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I move, therefore I am (?) visuomotor information modulates the senses of ownership and agency in a moving Virtual Hand Illusion paradigm

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I MOVE, THEREFORE I AM (?) VISUOMOTOR INFORMATION MODULATES THE SENSES OF OWNERSHIP AND AGENCY IN A MOVING VIRTUAL HAND ILLUSION PARADIGM

Tese de Candidatura ao grau de Doutor em Biologia Básica e Aplicada;
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“’Tell me one last thing’, said Harry.
’Is this real? Or has this been happening inside my head?’
Of course it is happening inside your head, Harry,
but why on Earth should that mean that it is not real?’”
J.K. Rowling,
Harry Potter and the Deathly Hallows

Pel Pol,
per que tot adult necessita d'un infant
que li recordi el que és realment important

To Pol,
because every grown-up is in need of a child
to remind them what really matters

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"And now for something completely different..." (Python, 1969)

Abstract

The senses of ownership (i.e., attributing a body part or body to ourselves) and agency (i.e., feeling authorship over the actions performed by a body part) are fundamental elements of the recognition of the self. The sense of ownership has been proposed to arise from the afferent sensory information, while the sense of agency depends on the efferent information derived from intentional movement. However, the role of active control over the movements of a fake and goal-achievement in the eliciting a sense of ownership is still up for debate.

In this thesis, we aimed to test the role of visuomotor information and how it interacts with other sensory sources (e.g., proprioception and visual appearance of the virtual limb) to generate a sense of ownership. To this end, we took advantage of Virtual Reality systems, which allowed us to control a wide range of experimental variables while maintaining ecological validity. In a custom-made virtual environment, we assessed the reported senses of ownership and agency over a gender-matched right arm, which the participants could control in a goal-directed task.

First, we found that, under active control, the reported senses of ownership and agency are resistant to seeing the hand in a discontinuous form (i.e., missing the forearm). Conversely, we found that the senses of ownership and agency decreased when passively observing a discontinuous static limb. Additionally, active control was found to increase the reported sense of ownership over the virtual hand only when it was presented in a discontinuous form. This interesting observation leads us to believe that, once present, movement-related information is important for the reported sense of ownership, but only when the evidence that the limb belongs to the self is decreased.

Secondly, we found that the reported sense of agency over a body part is affected by the achievement of the goal of the action. Specifically, the sense of agency decreased when the observed consequence of the action did not match the expected outcome. The sense of ownership, on the other hand, showed a less consistent reduction depending on the information that was manipulated simultaneously (e.g., body discontinuity or movement incongruence). Thus, suggesting that the effect of the incongruent outcome depended on the available evidence for the sense of ownership.

Altogether, our results are consistent with a framework where active control and congruent observed and expected consequences of the action act as evidence for the sense of ownership. Furthermore, we propose that the effect of the manipulations on the senses of ownership and agency is contingent on the available sensory information. Thus, our results help reconcile the discrepancies reported in previous literature regarding the role of movement and consequences of the action.

Resumo

Os sentidos de propriedade (ou seja, a atribuição uma parte do corpo ou corpo a nós mesmos) e agência (ou seja, sentir a autoria sobre as ações realizadas por uma parte do corpo) são elementos fundamentais do reconhecimento do próprio. O sentido de propriedade foi proposto ter a sua fonte na informação sensorial aferente, enquanto o sentido de agência depende da informação eferente proveniente do movimento intencional. No entanto, o papel que o controlo ativo sobre os movimentos de um braço falso e que a obtenção do objetivo na geração de um sentido de propriedade ainda é um tópico de debate.

Nesta tese, pretendemos testar o papel da informação visuomotora e da sua interçãoe com outras fontes sensoriais (por exemplo, propriocepção e aparência visual do membro virtual) para a obtenção de um sentido de propriedade. Para esse objectivo, utilizámos sistemas de Realidade Virtual, o que nos garantiu controlo sobre uma ampla gama de variáveis experimentais enquanto mantendo a validade ecológica da experiência. No ambiente virtual desenvolvido, avaliámos os sentidos de propriedade e agência sobre um braço direito virtual, que os participantes podiam controlar para realizar numa tarefa.

