agency questionnaire in *Embodiment* and *Embodiment+TMS* condition. Error bars represent standard error of means; * = significant.

As regards subjective agency ratings, 2*2 repeated measures ANOVA for CONDITION (*Embodiment, Embodiment+TMS*)*TYPE (*Real, Control*) as within-subject factors did not show any significant differences (F=.49, p=.50). This shows that participants did not experience strong agency over the movements of the embodied fake hand, although there was a trend for it - the scores in *Real* questions were positive in both conditions (mean=.14±1.6 in *Embodiment* condition, and .20±1.85 in *Embodiment+TMS* condition). Additionally, TMS over the SMA did not affect the subjective sense of agency, since the ratings in *Real* questions were not different between conditions (see Fig. 8D).

As regards subjective ownership ratings, Wilcoxon signed-rank test showed that, in *Embodiment* condition, the ratings in *Real* statements (mean=2.49±.70) were significantly higher than in *Control* statements (mean=-.17±1.96; Z=3.41, p=.001, r=.60). Similarly, in *Embodiment+TMS* condition, the ratings in *Real* statements (mean=2.36±.77) were significantly higher than in *Control* statements (mean=-.18±2.01; Z=3.46, p<.001, r=.61). On contrary, the ratings in *Real* (Z=.12, p=.41) or *Control* (Z=3.41, p=.91) statements were not different between conditions (see Fig. 8C). This shows that the TMS pulse over SMA did not affect embodiment.

2.3 Control experiment

2.3.1 Methods

2.3.1.1 Participants

Ten right-handed (Oldfield, 1971) healthy participants (seven females, age range 20-30 years) with no previous history of neurological disease gave written informed consent to participate in the study approved by the Bioethical Committee of the University of Turin. The study was carried out in accordance with relevant guidelines and regulations for the protection of human participants. All participants were screened against inclusion/exclusion criteria for a safety use of TMS (Rossi et al., 2009).

2.3.1.2 Procedure

The experimental procedure was the same as in the *SA paradigm* in the main experiment. Participants were required to rate the intensity of somatosensory electrical stimuli that were delivered to their right hand either by their own button press (performed by the left hand) or by a button press performed by a non-embodied fake hand. In this case, single-pulse TMS was delivered over the vertex (the location corresponding to the Cz,

according to the 10-20% system), a site that is often chosen as control site, since it should not be expected to induce any specific effects (Heinen et al., 2011; Ricci et al., 2012).

Before the experimental session, the coil was positioned over the left motor hotspot to determine the individual resting motor threshold (rMT), that was determined as the lowest stimulus intensity that induced at least three visible muscle twitches out of six consecutive TMS pulses (Rossi et al., 2009). Mean rMT was 57.4 (SD=4.81) (ranging from 49% to 64%) of maximum stimulator intensity.

During the experimental session, stimulation intensity was set at 100% of the rMT. As in the main experiment, within the experimental block, some trials contained "effective" TMS pulses, while others included "ineffective" TMS pulses. During the effective TMS trials, the coil center was placed over the vertex. In the ineffective TMS trials, the coil was positioned perpendicularly to the scalp over the vertex.

The somatosensory electrical stimuli were delivered through the buttons connected to an electrical stimulator (Digitimer DS7A). The stimulator delivered electrical stimuli (with the same intensity as in the main experiment, i.e., 2.5 subjective threshold + 4 mA with 300V voltage) to the lateral digital nerve of the right hand by means of 5-mm-diameter classical bipolar Ag/AgCl surface electrodes.

As in the *SA paradigm*, the participants were either instructed to press the button with their left index finger following the cue presented on the computer screen (*Self* and *Self+TMS* conditions) or to look at the index finger of the fake hand as it pressed the button (*Other* condition). In half of the trials of *Self* condition, a single TMS pulse was delivered over the vertex (100% of the rMT) 10 ms before the cue to move (i.e., *Self+TMS* condition); the timing of the TMS pulse was the same as in the main experiment. In order to control for the perception of the TMS pulse per se, single TMS pulse was also included in the remaining half of the trials in *Self* condition and in *Other* condition (where it was delivered 10 ms before the onset of fake-hand's movement), but in these cases, the TMS pulses were ineffective. In each trial, the button press caused the electrical stimulus to the participant's right index finger, and the participants were instructed to rate the perceived intensity of the stimulus on a 0-7 Likert scale (0 indicating absence of stimulation, 7 – highest intensity).

The conditions were administered in a single block with randomized order of trials; each condition included twenty trials and four catch trials (i.e. without electrical stimulation), i.e., seventy-two trials in total. The position of the electrodes along the later digital nerve was changed every 7-10 trials.

2.3.1.3 Statistical analysis

The stimuli intensity ratings were compared between *Self*, *Other* and *Self+TMS* conditions. Since at least one variable violated the criteria of normal distribution (Shapiro-Wilk test), we used nonparametric analysis. The p values were Bonferroni corrected for three comparisons (i.e. alpha level for statistical significance was set at p = .017).

2.3.2 Results

The results are presented in Fig. 9. Friedman's test for condition (*Self, Other, Self+TMS*) resulted to be significant ($\chi 2 = 15.85$, df = 2, n = 10, p<.001). Post-hoc Wilcoxon signed-rank test showed that the ratings in *Self* condition (mean=3.40±1.33) were significantly lower than in *Other* (mean=4.38±1.27; Z=2.80, p=.005, r=-.63). Moreover, the ratings in *Self+TMS* (mean=3.31±1.43) were also significantly lower than in *Other* (Z=2.80, p=.005, r=-.63). In turn, there were no significant differences between the ratings in *Self* and *Self+TMS* (Z=.24, p=.81).

These results show that the participants presented typical SA effect, which was not affected by the single-pulse TMS over the vertex.

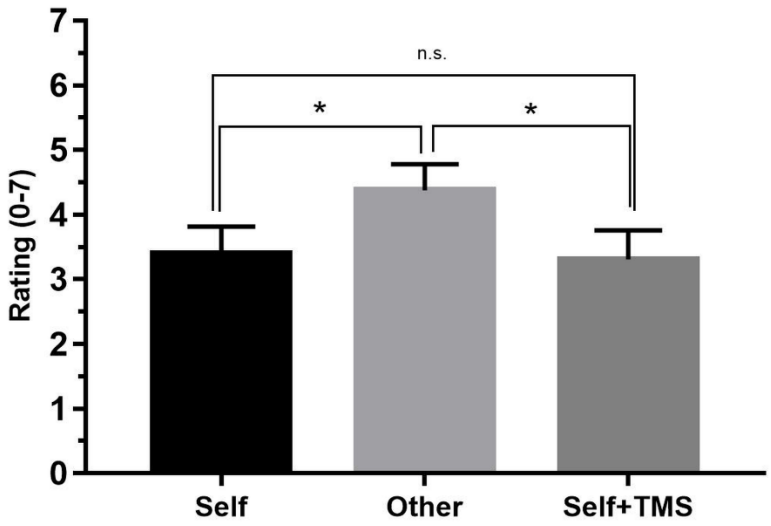


Figure 9. Results of SA paradigm (mean ratings of the somatosensory electrical stimuli intensity): mean intensity ratings in *Self*, *Other* and *Self+TMS* conditions. Error bars represent standard error of means; * = significant.

2.4 Discussion

Here we tested whether body-related signals subserving body ownership act upon agency attribution as motor-related signals are known to do. We compared attenuation of somatosensory stimuli generated by the movements of one's own hand, a fake hand and an embodied fake hand with or without TMS applied over the SMA.

Firstly, in the baseline condition, that is when body ownership (RHI) was evaluated separately from SA, our sample presented the typical RHI effects (i.e., the fake hand was embodied at both implicit and explicit levels when stimulated synchronously with the participant's own hand). These results are in line with previous literature pinpointing the importance of spatio-temporal integration of incoming sensory signals in the experience of the body as one's own (Botvinick & Cohen, 1998; Burin, Garbarini, et al., 2017; Burin, Pyasik, et al., 2017; Costantini & Haggard, 2007; Ehrsson, Holmes, & Passingham, 2005; Holmes & Spence, 2005; Longo, Schüür, Kammers, Tsakiris, & Haggard, 2008; Petkova et al., 2011; Pyasik, Burin, & Pia, 2018; Tsakiris & Haggard, 2005). Furthermore, participants displayed the SA effect (i.e., the perceived intensity of self-produced somatosensory electrical stimuli resulted to be reduced with respect to the intensity of the same stimuli generated externally). These findings are consistent with previous data (Bays, Wolpert, & Flanagan, 2005; Blakemore et al., 1998; Stenner et al., 2014; Timm, SanMiguel, Keil, Schröger, & Schönwiesner, 2014; Voss, Ingram, Haggard, & Wolpert, 2006; Voss, Ingram, Wolpert, & Haggard, 2008) and further support the idea that SA is one of the key components of experiencing authorship over willed actions.

Secondly, when RHI and SA were combined within the same setup and the embodied fake hand delivered the stimuli, attenuation was also present and comparable with the one observed in the SA paradigm. These findings are consistent with those obtained in two previous behavioral studies (Burin et al., 2018; Burin, Pyasik, et al., 2017). In those studies, SA and subjective experience of agency were measured in three different conditions: over the movements of one's own hand, an embodied fake hand (synchronous stimulation) or a non-embodied fake hand (no stimulation/asynchronous stimulation/synchronous stimulation of incongruently located fake hand) when they pressed a button delivering a stimulus to the participant's body. As in the present study, the stimulus intensity was attenuated when one's own or the embodied fake hand delivered the stimulus, but not when the non-embodied fake hand delivered the stimulus (which, in turn, meant that attenuation was not related to the kind of stimulation – synchronous or asynchronous – but rather to ownership *per se*). Considering these findings, here we administered the only condition that evoked ownership, i.e.,

synchronous stimulation with congruent location of the fake hand. However, contrary to those studies, here we did not find that movements of the embodied fake hand were also subjectively attributed to one's own will (explicit sense of agency), although there was a trend for it, i.e., the ratings in the questionnaire statements that described the feeling of agency were positive. Hence, one might argue that, in this case, SA alone might reflect some process unrelated to the sense of agency. Despite the fact that some authors agreed with this view (Dewey & Knoblich, 2014; Hughes, Desantis, & Waszak, 2012; Weller, Schwarz, Kunde, & Pfister, 2017), the majority of the existing literature pinpoints the idea that a necessary condition of SA is the presence of the signals related to the preparation of a voluntary action (Timm et al., 2014; Voss et al., 2006, 2008), even in the absence of a subjective explicit representation of sense of agency (e.g., (Borhani et al., 2017)).

Another key point to emphasize is that our setup allowed eliminating any actual or even potential efferent signals. Indeed, participants neither performed, nor intended any movements, and the use of a quick, one-shot movement achieved by the fake hand's finger prevented even priming such signals. On the contrary, with the exception of Burin and co-workers' study (Burin, Pyasik, et al., 2017), previous above-mentioned experiments entailed, in one way or another, at least some efferent signals: actual (Banakou & Slater, 2014; Kilteni & Ehrsson, 2017)/primed (Kokkinara et al., 2016) movements or actual motor intentions (Garbarini et al., 2013, 2015). This, in turn, suggests that those studies could not provide unequivocal evidence of the role of body ownership *per se* in the experience of voluntary actions. In other words, the present setup, clearly allows to provide evidence of the role of body ownership in the subjective awareness of voluntary actions independently from any kind of motor-related signals.

Thirdly, and most importantly, single-pulse TMS over the SMA disrupted somatosensory attenuation, regardless of whether the stimuli were generated by one's own movement or the movement of the embodied fake hand. Hence, we confirmed that TMS over the SMA eliminates SA of self-generated stimuli (Haggard & Whitford, 2004). Crucially, here we also showed that the SA driven by body-related signals (i.e., the embodiment of the fake hand) was affected similarly to the SA triggered by motor-related signals (i.e., one's own intended movements), which might suggest that they share at least some neural signatures. It is worth noticing that motor intention and motor awareness have been linked also to the activity of the inferior parietal lobule (Desmurget & Sirigu, 2012), rostral cingulate cortex, superior parietal cortex and insular cortex (Cunnington et al., 2002). However, here we aimed at investigating whether agency triggered by body-related afferent

signals and agency triggered by motor-related efferent signals share some neural signatures, rather than pinpointing all of the brain structures subserving SA, or the sense of agency in general. For this reason, we capitalized on the only TMS study related to motor intention/sensory attenuation, which indeed targeted the SMA (Haggard & Whitford, 2004). In order to exclude the possibility that our results might be related to a non-specific stimulation effect, rather than to the interference with the target area, we added a control TMS condition. We recruited a different group of participants and performed the SA baseline paradigm (i.e. the comparison between the subjective intensity of self-generated and other-generated somatosensory stimuli) with the single-pulse TMS over the vertex. The results showed that the TMS over the vertex did not modulate the SA, thus confirming that the results of the main experiment are related to the interference with the brain area involved in motor intention and SA.

2.5 Conclusions

In summary, by demonstrating the same TMS-driven pattern when somatosensory stimuli were generated by one's own action and by the movement of the embodied fake hand, we showed that body-related signals act upon the SA as motor-related signals do and that these two processes depend, at least in part, on the activity of the same neural structures. Interestingly, the sense of body ownership was not affected by the interference with the SMA activity, suggesting that while agency is modulated by ownership, ownership is not affected by changes in agency ("when a hand is mine, it remains mine even when I do not recognize the agency of the action").

Appendix 1

Ownership questionnaire

Q1: I felt as if I was looking at my own hand;

Q2: It seemed that the touches that I felt were caused by the paintbrush that was touching the fake hand;

Q3: I felt as if the fake hand was part of my body;

Q4: It appeared as if my real hand was drifting towards the fake hand;

Q5: It seemed as if the touch I was feeling came from somewhere between my own hand and the fake hand;

Q6: It felt as if my real hand was turning "rubbery".

Agency questionnaire

Q1: The fake hand was obeying my will and I could make it move just like I wanted it;

Q2: I felt as if I could control movements of the fake hand;

Q3: I felt as if the fake hand was controlling my will;

Q4: I felt as if the fake hand was controlling me.

3. EEG study

3.1 Methods

3.1.1 Participants

Fourteen healthy right-handed 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.

Sample size was determined using a priori power analysis. The power analysis was conducted in G-POWER using the alpha level and effect size from a previous behavioral study (Burin, Pyasik, Salatino, & Pia, 2017) and a power of 0.80 for a two-tailed test. The required sample size was determined to be twelve.

3.1.2 Experimental Design

Similarly to the TMS study, this study was composed of two parts. In the first, we obtained baseline measures of both body ownership and sense of agency by administering to the participants the RHI paradigm and the SA paradigm. In the second, we combined together these two paradigms (hereinafter RHI+ SA), where we compared self-produced stimuli with stimuli generated by the embodied fake hand or the non-embodied fake hand (registering both subjective intensity ratings and the SEPs).

3.1.3 Behavioral setup and procedure

The experiment included four conditions (the setup and procedure are summarized in Figure 10). The first two conditions served as SA baseline, i.e. included the comparison between self- and other-generated stimuli (Self and Other conditions, respectively). The other two conditions were related to the SA of the stimuli produced by an embodied fake hand (Synch_Ego and Syn_Allo conditions). Each condition was presented in two consecutive

blocks of 12 trials (10 trials and 2 randomly presented catch trials without electrical stimulation), i.e. total of 24 trials per condition; the structure of a single trial was identical throughout conditions (see Figure 10E). The order of 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 stimulation intensity was set at 2.5 times the subjective threshold + 4mA 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 SA paradigm (Burin, Battaglini, et al., 2017). The stimulation intensity was the same for each participant in all conditions. In order to avoid habituation and control for phantom sensations, the position of the electrodes was changed approximately every 7 trials in each block of each condition.

In Self and Other 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 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 Figure 10A), 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-second interval that was included in order to make the trial structure identical in all conditions (the 50-second interval contained synchronous visuotactile stimulation in Synch_Ego and Synch_Allo 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 the SA in a previous methodological paper (Burin 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 condition (see Figure 10B), the button press was executed by the fake left hand. The fake hand was placed on the button in allocentric position (i.e. rotated 180° with

respect to the participant's body). The participant's left hand was covered (placed under the table). As in the Self condition, each trial was preceded by the 50-second interval, and the participants were asked to maintain their gaze on the fake hand. After the interval, the fake hand pressed the button with its index finger (the movement was executed by a computer-controlled servomotor that was placed at the base of the fake-hand's index finger), which produced the somatosensory electrical stimulus to the participant's right hand after the delay of 1000 ms. The participants rated the stimuli intensity on the 0-7 Likert scale, as in the Self condition.

In Synch_Ego and Synch_Allo conditions, a vertical RHI setting (as in Kalckert & Ehrsson, 2012, 2014) was introduced. A wooden box (40 x 30 x 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 Synch_Ego condition (see Figure 10C), the fake hand was placed in the egocentric position with respect to participant's body, and it 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. The 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 fake-hand's index finger by the strokes of paintbrushes performed by the co-experimenter (the strokes were administered synchronously at approximately 1 Hz frequency); the stimulation phase lasted 50 s. Immediately after, the fake hand pressed the button with its index finger, 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 Synch_Allo condition (see Figure 10D), the setup was the same as in the Synch_Ego 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 was the same as in Synch_Ego 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 (a real statement; “It felt as if I were 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 & Ehrsson (2014) and adapted to be appropriate for all experimental conditions. 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 full 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 kΩ. 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).

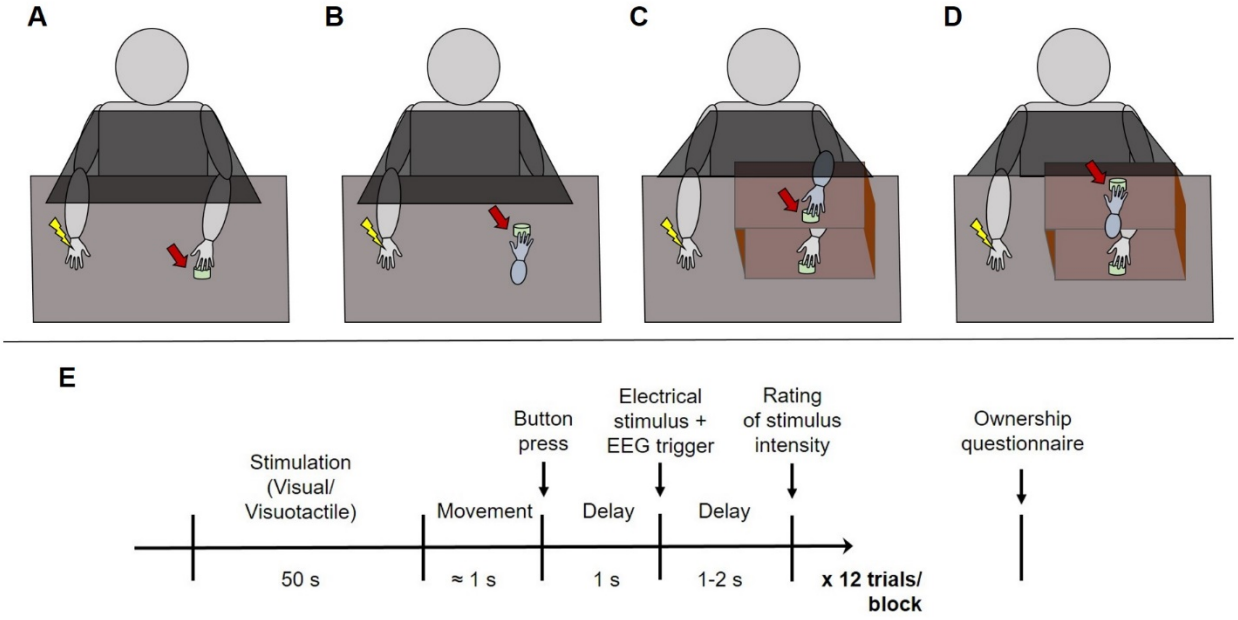


Figure 10. Experimental setup and procedure. **A** – *Self* condition; **B** – *Other* condition; **C** – *Synch_Ego* condition; **D** – *Synch_Allo* condition; **E** – timeline of a single trial.

3.1.4 Statistical analysis

Behavioral data

Firstly, all subjective ratings (both in SA procedure and ownership questionnaire) were transformed into z scores for each subject.

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 ηp2 or Pearson's correlation coefficient r (for nonparametric tests).