Primeiro, descobrimos que, com controlo ativo, os sentidos de propriedade e agência são resistentes a observar o braço na forma descontínua (ou seja, sem o antebraço). Por outro lado, descobrimos que os sentidos de propriedade e agência diminuiuram ao observar passivamente um braço estático na forma descontinua. Além disso, descobriumos que o controlo ativo aumenta o sentido de propriedade sobre a mão virtual apenas quando ele é apresentado na forma descontínua. Esta interessante observação leva-nos a concluir que, uma vez presentes, as informações relacionadas com o movimento são importantes para o sentido de propriedade repoortado, mas somente quando a evidência de que o membro pertence ao próprio diminuí.

Em segundo lugar, descobrimos que o sentido de agência reportado sobre uma parte do corpo é afetado pela capacidade de obtenção dos objetivos da ação. Especifícamente, o sentido de agência diminuiu quando a consequência observada do não correspondeu ao resultado esperado. O sentido de propriedade, por outro lado, apresentou uma redução menos consistente e dependente da restante informação a

ser manipulada em simultaneamentâneo (por exemplo, descontinuidade corporal ou incongruência de movimento). Assim, sugerindo que o efeito da incongruência das consequências depende da evidência disponível a favor do sentido de propriedade.

Em conjunto, os nossos resultados são consistentes com uma estrutura em que o controlo ativo e a congruência entre as consequências observadas e asv esperadas atuam como evidência para a obtenção do sentido de propriedade. Além disso, propomos que o efeito das manipulações sobre os sentidos de propriedade e agência está contingente à informação sensorial disponível. Assim, os nossos resultados ajudam a reconciliar as discrepâncias existentes na literatura anterior sobre o papel do movimento e das consequências da ação no reconhecimento do próprio.

Contents

List of Figures

List of Tables

List of Abbreviations

BOI	**B**ody **O**wnership **I**llusion
GSR	**G**alvanic **S**kin **R**esponse
HMD	**H**ead **M**ounted **D**isplay
IQR	**I**nter**Q**uartile **R**ange
IVS	**I**mmersive **V**irtual **S**ystems
RHI	**R**ubber **H**and **I**llusion
SM	**S**tate **M**achine
VHI	**V**irtual **H**and **I**llusion
VR	**V**irtual **R**eality

Publications

This thesis resulted in the publication of two works in peer-reviewed journals

1. **Brugada-Ramentol V***, Clemens I, de Polavieja GG* (2019). Active control as evidence in favor of sense of ownership in the moving Virtual Hand Illusion. Consciousness and Cognition 71:123-135. doi: 10.1016/j.concog.2019.04.003

   **shared corresponding authorship*

   In this Original Research article, we show how active control enhances sense of ownership over the virtual limb, but this effect is contingent on the visual information related to the hand.

2. **Brugada-Ramentol V**, de Polavieja GG* and Román Á-C* (2016). Toward a Molecular Profile of Self-Representation. Front. Hum. Neurosci. 10:602. doi: 10.3389/fnhum.2016.00602

   **shared corresponding authorship*

   In this Perspective article, we propose a mechanism to explore the molecular correlates of self-representation.

1 | General Introduction

"Je suis qui je suis, et j'ai le besoin pour l'être."
"I am who I am and I have the need to be."

Antoine de Saint Exupéry,
The Little Prince

1.1 Experimental manipulation of the self

Recognizing our body as ourselves is crucial to interact with the environment and with others optimally. Similarly, distinguishing our self-generated actions from other generated actions is critical for self-recognition (Jeannerod, 2003). Thus, two key components in the sense of self can be identified: the sense of ownership and the sense of agency (Kilteni et al., 2015; Gallagher, 2000; Gallagher, 2005).