Intensity ratings of somatosensory electrical stimuli were compared between the four conditions (Self, Other, Synch_Ego and Synch_Allo) using a 2x2 repeated-measures ANOVA with Stimulation (Presence, Absence) and Perspective (Egocentric, Allocentric) as within-subject factors.

In the ownership questionnaire, Wilcoxon signed-rank test was used to compare the ratings in real statement with the ratings in control statement within each condition, and the ratings in real 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 preprocessing and statistical analyses

SEPs were pre-processed and analyzed using Letswave v.6 (http://www.nocions.org/letswave/, (Mouraux & 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 (ICA – 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, Synch_Ego and Synch_Allo).

To explore the presence of SA across conditions, we performed one point-by-point, repeated-measures, 2x2 ANOVA on SEPs, with two within-subject factors: Stimulation (Presence, Absence) and Perspective (Egocentric, Allocentric). Point-by-point analyses represent a statistical approach common in EEG studies (Harris et al. 2018; Novembre et al. 2018), directed to highlight significantly different ERP time windows among different experimental conditions, without any a-priori assumption. One statistical comparison for each time point composing a waveform is performed. In order to correct for multiple comparison, cluster-based permutation testing approach (1000 random permutations) is employed to each point-by-point analysis (Maris & Oostenveld, 2007).

3.2 Results

3.2.1 Behavioral results

Intensity ratings

The ANOVA on the stimuli intensity ratings showed a significant main effect of Perspective [F(1,13) = 31.84262; p = .000080; ηp2 = .999], with higher ratings for Allocentric (mean ± SE = .26±.06) compared to Egocentric (mean ± SE = -.31±.06) perspective. Neither the Stimulation x Perspective interaction [F(1,13) = .006034; p = .906744; ηp2 = .051], nor the Stimulation factor [F(1,13) = .200284; p = .419586; ηp2 = .121] were significant: the ratings were comparable between Absent Stimulation x Egocentric Perspective (mean ± SE = -.38±.11), Absent Stimulation x Allocentric Perspective (mean ± SE = .21±.14), Present Stimulation x Egocentric Perspective (mean ± SE = -.24±.09), Present Stimulation x Allocentric Perspective (mean ± SE = .31±.15), as well as between Absent (mean ± SE = -.09±.07) and Present (mean ± SE = .03±.08) stimulation (see Figure 11).

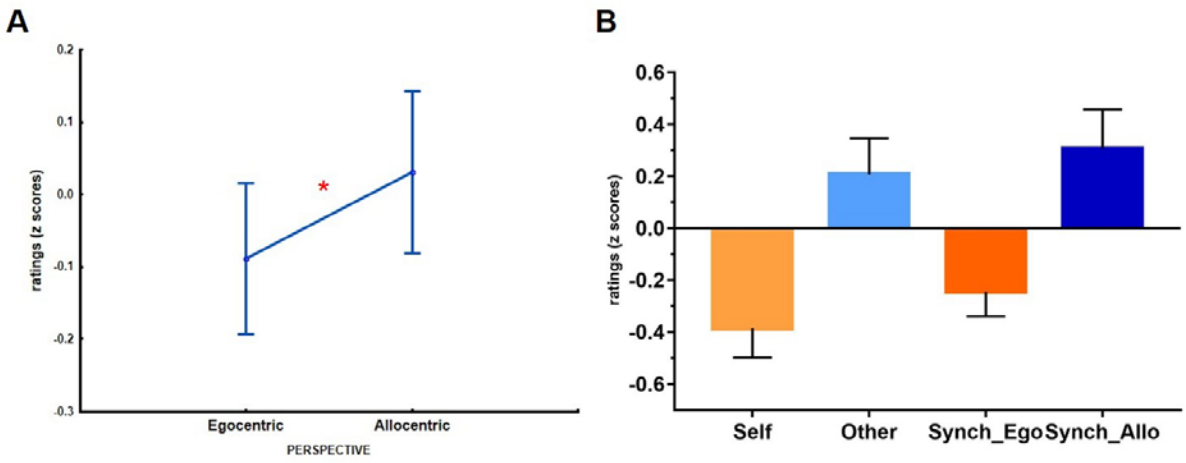


Figure 11. Ratings of somatosensory stimuli intensity: A – results of ANOVA for Perspective (Egocentric, Allocentric); B – ratings in the four experimental conditions (z scores). Error bars represent standard errors of means; * - significant differences.

Ownership questionnaire

Wilcoxon signed-rank test showed that the ratings in the real statement were significantly higher than in the control statement in Self (n = 14; Z = 3.30; p < .001; r = .62; Real: mean ± SD = 1.96±.68; Control: mean ± SD = -.65±.21) and Synch_Ego (n = 14; Z =

3.17; p = .002; r = .61; Real: mean ± SD = 1.36±.40; Control: mean ± SD = .05±.75) conditions, but not in Other (n = 14; Z = 1.07; p = .29; Real: mean ± SD = -.67±.20; Control: mean ± SD = -.51±.50) and Synch_Allo (n = 14; Z = 1.68; p = .09; Real: mean ± SD = .13±.80; Control: mean ± SD = -.30±.48) conditions.

The comparison of the ratings in the real statement between conditions showed that the ratings in Self condition were significantly higher than in Other (n = 14; Z = 3.30; p < .001; r = .60) and Synch_Allo (n = 14; Z = 3.23; p = .001; r = .59) conditions, but not different from Synch_Ego (n = 14; Z = 2.41; p = .016 (not significant with Bonferroni correction)) condition. Similarly, the ratings in Synch_Ego conditions were significantly higher than in Other (n = 14; Z = 3.30; p < .001; r = .60) and Synch_Allo (n = 14; Z = 3.11; p = .002; r = .58). Finally, the ratings in Other and Synch_Allo conditions were not significantly different (n = 14; Z = 2.52; p = .011 (not significant with Bonferroni correction)). See Figure 12.

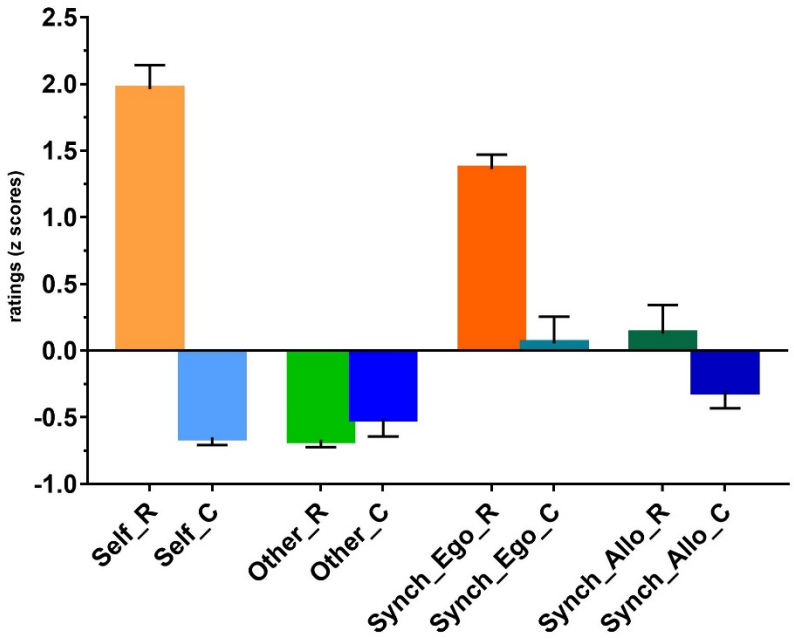


Figure 12. Ratings in real and control statements of the ownership questionnaire in the four experimental conditions (z scores). Error bars represent standard errors of means.

3.2.2 Electrophysiological results

The 2x2 point-by-point ANOVA revealed a main effect of Perspective over frontal, central and parietal channels, with overall larger amplitude in response to allocentrinc as compare to egocentric condition. At Cz, Perspective was a significant source of variance within two different time intervals: 84-166 ms ($F_{1,15}=33.01$, $p<0.001$), coinciding with the latency of the N140 wave; 194-281 ms ($F_{1,15}=25.10$, $p<0.001$), coinciding with the latency

of the P200 wave. Crucially, we did not find a significant effect of Stimulation, nor any significant interaction Perspective x Stimulation (see Figure 13).

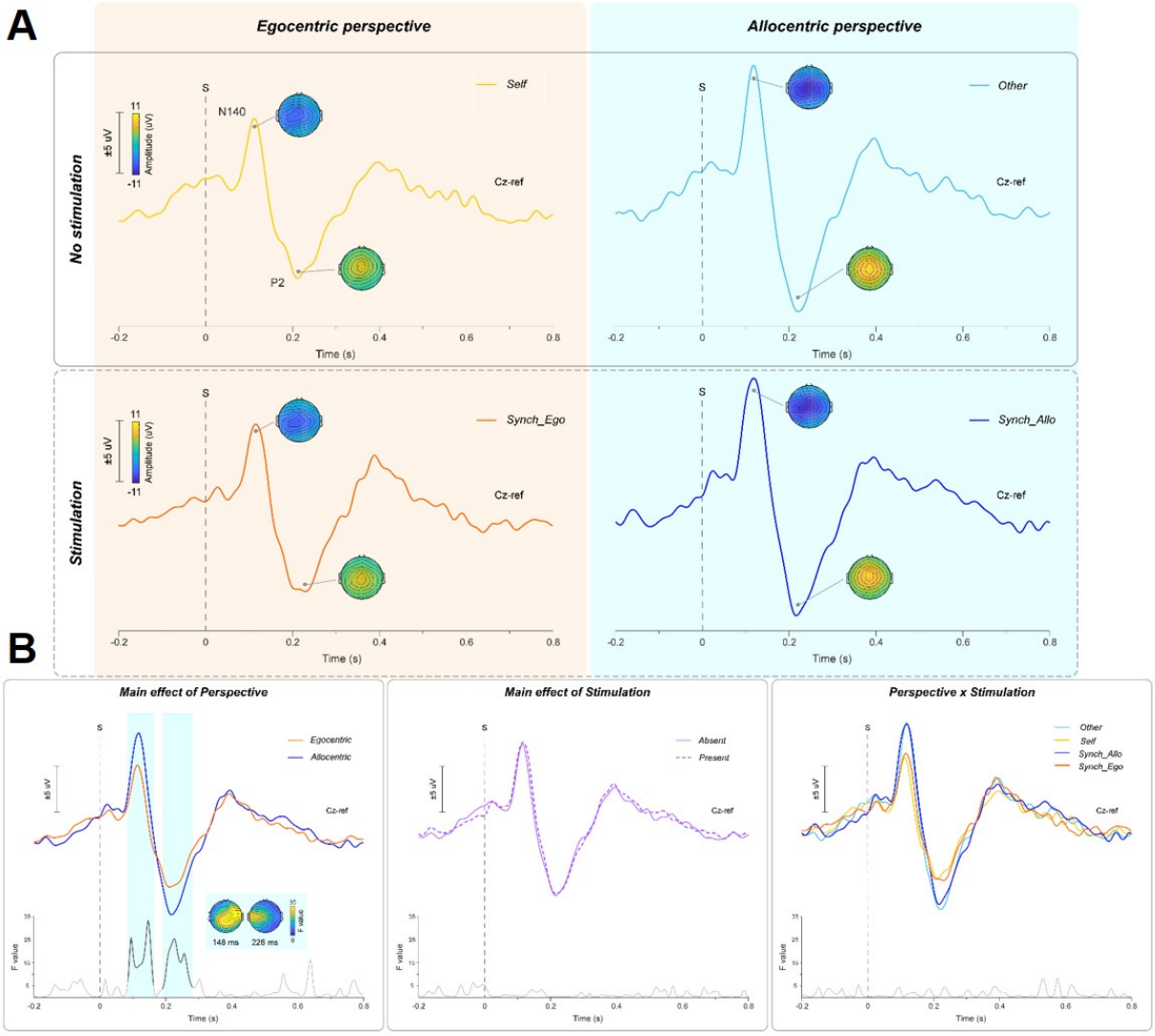


Figure 13. Somatosensory evoked potentials: **A.** SEPs group-averaged waveforms and scalp maps for Cz in the four experimental conditions; **B.** Point-by-point ANOVA results for Perspective (left panel), Stimulation (middle panel) and Perspective x Stimulation (right panel).

3.3 Discussion

In the present study, we further explored the neurophysiological mechanisms of SA triggered by body-related signals in comparison with SA triggered by motor-related signals. In particular, we recorded and compared subjective intensity ratings and SEPs for somatosensory electrical stimuli that were triggered by the participant, by a non-embodied fake hand or by an embodied fake hand.

In a sample of participants that had both baseline effects, i.e., embodiment of the fake hand in the RHI (Botvinick & Cohen, 1998) and attenuation of self-produced stimuli in the

SA paradigm (Blakemore, Wolpert, & Frith, 1998), we showed comparable attenuation of self-produced stimuli and stimuli generated by the embodied fake hand (in terms of the subjective intensity ratings). This result replicated our previous findings (Burin et al., 2018; Burin, Pyasik, et al., 2017; Pyasik, Salatino, et al., 2019) and confirmed again that SA could be driven by body-related signals alone.

As for the EEG results, firstly, we found the reduction of N140 and P2 SEPs components for self-produced stimuli in comparison with the externally-generated ones, which corresponded with the subjective ratings. Such SEPs attenuation corresponds with the previous EEG studies on attenuation of auditory stimuli (Bass, Jacobsen, & Schroger, 2008; Horváth, 2013b, 2013a; Martikainen, Kaneko, & Hari, 2005; SanMiguel, Todd, & Schröger, 2013; Timm, SanMiguel, Keil, Schröger, & Schönwiesner, 2014; Timm, SanMiguel, Saupe, & Schröger, 2013). Those 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. Therefore, the reduction of N1-P2 complex has been linked to predictive processes, such as the match between predicted and actual sensory outcome within the comparator model. To our knowledge, our study was the first to describe SEPs for somatosensory stimuli, so here we showed, for the first time, a similar reduction of N140 and P2 SEPs components. It is possible to hypothesize that N140 and P2 components of the SEPs are functionally similar to N1 and P2 components of the AEPs.

Secondly, we found 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 corresponded with the behavioral data. Crucially, when the fake hand performed the movement to produce the stimuli, participant did not move, or even intended to move. Therefore, in this condition, the SA was triggered by body-related signals without any motor intention or prediction, and yet, it had a neurophysiological response typical for intention-driven SA. Considering that, as described above, the reduced SEPs amplitudes during SA are explained through the predictive processes, it might be possible to suggest that the feeling of ownership of the fake hand also entails the feeling of ownership and agency over its potential movements. Indeed, it might be possible that, after the fake hand is embodied, its movements are retrospectively attributed to the participant's own will, which activates the same neural processes as the real intended actions (as also suggested by Banakou & Slater, 2014; Burin, Pyasik, et al., 2017; Pyasik, Salatino, et al., 2019), for review see Pyasik, Furlanetto, & Pia, 2019).

3.4 Conclusions

To summarize, we showed that the SA triggered by body ownership and the SA triggered by motor intention had similar neurophysiological correlates (in form of the reduction of N140 and P2 SEPs components). This further confirms that body ownership and body-related signals contribute to the construction of the sense of agency, to the extent of triggering motor intention and prediction (possibly, in a retrospective way).

4. General conclusions

Taken together, the results of the TMS and the EEG experiment, firstly, further confirm that the sense of agency can be triggered by body-related signals alone. Secondly and most importantly, our data suggest that such ownership-driven agency has similar neural signatures as the agency driven by motor-related signals. Interfering with the SMA activity using single-pulse TMS similarly disrupted the SA of self-produced stimuli and stimuli produced by an embodied fake hand. Moreover, the EEG showed comparable attenuation of SEPs amplitudes in those two conditions. This suggests that ownership-driven SA and motor-related SA might rely on the activity of the same brain structures (at least in part) and have a similar neurophysiological signature.

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Chapter 3. Do movements contribute to sense of body ownership? Rubber hand illusion in expert pianists

1. Introduction

Having shown in the previous chapter that body ownership has a role in constructing the sense of agency, in the present chapter I will explore the opposite relation, i.e., the possible role of sense of agency and motor-related signals for the sense of body ownership.

As described in the previous chapters, body ownership is defined as the conscious experience that one's body belongs to oneself (Gallagher, 2000). Such omnipresent perceptual status stands at the root of human nature, since each human being senses what it is like to have the body and what are its boundaries with respect to the environment (James, 1890).

There is a large consensus on the fact that body ownership is strongly rooted in both bottom-up and top-down signals. With respect to the former source, it emerges whenever incoming afferent sensory information (e.g., visual, tactile, proprioceptive, interoceptive, etc.) that continuously reaches our own body is integrated in both spatial and temporal terms (Kilteni, Maselli, Kording, & Slater, 2015; Pyasik, Burin, & Pia, 2018; Tsakiris, 2010). This interpretation comes from neurologically-based alteration of body ownership (e.g., Bottini et al., 2009; Jenkinson, Haggard, Ferreira, & Fotopoulou, 2013; Pia, Garbarini, Fossataro, Burin, & Berti, 2016; Pia et al., 2014; Piedimonte, Garbarini, Pia, Mezzanato, & Berti, 2016; Vallar & Ronchi, 2009), and mainly from the most employed experimental manipulation of normal body ownership, the rubber hand illusion (RHI) (Botvinick & Cohen, 1998; Burin et al., 2018; Burin, Pyasik, Salatino, & Pia, 2017; Costantini & Haggard, 2007; Ehrsson, Spence, & Passingham, 2004; Farnè, Pavani, Meneghello, & Ladavas, 2000; Kalckert & Ehrsson, 2014; Kammers, de Vignemont, Verhagen, & Dijkerman, 2009; Longo, Schüür, Kammers, Tsakiris, & Haggard, 2008; Makin, Holmes, & Ehrsson, 2008). As described in Chapter 1, during the RHI, a realistic human-like fake hand is placed congruently with the participant's body (aligned with the shoulder and parallel to the matching real hand), while the real hand is hidden from the view. When the two hands are synchronously stroked, a compelling feeling of ownership over the fake hand arises; on the contrary, if the strokes are asynchronous, the illusion does not occur (although several studies reported some degree of embodiment also after the asynchronous stimulation (Costantini et al., 2016; Ismail & Shimada, 2016; Shimada, Fukuda, & Hiraki, 2009)). The illusory effects, which are measured

by the perceived mislocalization of the own hand towards the fake hand (i.e., proprioceptive drift) and/or by the subjective experience of owning the fake hand (an ad hoc questionnaire), are explained by the fact that vision, with respect to touch and proprioception, is given a higher weighting in the construction of the final percept (Costantini & Haggard, 2007; Makin et al., 2008; Tsakiris, 2010). Therefore, the initial conflict between vision of the rubber hand and tactile and proprioceptive sensation of the own hand is resolved by shifting the perceived location of the own hand towards the rubber hand. It is worth emphasizing, however, that the human body receives afferent signals not only in static conditions but also during movements. Indeed, under these circumstances, vision, proprioception and touch are complemented with some additional signals, such as those coming from skin/joint receptors and muscle spindles. Hence, one might wonder whether the integration of sensory signals processed during passive and active movements also contributes to the sense of body ownership. As regards the role of top-down information in body ownership, it is known that some efferent signals impose constraints on what can, or cannot, be embodied during the RHI. Indeed, the illusion does not occur when the fake hand is placed in an incongruent position (e.g., rotated 180° or located far from the participant's body midline and real hand) (Botvinick & Cohen, 1998; Burin, Pyasik, et al., 2017; Costantini & Haggard, 2007; Lloyd, 2007; Preston, 2013). Given the fact that voluntary movements are based on efferent signals (e.g., centrally-generated motor commands, forward models and sensory predictions (Blakemore, Frith, & Wolpert, 1999; Blakemore, Wolpert, & Frith, 1998; Frith, 2005)), one might ask whether motor-related efferent signals also contribute to the emergence of body ownership.