The sense of ownership is defined as the feeling that a body or body part belongs to ourselves, and that we are the one undergoing a sensory experience (Gallagher, 2000; Longo et al., 2008; Tsakiris, 2010). The sense of ownership relies on integrating interoceptive and exteroceptive, body-related sensory signals (Costantini and Haggard, 2007; Petkova, Khoshnevis, and Ehrsson, 2011; Tsakiris and Haggard, 2005a). This multisensory integration (Holmes and Spence, 2005) creates and continuously updates the representation of the body in the brain (Gallagher, 2005; Metzinger, 2003).

As a result of its dependence on the sensory information, the sense of body ownership is dynamic and malleable (Graziano and Botvinick, 2002). This malleability allows experimentally inducing a sense of ownership over a fake body part by manipulating the sensory signals. Such is the case of the Rubber Hand Illusion (RHI, Botvinick and Cohen, 1998), in which illusory ownership over a rubber hand was elicited through synchronous visuotactile stimulation of both the participant's physical and a rubber hand. In this classical paradigm, the participants are presented with a rubber hand in an anatomically plausible position, while their real hand is hidden from their sight. The experimenter then applies spatial and temporal synchronous tactile stimulation on the rubber hand and the participant's physical hand. Thus, generating a sensory conflict between the felt tactile stimulation on the hidden real hand and the seen stimulation on the fake hand. The integration of the visual, tactile, and proprioceptive information results in a vast majority of the participants referring to the felt touch as emerging from the rubber hand and consequently experiencing the rubber hand as if it were their own.

The RHI can be used as a method to study multisensory integration and also to investigate the interplay of vision, proprioception, and touch in self-perception and how they contribute to the representation of the bodily-self. The experience of our body is intrinsically linked to the body itself. By dissociating the experience of the body from the physical body, ownership illusions such as the RHI provide a replicable paradigm that allows the study of the underlying mechanisms of body representation.

The classical paradigm has been extensively replicated (Armel and Ramachandran, 2003; Ehrsson, Spence, and Passingham, 2004; Longo et al., 2008; Tsakiris et al., 2010; Tsakiris and Haggard, 2005b; Ehrsson et al., 2007; Costantini and Haggard, 2007) and extended to different experimental setups, such as using Virtual Reality (VR) (Slater et al., 2008; Maselli and Slater, 2013). In the Virtual Hand Illusion (VHI), synchronous visuotactile stimulation elicited a sense of ownership over a virtual limb (Slater et al., 2008). Additionally, it has been replicated using visuomotor correlations instead of visuotactile stimulation (Sanchez-Vives et al., 2010; Kalckert and Ehrsson, 2012; Kalckert and Ehrsson, 2014; Tsakiris, Prabhu, and Haggard, 2006), robotic limbs instead of rubber hands (Caspar et al., 2015; Romano et al., 2014), and through brain-computer interfaces (Perez-Marcos, Slater, and Sanchez-Vives, 2009). Furthermore, visuotactile stimulation can result in the embodiment of full fake bodies (Slater et al., 2009; Rubo and Gamer, 2019). For example, synchronous stroking of the participant's chest resulted in illusory experience of ownership towards a mannequin body (Petkova and Ehrsson, 2008). Finally, the perception of the own body is also malleable by tool-use. Successful completion of a reaching-task using a tool resulted in the perception of an increased arm length (Sposito et al., 2012; Cardinali et al., 2009). Additionally, the attribution of external body parts has also been extended to the face (Tsakiris, 2008). Interestingly, the RHI has also been replicated in mice (Wada et al., 2016; Buckmaster et al., 2020), in what has been dubbed as the Rubber Tail Illusion (RTI). After stroking the animal's hidden physical tail and a seen rubber tail synchronously, the rodents reacted to a pinching of the fake tail like if their physical tail has been pinched.