So far, most of the literature that attempted to answer the question of whether movements contribute to body ownership modified the original RHI paradigm in order to compare the conditions of passive and/or active movements with static conditions (Dummer, Picot-Annand, Neal, & Moore, 2009; Kalckert & Ehrsson, 2012, 2014; Kammers et al., 2009; Longo & Haggard, 2009; Riemer, Kleinbohl, Holzl, & Trojan, 2013; Tsakiris, Prabhu, & Haggard, 2006; Walsh, Moseley, Taylor, & Gandevia, 2011). The rationale of such approach was investigating whether movements further modulate body ownership. Overall, these studies reported contrasting findings. Indeed, some of them showed that the illusion was equally strong when it was evoked by tactile stimulation, active or passive movements (Kalckert & Ehrsson, 2014); others showed that movements increased the feeling of ownership (Dummer et al., 2009; Ma & Hommel, 2015; Manos Tsakiris et al., 2006); and others more demonstrated that the sense of ownership decreased in the presence of movements (Walsh et al., 2011). Other studies employed a different approach that consisted

in investigating whether the prolonged absence of movements affects body ownership. Accordingly, the RHI has been investigated in paraplegia/tetraplegia caused by spinal cord injury (Scandola et al., 2014), stroke-induced limb paralysis (Burin et al., 2015), and in healthy participants after a period of mechanical limb immobilization (Burin, Garbarini, et al., 2017). In all of those cases, the susceptibility to the illusion was affected by the absence of movements. Specifically, tetraplegic patients did not present proprioceptive drift, but experienced embodiment of the fake hand on the subjective level even after asynchronous stimulation (Scandola et al., 2014); hemiplegic patients experienced stronger illusion for their plegic hand (Burin et al., 2015); and healthy participants had more illusory effects for the hand that had been immobilized for one week (Burin, Garbarini, et al., 2017).

Findings obtained in the conditions of long-lasting periods of movement absence seem to suggest that motor-related signals are necessary for the construction of the coherent sense of body ownership. However, those studies did not clarify the specific role of afferent (e.g., vision, proprioception, kinesthetic information) and efferent (e.g., motor intention and sensory predictions) signals. Additionally, they provided only indirect evidence, since the role of movements was inferred from their absence. In order to fill this gap, in the present study we employed the opposite, direct logic, that is investigating the illusion in a condition where movements are naturally boosted, and therefore, there is an objective increase in the amount of motor-related signals. We capitalized on the condition of long-term motor practice of professional pianists. We therefore compared the RHI with three different types of stimulation (visuotactile, active movements and passive movements) in a group of expert pianists and in a group of non-musicians. Indeed, comparing different types of movement conditions would allow to clarify the role of efferent signals, such as motor intention, and afferent motor-related signals. Specifically, in the active moving RHI, the illusion is evoked by participant's voluntary movements (hence, it implies both efferent and afferent signals); in the passive moving RHI, there are no motor intentions or predictions but there are afferent motor-related signals, while neither type of motor-related signals is present in the visuotactile RHI (Kalckert & Ehrsson, 2014). Firstly, we predicted that pianists would experience less (or none) illusory effects in all types of the RHI because of the long-lasting increase of motor-related signals. We reasoned that, if in the condition of movements reduction (e.g., hemiplegia or movement prevention with a cast), the RHI effects were stronger because the multisensory conflict was more likely to be resolved in favor of vision due to the lack of motor-related signals to the hand (Burin, Garbarini, et al., 2017; Burin et al., 2015), then an increased amount of those signals should result in the opposite pattern, i.e. lower

susceptibility to the illusion. Secondly, we predicted a further decrease of the illusory effects in the active movement condition, because efferent motor-related signals, such as motor intention and planning, might additionally contribute to the construction of ownership of one's own hand.

2. Methods

2.1 Participants

Twenty expert pianists (nine females, eleven males; right-handed (Oldfield, 1971), mean age – 24.6±6.3 years, mean number of years of playing the piano – 13.5±5.0, mean time currently spent playing the piano – 11.2±11.9 hours/week) and twenty age- and gender-matched control participants without any experience in playing a musical instrument (nine females, eleven males; right-handed (Oldfield, 1971), mean age – 23.6±1.8) participated in the study. Informed consent was obtained from all individual participants included in the study.

2.2 Experimental design

We used the moving RHI procedure (Kalckert & Ehrsson, 2012, 2014), which included three types of the RHI – visuotactile, active moving and passive moving, and two types of stimulation – synchronous and asynchronous, in a within-subject design. Therefore, there were total of six experimental conditions (3*2) administered in two groups of participants. We tested only the right (dominant) hand, since it has been shown that the RHI susceptibility is not affected by the hand laterality (Adamo, Scotland, & Martin, 2012; Ocklenburg, Rüther, Peterburs, Pinnow, & Güntürkün, 2011; Smit, Kooistra, van der Ham, & Dijkerman, 2017). The experiment was performed in a single session that lasted approximately one hour.

2.3 Setting

The setting is presented in Figure 14. Participants sat in front of a wooden box (40 cm x 30 cm x 20 cm) that was set on a table. A life-sized model right hand (a plastic glove filled with flour) was placed on an upper shelf of the box, while the participant's right hand (wearing an identical plastic glove) was placed on a lower shelf, 15 cm below the fake hand and vertically aligned with it. The two hands were placed congruently with the participant's body, and a barber cape covered the space between participant's neck and the wrist of the fake hand; thus, the participant's hand and arm were hidden from the view, which created the impression that the fake hand was the participant's own outstretched hand. During the active and passive moving RHI procedures, a plastic ring was placed on the participant's and the fake-hand's

index fingers. Then, a plastic stick was attached to both rings in order to connect the participant's index finger with the index finger of the fake hand.

2.4 Procedure

The three types of RHI had the same procedure, except for the type of stimulation. In each type of RHI, the illusory effects were measured behaviorally (i.e., proprioceptive drift) and subjectively (i.e., questionnaire on the sense of body ownership).

In each type of RHI, firstly, participants were blindfolded and asked to indicate the perceived position of their right index finger by pointing their left index finger towards a rectangular piece of cardboard that was placed vertically on the left side of the box (six trials). Between the trials, the participants were asked to return their left hand to the initial position (placing it on the lap and keeping it relaxed) in order to avoid stereotypic responses. In each trial, the indicated position was recorded on a ruler that was attached to the piece of cardboard, and the recorded values were averaged between the six trials and referred to as pre-stimulation proprioceptive judgment. This measurement was followed by the stimulation phase that lasted for two minutes.

In the *visuotactile RHI* (Figure 14A), the participants were asked to maintain their gaze on the index finger of the fake hand and to remain still; then, the touches were applied to the participant's and fake-hand's index fingers with two paintbrushes. In the condition of *synchronous* stimulation, the touches were applied simultaneously at 1 Hz frequency with randomly applied faster touches and occasional double touches at the tip of finger, while in the condition of *asynchronous* stimulation, the stimulation was temporally incongruent, i.e., the visual stimuli preceded the tactile ones by approximately 500-1000 ms (the experimenter was trained in advance with the backdrop of metronome beats occurring accordingly to the above-mentioned intervals).

In the *active RHI* (Figure 14B), the participant's index finger was connected to the fake-hand's index finger with a plastic stick. The participants were asked to perform a tapping movement with their right index finger in a semi-regular rhythm of approximately 1 Hz with occasional double taps (since it has been shown that regular rhythm produced weaker illusion (Kalckert & Ehrsson, 2012)). Before the beginning of this RHI procedure (i.e., during the instructions before pre-stimulation proprioceptive judgments), the participants were briefly trained to perform the tapping in the requested rhythm by following a metronome (which was no longer present during the experimental phase). During the experimental phase, in the condition of *synchronous* stimulation the participants performed the tapping

movements and were instructed to keep their gaze on the index finger of the fake hand, which moved synchronously with the participant's movements. In the condition of *asynchronous* stimulation, the plastic stick between participant's and fake-hand's index fingers was disconnected in the middle. The participants followed the same instructions as in the *synchronous* condition, but the index finger of the fake hand was moved by the experimenter (who sat opposite from the participant and moved the finger using the plastic stick inside the box) in asynchrony with the participant's finger movements, i.e. the experimenter moved the fake finger as soon as the participant completed the movement of her finger.

In the *passive RHI* (Figure 14C), participants were instructed to maintain their gaze on the index finger of the fake hand and keep their hand still and relaxed. In the *synchronous* condition, the participant's and fake-hand's index fingers were connected with the plastic stick, and the experimenter (seating opposite from the participant) moved the plastic stick, thus synchronously moving both fingers up and down. In the *asynchronous* condition, the stick was disconnected in the middle, and the experimenter first performed the complete movement of the participant's finger and then the complete movement of the fake finger.

Then, in each type of RHI and in each stimulation condition, immediately after the stimulation phase, the participants were blindfolded again and asked to indicate the perceived position of their right index finger by pointing towards the piece of cardboard on the left side of the box with their left index finger (six trials). The indicated position was averaged between the six trials and referred to as post-stimulation proprioceptive judgment. After that, the participants were presented with a questionnaire on the subjective experience of ownership over the fake hand. The questionnaire consisted of six statements – three illusion statements, which reflected the experience of different aspects of the illusion, and three control statements (see Table 2). The statements were read to the participants by the experimenter, and the participants were asked to verbally report their agreement with each statement by using a 7-point Likert scale from -3 ("completely disagree") to +3 ("completely agree"). The statements were selected from a previous study (Kalckert & Ehrsson, 2014), and their order was randomized for each participant in each experimental condition.

Table 2. Questionnaire on the sense of body ownership

Real	Q1. I felt as if I was looking at my own hand
	Q2. I felt as if the fake hand was part of my body
	Q3. I felt as if the fake hand was my hand

Control	Q4. It seemed as if I had more than one right hand	
	Q5. It felt as if I had no longer a right hand, as if my right hand had disappeared	
	Q6. I felt as if my real hand was turning rubbery	

Between the experimental conditions (i.e., between each type of RHI and stimulation), participants were instructed to take their hand out of the box and move it in order to avoid possible lasting effects of the illusion from the previous condition. The order of experimental conditions was counterbalanced between participants.

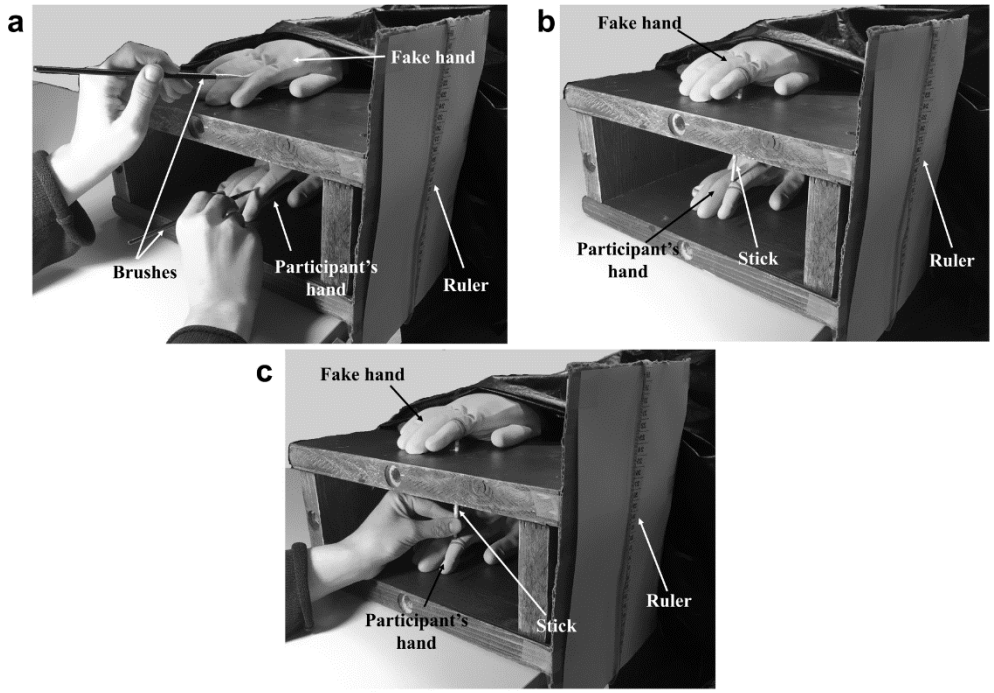


Figure 14. Experimental setup: **a.** Visuotactile RHI; **b.** Active moving RHI; **c.** Passive moving RHI.

2.5 Statistical analysis

Firstly, we compared pre-stimulation proprioceptive judgments in each type of RHI between the groups of participants in order to evaluate whether the groups were comparable in terms of initial proprioceptive accuracy.

Then, in each experimental condition, pre-stimulation proprioceptive judgments were subtracted from post-stimulation judgments, and this value was referred to as proprioceptive drift (Manos Tsakiris et al., 2006). Within the ownership questionnaire in each condition, the ratings were averaged for the illusion statements (Q1-Q3) and the control statements (Q4-Q6).

Proprioceptive drift and subjective ownership ratings (represented by the ratings in the illusion statements of the questionnaire) were compared between the groups of participants

for each type of the RHI in the synchronous condition (i.e., the condition that is supposed to induce the illusion (Botvinick & Cohen, 1998)). Then, within each group, for each type of the RHI the proprioceptive drift was compared between synchronous and asynchronous condition, and the ratings in illusion and control statements of the questionnaire were compared within synchronous and asynchronous condition, in order to evaluate whether each group of participants experienced each type of the illusion. Within each group, we also compared the illusion susceptibility (proprioceptive drift and the ratings in illusion statements of the questionnaire in synchronous condition) between the three types of RHI.

Since at least one variable for each required analysis failed to meet the criteria for normality of distribution on a Shapiro-Wilk test ($p > .05$), we performed nonparametric tests. The effect size was estimated with *r*. Bonferroni correction for multiple comparisons was used to adjust the alpha level for statistical significance according to the number of comparisons performed in each analysis.

3. Results

3.1 Proprioceptive drift

According to Mann-Whitney U test, pre-stimulation proprioceptive judgments did not differ between the groups of participants in any type of RHI in any condition: *visuotactile synchronous* (Z = .70, p = .48; pianists median = 3.08, IQR = 2.83, control group median = 2.58; IQR = 3.00), *visuotactile asynchronous* (Z = -1.26, p = .21; pianists median = 2.33, IQR = 3.50, control group median = 4.08; IQR = 4.42), *active synchronous (*Z = .89, p = .37; pianists median = 2.75, IQR = 2.92, control group median = 2.17; IQRIQR = 3.67), *active asynchronous (*Z = .27, p = .80; pianists median = 2.08, IQR = 2.52, control group median = 3.08; IQR = 4.08), *passive synchronous* (Z = -.32, p = .75; pianists median = 2.00, IQR = 2.42, control group median = 2.25; IQR = 2.42), *passive asynchronous* (Z = -1.18, p = .24; pianists median = 2.08, IQR = 3.75, control group median = 4.33; IQR = 4.33). These results show that there was no a-priori between-groups difference in the ability to localize one's own hand.

The results of proprioceptive drift are presented in Figure 15. As regards the between-groups differences, Mann-Whitney U test showed that pianists presented significantly lower drift in *visuotactile* (Z = -2.60, p = .001, *r* = -.41; pianists median = -.17, IQR = 2.83, control group median = 1.83, IQR = 3.83) and *active* (Z = -3.72, p < .001, *r* = -.59; pianists median = .17, IQR = 1.83, control group median = 2.00, IQR = 2.17) RHI in the condition of synchronous stimulation, compared to the control group. As for the *passive* RHI, the groups

of participants did not differ significantly (Z = -1.28, p = .20; pianists median = -.33, IQR = 1.33, control group median = .75, IQR = 3.67).

As for the within-group analysis, in the group of pianists, Wilcoxon signed rank test showed no significant differences between proprioceptive drift in the condition of *synchronous* and *asynchronous* stimulation in any type of the RHI: *visuotactile* RHI – Z = .34, p = .74; *synchronous* median = -.17, IQR = 2.83, *asynchronous* median = -.42, IQR = 1.50; *active* RHI – Z = 1.43, p = .15; *synchronous* median = .17, IQR = 1.83, *asynchronous* median = -.08, IQR = 1.50; *passive* RHI – Z = 1.75, p = .08; *synchronous* median = -.33, IQR = 1.33, *asynchronous* median = -.50, IQR = 1.08. The proprioceptive drift in *synchronous* condition did not differ significantly between the three types of RHI (*visuotactile* vs *active* RHI: Z = .06, p = .95; *visuotactile* vs *passive* RHI: Z = .11, p = .91; *active* vs *passive* RHI: Z = .54, p = .59).

In the control group in all types of RHI, proprioceptive drift was significantly higher in the condition of *synchronous* stimulation compared to *asynchronous*: *visuotactile* RHI – Z = 3.17, p = .002, *r* = .50; *synchronous* median = 1.83, IQR = 3.83, *asynchronous* median = -.17, IQR = 2.75; *active* RHI – Z = 3.47, p < .001, *r* = .55; *synchronous* median = 2.17, IQR = 2.17, *asynchronous* median = .50, IQR = 2.17; *passive* RHI – Z = 2.15, p = .03, *r* = .34; *synchronous* median = 0.75, IQR = 3.67, *asynchronous* median = -.42, IQR = 1.75. Similarly to the group of pianists, there were no significant differences in proprioceptive drift in *synchronous* condition between the three types of RHI (*visuotactile* vs *active* RHI: Z = .09, p = .93; *visuotactile* vs *passive* RHI: Z = 1.62, p = .10; *active* vs *passive* RHI: Z = 1.47, p = .14).

In summary, these results show that after the synchronous stimulation in *visuotactile* and *active* RHI, the group of pianists had significantly less proprioceptive drift with respect to the control group. Moreover, pianists did not experience the proprioceptive drift in any type of the RHI, while the control group, on the contrary, presented typical drift in all types of the illusion; neither of the groups had significant differences between the three types of RHI.

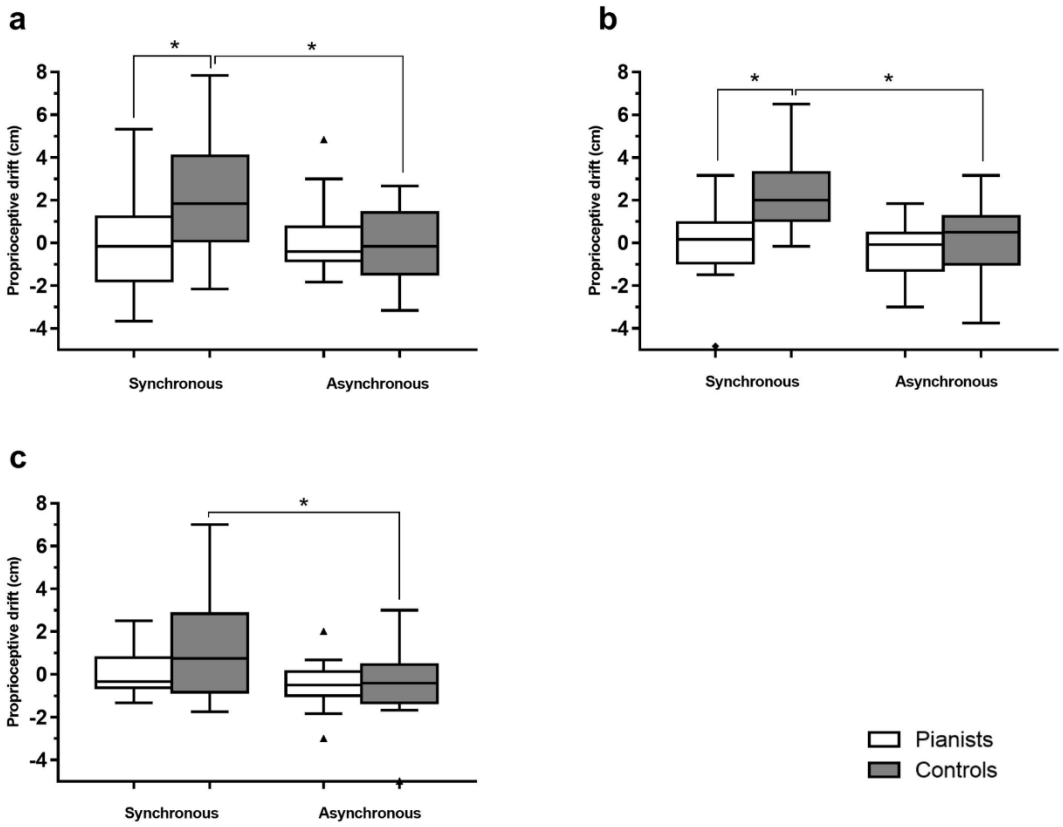


Figure 15. Proprioceptive drift (cm) in the condition of synchronous and asynchronous stimulation in the group of pianists and the control group: **a.** Visuotactile RHI; **b.** Active moving RHI; **c.** Passive moving RHI. The box represents the first and the third quartile with the line in the middle of the box representing the median, and the bottom and top whiskers represent the first quartile minus 1.5*IQR and the third quartile plus 1.5*IQR; * represents significant differences.