The effects of the RHI can be measured both by subjective and objective measures. Subjective measures require the explicit report of the experience by answering a set of questions that assess the sense of ownership over the fake limb (i.e., 'I felt as if the rubber hand were my hand.' (Botvinick and Cohen, 1998)). The illusion of ownership can also be measured through behavioral measures. A typical example is the proprioceptive drift, the perceptual mislocalization of the physical arm's perceived position towards the fake arm that results from the illusion (Botvinick and Cohen, 1998; Romano et al., 2014; Costantini and Haggard, 2007; Kalckert and Ehrsson, 2012; Tsakiris and Haggard, 2005a). Furthermore, the experience of ownership over a body or a body part has also been assessed using physiological measures, such as Galvanic Skin Response (GSR) (Tieri et al., 2015b; Armel and Ramachandran, 2003; Kilteni et al., 2012; Ehrsson et al., 2008).

1.2 Mechanisms underlying the RHI

A three-way sensory interaction (i.e., visual, tactile, and proprioceptive information) that reconciles the sensory conflict when tactile and visual stimulation is synchronous has been proposed to explain the RHI (Botvinick and Cohen, 1998; Tsakiris and Haggard, 2005a). An extended model included the need for the hand to be in an anatomically plausible position (Makin, Holmes, and Ehrsson, 2008). The visual information from the fake hand and proprioceptive information from the physical hand are combined to estimate the hand position. When the rubber hand is in an anatomically plausible position, visual information is strongly weighted in favor of the fake limb being part of the body. Then, visuotactile information of the seen and felt stimuli is processed. If all the information is integrated correctly, the sensation of touch is inferred as arising from the rubber hand (Makin, Holmes, and Ehrsson, 2008), and the illusion of ownership occurs. When the stimulation is synchronous, visual information dominates over the proprioceptive information, resulting in an illusion of ownership over the fake limb. These models suggest that a bottom-up modulation would be sufficient for the illusion to take place.

Top-down influences, however, have also been proposed strongly to influence the RHI (Tsakiris, 2010). Thus, a further extended model also accounts for the need for the fake hand to fit a pre-existing internal model of the hand. The illusion does not occur for non-corporeal objects (Tsakiris, Longo, and Haggard, 2010; Makin, Holmes, and Ehrsson, 2008). Finally, a Bayesian causal inference model has been proposed to explain the computational mechanism underlying the RHI (Kilteni et al., 2015; Samad, Chung, and Shams, 2015). In this model, the sensory conflict generated by the synchronous visuotactile stimulation can be resolved in two ways: either the sensory information comes from one common source (i.e., rubber hand), which results in the illusion, or from two different sources (i.e., rubber and physical hand). Which scenario occurs depends on the likelihood of the origin of the tactile information, the semantic information (i.e., morphological appearance), the anatomical constraints, and the prior expectations of only one hand being the source of all the information (Kilteni et al., 2015).

These models highlight the importance of synchronous visual and tactile information. The illusions of ownership are abolished by temporal and spatial visuotactile asynchronous stimulation (Botvinick and Cohen, 1998; Perez-Marcos, Sanchez-Vives, and Slater, 2012; Kammers et al., 2009b; Slater et al., 2008), when delays are larger than 300ms between the seen and felt touch (Shimada, Fukuda, and Hiraki, 2009). Furthermore, a mismatch on the location of the seen and felt touch also abolishes the illusion (Kammers et al., 2009b; Kammers et al., 2009a; Riemer et al., 2013). Even though a single study has shown ownership over non-hand objects (Armel and Ramachandran, 2003), the consensus goes against the possibility of the attribution of non-bodily shaped objects (Tsakiris et al., 2010; Pyasik, Tieri, and Pia, 2020). Thus, self-attribution of the rubber hand to one's body arises as an interaction between bottom-up processes (synchronous spatiotemporal stimuli) and top-down representations of a coherent body-schema in both posture and morphology (Ehrsson, Spence, and Passingham, 2004; Tsakiris and Haggard, 2005b).