3.2 Ownership questionnaire

The results are presented in Figure 16. As regards the between-groups differences, on a Mann-Whitney U test, the ratings in illusion statements of the ownership questionnaire were significantly lower in the group of pianists in in *active* (Z = -3.12, p = .002, *r* = -.50) and *passive* RHI (Z = -2.06, p = .04, *r* = -.33) RHI with synchronous stimulation. In *visuotactile* RHI, the ratings did not differ significantly between the groups of participants (Z = -1.77, p = .08).

In the within-group analysis we compared the ratings in illusion and control statements in each experimental condition using the Wilcoxon signed rank test. In the group of pianists, the ratings in illusion statements were significantly higher than in control statements in *synchronous* condition in all types of RHI (*visuotactile*: Z = 3.11, p = .002, *r* = .52; illusion median = -.67, IQR = 4.17; control median = -2.67, IQR = 1.00; *active*: Z = 2.97, p = .003, *r*

= .48; illusion median = -1.83, IQR = 2.00; control median = -2.67, IQR = .50; *passive*: Z = 3.39, p = .001, *r* = .53; illusion median = -1.17, IQR = 2.17; control median = -2.67, IQR = 1.33). In *asynchronous* condition, the ratings in illusion statements were significantly higher only in *visuotactile* RHI (Z = 2.01, p = .04, *r* = .32; illusion median = -2.83, IQR =1.17; control median = -3.00, IQR = .50), but not in *active* (Z = .21, p = .83; illusion median = -3.00, IQR = .50; control median = -2.83, IQR = .50) or *passive* (Z = 1.77, p = .08; illusion median = -3.00, IQR = 1.17; control median = -3.00, IQR = .50). The ratings in illusion statements in *synchronous* condition did not differ significantly between the three types of RHI: *visuotactile* vs *active* RHI: Z = 2.33, p = .02 (N.S. after Bonferroni correction; alpha level: p=.017); *visuotactile* vs *passive* RHI (Z = 1.44, p = .15); *active* vs *passive* RHI (Z = .57, p = .57).

In the control group, the pattern of significant differences was the same as in pianists: in *synchronous* condition, the ratings in illusion statements were significantly higher than in control statements in all types of RHI (*visuotactile*: Z = 3.59, p < .001, *r* = .58; illusion median = 1.67, IQR = 1.83; control median = -.83, IQR = 2.33; *active*: Z = 3.18, p = .001, *r* = .50; illusion median = 1.50, IQR = 2.00; control median = -1.33, IQR = 3.50; *passive*: Z = 2.37, p = .02, *r* = .36; illusion median = .67, IQR = 2.83; control median = -1.17, IQR = 2.83). In turn, in *asynchronous* condition the significant difference was observed only in *visuotactile* RHI (Z = 2.76, p = .006, *r* = .47; illusion median = -.83 IQR = 4.33; control median = -2.33, IQR = 3.00), but not in *active* (Z = 1.44, p = .15; illusion median = -1.33, IQR = 3.50; control median = -2.00, IQR = 2.83) or *passive* (Z = .82, p = .41; illusion median = -2.00, IQR = 2.33; control median = -2.50, IQR = 1.83). As in the group of pianists, the ratings in illusion statements in *synchronous* condition did not differ significantly between the three types of RHI: *visuotactile* vs *active* RHI: Z = .95, p = .34; *visuotactile* vs *passive* RHI: Z = 2.07, p = .04 (N.S. after Bonferroni correction; alpha level: p=.017); *active* vs *passive* RHI (Z = 1.63, p = .10).

In summary, pianists experienced significantly less ownership of the fake hand in *active* and *passive* RHI, but not in *visuotactile* RHI in synchronous condition. Within-group analysis showed the same pattern of differences between illusion and control statements within *synchronous* and *asynchronous* condition in each type of the RHI in the two groups of participants. However, in the group of pianists, the median ratings in illusion statements were negative in all experimental conditions, while in the control group they were positive in *synchronous* condition in all types of RHI. These results suggest that pianists did not

experience subjective ownership of the fake hand, while the control group embodied the fake hand in all types of the illusion.

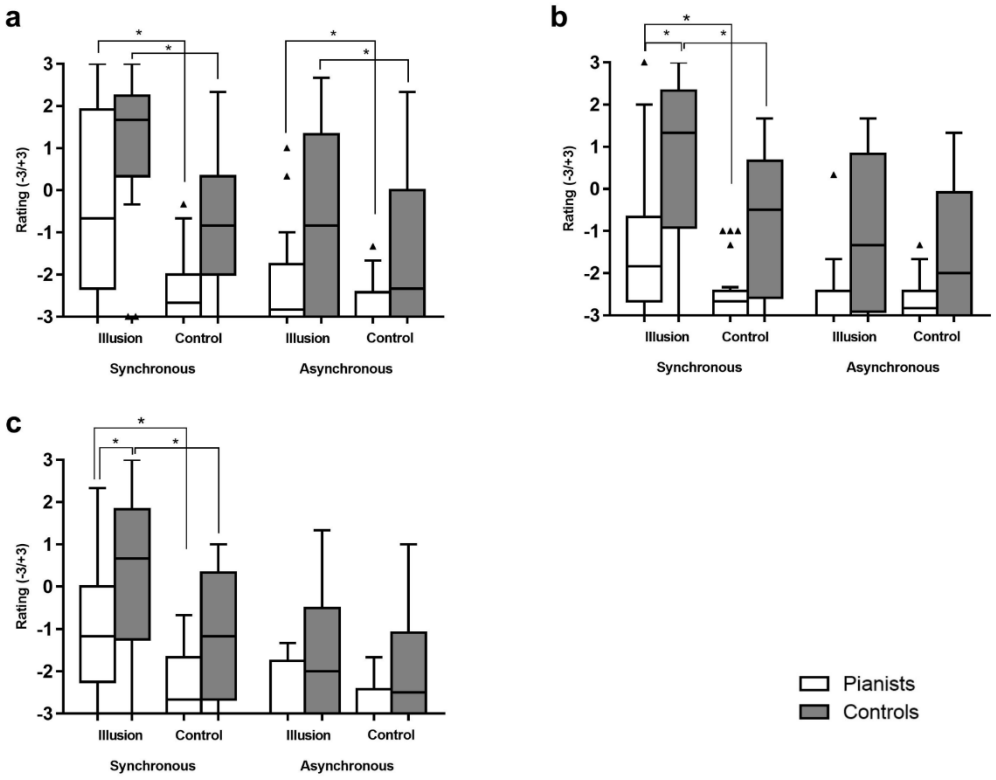


Figure 16. Ownership questionnaire (ratings in illusion and control statements; -3/+3 Likert scale) in the condition of synchronous and asynchronous stimulation in the group of pianists and the control group: **a.** Visuotactile RHI; **b.** Active moving RHI; **c.** Passive moving RHI. The box represents the first and the third quartile with the line in the middle of the box representing the median, and the bottom and top whiskers represent the first quartile minus 1.5*IQR and the third quartile plus 1.5*IQR; * represents significant differences.

4. Discussion

In present study, we aimed at investigating the role of movements in the construction of body ownership. In order to answer this question, we examined whether, and to what extent, long-term motor practice affected the sense of body ownership measured by the RHI. Specifically, we experimentally manipulated the sense of body ownership with three different types of stimulation (visuotactile, active movements and passive movements) in expert pianists and a control group of people without any experience in playing musical instruments. Then, we compared different indices of the illusion (proprioceptive drift and ownership questionnaire) between groups. We predicted that pianists would experience less (or none) embodiment in

any type of the RHI and that the illusory effects would be even lower in the condition of active movements.

The first prediction was confirmed, since the pianists were significantly less susceptible to the RHI of any type. Specifically, while they did not differ significantly from the control participants in the accuracy of pre-stimulation proprioceptive judgments (i.e., there was no a-priori difference), after the stimulation phase, pianists had significantly less proprioceptive drift in the *visuotactile* and *active* RHI, and lower ratings of ownership of the fake hand in the *active* and *passive* RHI. Crucially, within-group analysis showed that pianists did not experience either subjective ownership of the fake hand (i.e., they had negative scores in the questionnaire), or the proprioceptive drift in any type of the RHI. On the contrary, the control participants presented the typical RHI pattern in all types of RHI: in the condition of synchronous stimulation, the perceived location of their own hand shifted towards the fake hand (proprioceptive drift), and the participants agreed with the ownership questionnaire statements that described different aspects of illusory ownership (consistently with previous data (Kalckert & Ehrsson, 2014)). Contrary to our second prediction, however, pianists did not present any significant differences in the proprioceptive drift or the subjective ownership between the three types of the RHI, and neither did the control group. In case of the control group, such absence of differences is consistent with the previous studies that used the same RHI procedure (Kalckert & Ehrsson, 2012, 2014). In turn, the pianists did show a trend for lower subjective ownership ratings in the *active* RHI, although it was not significant.

In the rest of the discussion, we will argue that these results might be explained as due to the long-term motor practice in pianists. This, in turn, would support the view that movements *per se* contribute to the coherence of body ownership (Burin et al., 2015; Burin, Pyasik, et al., 2017; Fiorio et al., 2011; Tidoni, Grisoni, Liuzza, & Aglioti, 2014). Broadly speaking, any kind of prolonged and regular motor practice automatically increases the amount and the variety of motor-related afferent and efferent signals to the body. As regards pianists, these perceptual and motor changes are represented by anatomo-functional plastic changes in the brain for both somatosensory (Schulz, Ross, & Pantev, 2003) and motor (Gaser & Schlaug, 2003; Vaquero et al., 2016) cortex regions, and increased functional connectivity in multisensory and motor cortices (Luo et al., 2012). One study that addressed motor and somatosensory functions in expert pianists (Hosoda & Furuya, 2016), showed that more precise motor control was positively covariated with higher somatosensory acuity. Here we argue that this increase of motor-related afferent and efferent signals affects body ownership as follows. As stated above, in normal circumstances, the rubber hand illusion

emerges because vision overcomes touch and proprioception – a pattern consistent with a visual dominance over touch (Hartcher-O'Brien, Gallace, Krings, Koppen, & Spence, 2008). Specifically, when visual and tactile stimuli are presented simultaneously, control participants typically respond only to the visual component of the bimodal stimuli and fail to recognize the tactile one (Hartcher-O'Brien et al., 2008). Furthermore, this dominance becomes even stronger when the visual stimuli are presented on the body, and it remains present not only for one's own body parts but also for a congruently located fake hand (Hartcher-O'Brien, Levitan, & Spence, 2010). Accordingly, the absence of the illusion in pianists would follow a decrease of such dominance. Indeed, the musical skills of expert pianists require many years of motor training with constant presence of kinesthetic/tactile signals, without a corresponding increase of visual signals. Hence, the higher weight given to kinesthesis and touch would prevent the visual information from dominating (therefore not allowing the fake hand to be embodied). In fact, in pianists, the proprioceptive drift (which relies on the perceived location of participant's real hand) was almost equal to zero in all types of the RHI in the condition of synchronous stimulation.

Our results are not trivial but rather consistent with previous studies. Indeed, hemiplegic patients showed absence of RHI effects for the healthy hand, suggesting that the increased use of the healthy hand provided more motor-related signals, which enhanced body ownership (Burin et al., 2015). On the contrary, for the immobile plegic hand the illusory effects were significantly stronger than in healthy participants. Similar results were observed in healthy participants after a week of mechanical limb immobilization. After such period, the RHI effects were stronger for immobilized hand and weaker for the non-immobilized hand (Burin, Garbarini, et al., 2017). To sum up, the RHI effects seem to be absent or decreased in any condition of increased amount of movements and motor-related signals.

It is worth emphasizing that our interpretation should be taken cautiously and alternatives need to be considered. Firstly, one might argue that the absence of RHI in pianists might be a consequence of better hand proprioception *per se*. Although our results cannot entirely rule out such interpretation, together with the existing literature, they suggest that it is rather unlikely. Indeed, a more accurate hand perception would have caused pianists to differ from the control participants in proprioceptive judgments before the stimulation. Since this did not happen in any condition, our data are more compatible with a different susceptibility to the illusion, rather than with possible pre-existing differences. Specifically, after seeing the touches to the fake hand (or the movements of its finger) synchronously with feeling the touches on their own hand (or the movements of their own finger), pianists did not

feel any changes in the perceived location of their hand, therefore, their proprioception was not affected by the synchronous visual information. At the subjective level, this resulted in the absence of illusory ownership of the fake hand. Such interpretation is also supported by the fact that populations with superior proprioception but without specific motor training of the hands (advanced yoga practitioners (David, Fiori, & Aglioti, 2014) and people that practiced Tai Chi (Kerr, Agrawal, & Nayak, 2016)) did not present modulations in the RHI. Furthermore, the nature of piano practice itself suggests that pianists' superior somatosensory functions (Ragert et al., 2004; Schulz et al., 2003) are more likely to be related to the practice rather than to the pre-existing proprioceptive sensitivity (e.g., Hosoda & Furuya, 2016). In addition, it is known that the development of expert musical skills and the level of expertise strongly depend primarily on the amount of deliberate practice and related additional factors, such as motivation, rather than innate skills and "talent" (Ericsson, 2014; Ericsson, Krampe, & Tesch-Römer, 1993; Lehmann, 1997). Therefore, although it might be difficult to separate the input of motor and sensory signals in piano practice, our results support the idea that sensory signals alone do not account for the observed absence of the RHI in pianists. One might also argue that the pianists could have been less susceptible to the RHI because they were more familiar with and accustomed to the hand posture and movements of the RHI setup and procedure, compared to the control group. While this might be a contributing factor, it also does not account for the main results because, as described above, the pianists were not more accurate in pre-stimulation proprioceptive judgments.

5. Conclusions

Taken together, our results suggest that, despite the complex interaction of motor and somatosensory functions in piano practice, long-term motor training contributes to the construction of body ownership by providing additional motor-related afferent and efferent signals included in the multisensory integration. This conclusion is consistent with the fact that humans interact with the environment through the actions of their physical bodies (Gallese & Sinigaglia, 2010). Indeed, our own body allows to translate desires and goals into effects in the external world (Head & Holmes, 1911). To extend our results, future studies might focus on exploring this topic within a more cause-and-effect approach between variables (e.g., comparing different indices of body ownership before and after short-term non-musical motor training). Alternatively, body ownership might be further explored in other highly skilled individuals (e.g., dancers or athletes); in this case, it would be possible to

investigate ownership of the whole body, rather than of the hands, in a virtual environment (virtual body illusion (Lenggenhager, Tadi, Metzinger, & Blanke, 2007)).

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General conclusions

In my thesis, I explored the relation between the sense of body ownership and the sense of agency from different perspectives and approaches. Starting from the description of the existing findings that often reported controversial results and double dissociations between the two senses, I presented three studies on the mutual effects of body ownership and sense of agency and the underlying mechanisms that they might have in common. In particular, in the first study I explored whether the individual differences in body ownership and sense of agency measures (obtained in separate experimental settings) were correlated. The second and third studies addressed the causal relation between the two senses: in the second study, we experimentally manipulated body ownership and evaluated the effect of this manipulation on the sense of agency (represented by one of its implicit measures, the sensory attenuation) at the behavioral and neurophysiological level. Finally, in the third study, I explored the possible role of sense of agency and movement-related signals in the construction of body ownership by evaluating body ownership in a condition of naturally increased amount of movements, i.e., in expert pianists.

The results of the first study showed a significant positive correlation between the implicit measures of body ownership (proprioceptive drift in the RHI) and sense of agency (sensory attenuation of self-produced auditory stimuli), but not between their explicit measures. The second study demonstrated that sense of agency (represented by sensory attenuation) could be triggered solely by body ownership in the absence of any motor-related signals, and that it shared the neurophysiological mechanisms with the veridical sensory attenuation (i.e., the one based on motor-related signals). The third study showed that a sample with consistently increased amount of intended hand movements (expert pianists) was not susceptible to the RHI, regardless of whether the RHI was triggered by visuotactile stimulation, active or passive movements.

In essence, our findings suggest that, firstly, body ownership and sense of agency might partially rely on the same lower-level processes related to multisensory integration (at least, at the behavioral level). Secondly, each of the senses might be involved in the construction of the other one. Taken together, the results of the presented studies are more in line with the additive model, although they also partially support the independence one. On the other hand, the initially described additive model implied a one-way interaction ("sense of agency is body ownership, plus motor intention"; Tsakiris, 2010), while our data also

demonstrated the opposite effect of body ownership on agency. Therefore, it is possible to suggest a third model that would be based on the *interaction* of body ownership and sense of agency. Such model might consider ownership and agency as separate phenomena (which is indeed supported by the most common theoretical descriptions of each sense, i.e., the neurocognitive model of body ownership (Tsakiris, 2010) and the internal forward model (Blakemore & Frith, 2003), that do not share any common elements), but might also acknowledge the possible common constraints shared by the two senses and the role of each sense in the construction of the other one.

Indeed, from this perspective, the respective models that describe body ownership and sense of agency might be expanded to include some of the components from the other sense. In particular, as described in previous chapters, body ownership is typically explained by the integration of multisensory information (vision, touch and proprioception) and the comparison of the perceived signals and the pre-existing model of the body (Tsakiris, 2010). However, as showed in Chapter 3, motor-related signals might also contribute to the construction of ownership, possibly by altering both the multisensory integration (by shifting the balance between vision and proprioception) and the pre-existing model of the body (probably by making it more "stable"). Therefore, the existing neurocognitive model of body ownership might include the signals related to voluntary movements either at the level of multisensory integration, or a separate level that would include the comparison with the pre-existing model of the body not only static, but also in dynamic conditions.

As for the sense of agency, the internal forward model (Blakemore, Wolpert, & Frith, 1998; Blakemore, Wolpert, & Frith, 2000) is considered to be its key mechanism. Yet, the results in Chapter 2 suggest that agency can be triggered by body-related signals even without a forward model when any action preparation was prevented. Therefore, there might be a second mechanism involved in the sense of agency, an "inverse" model that might act in the opposite direction with respect to the forward model: it might predict the motor commands for a given goal by comparing the actual position of the body with the desired one. Possibly, whenever an actual body state closely matches the one associated with a specific motor program, it might retrospectively activate the same neural circuits of the real intended actions, thus creating the feeling of agency. In ecological situations, which include voluntary movements of the body, the forward and the inverse models should act together (making body-related signals crucial for the sense of agency).

Finally, even though body ownership and sense of agency might be mostly independent processes, they might rely on some common constraints in terms of spatial and

temporal integration at the implicit level; their higher-level explicit aspects, however, seem to be largely independent.

The presented results might also be useful in clinical practice, such as the rehabilitation of movement disorders, since it might be possible to develop new rehabilitation techniques based on the manipulation of body ownership (e.g., embodiment of a moving virtual avatar in immersive virtual reality). In particular, having shown that body ownership might be sufficient to trigger sense of agency even at the neural level (activating the same brain structures as the ones that are involved in motor intention and planning, such as the SMA (Cunnington, Windischberger, Deecke, & Moser, 2002)), I hypothesize that body-ownership manipulations might contribute to restoring motor functions, for example, in stroke patients. Ownership-based rehabilitation procedures might use immersive virtual reality (IVR, e.g. Maselli & Slater, 2013) to create strong feeling of ownership of a whole virtual body (avatar), which could then perform movements of any complexity and duration. Possibly, observing the movements of an embodied avatar would retrospectively activate the brain structures and neural pathways involved in actual motor execution and planning, and promote recovery. Another clinical application might be related to the therapy of body-image disturbances, for example, in eating disorders. Indeed, it has been previously shown that patients with anorexia nervosa were more susceptible to the RHI (Keizer, Smeets, Postma, van Elburg, & Dijkerman, 2014) and that their hand/body size estimation was modulated after embodiment of a fake hand/a virtual body, respectively (Keizer et al., 2014; Keizer, van Elburg, Helms, & Dijkerman, 2016). Taking this into account, it might be possible to develop rehabilitation procedures, for example, by manipulating the size of a virtual avatar and therefore affecting the patients' own body size perception. This would promote their readiness to accept their own body at a healthier weight.

To summarize, the presented findings shed light on the interaction of body ownership and sense of agency and provide opportunities for future theoretical and applied research on this topic.

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