1.3 The sense of agency

Another essential component of self-representation is the sense of agency (Gallagher, 2000): the feeling of authorship over one's actions and their consequences in the environment (Tsakiris, 2010; Haggard, 2017; Moore and Fletcher, 2012). The sense of agency relies on the internal cues of the motor actions and the sensory perception of the external consequences of those actions. The sense of agency is related to action awareness and planning (Vignemont, 2011) and the action-effect relationship (Caspar, Cleeremans, and Haggard, 2015).

The authorship over an action seems to arise from the interplay between predictive internal and postdictive external cues (Haggard, 2017; Synofzik, Vosgerau, and Voss, 2013). The predictive models defend that sense of agency heavily relies on the motor-related signals that precede the action (Wolpert, Ghahramani, and Jordan, 1995). The comparator model (Frith, Blakemore, and Wolpert, 2000; Blakemore, Wolpert, and Frith, 2002) suggests that the sense of agency arises from comparing an internal prediction about the sensory consequences of the action and the actual sensory consequences. In a voluntary action, motor commands and an efference copy are generated, which generated and internal model of the action (Wolpert, 1997; Wolpert, Ghahramani, and Jordan, 1995). The predictions made by the internal model regarding the efference copy is then compared to the sensory feedback from the action. A match between these two components registers the action as caused by oneself. On the other hand, a mismatch between the expected and actual sensory feedback disrupts the sensation of agency (Synofzik, Vosgerau, and Newen, 2008a) and registers the movement as externally generated.

On the other hand, the postdictive account proposes an inference of the sense of agency that occurs after the action has happened, assuming a critical role of context (Wegner, 2002). For instance, the expectation of a specific outcome is sufficient to elicit a sense of agency over other-generated movements when the proper outcome is provided (Wegner, Sparrow, and Winerman, 2004). Thus, suggesting that the sense of agency can occur in the absence of voluntary motor commands (Tieri et al., 2015a; Wegner, Sparrow, and Winerman, 2004). In the absence of motor commands, passively observing a moving limb generates vicarious agency over the arm's movements (Pezzetta et al., 2018; Tieri et al., 2015b). Furthermore, the sense of agency has been reported to be influenced by the feelings of ownership over the body (Burin et al., 2017; Burin et al., 2018). Seeing an embodied avatar walking primed an illusory feeling of walking even in the absence of movement (Kokkinara et al., 2016). Finally, the sense of agency can be modulated by prior beliefs (Desantis, Roussel, and Waszak, 2011) and the valence of the outcomes (Moretto, Walsh, and Haggard, 2011).

The sense of ownership and sense of agency can be defined as sensory and motor representation of the bodily self, respectively (Longo and Haggard, 2009). It has been suggested that the sense of agency has a strong efferent component, while the sense of ownership relies on afferent information. While evidence supports that in the absence of motor control, feelings of ownership over a virtual hand can elicit a sense of agency. The role of actively controlling the movements of a virtual hand in the reported sense of ownership remains unclear.

1.4 Aim and structure of this thesis

In the present dissertation, we are concerned with the role of active control over the movements in eliciting and maintaining the senses of ownership and agency over a virtual hand. Additionally, we aimed to understand the interplay between the different sensory information sources, such as visual information from the limb and congruent visuomotor information. We assessed the reported ownership and agency in a moving Virtual Hand Illusion (mVHI) paradigm in a custom-made virtual environment. This environment allowed for the independent manipulation of proprioceptive, visuomotor, and morphological information of the virtual hand and to assess its effects on the reported senses of ownership and agency.

First, in **Chapters 2** and **3** we present the custom-made VR environment and the experimental methodologies presented here. VR offers the unique opportunity to manipulate sensory information in a seemingly realistic manner that would not have been otherwise possible. In **Chapter 2**, we described the hardware and the software used during the experiments presented in the thesis. In this chapter, we describe the virtual environment designed utilizing the Unity 3D engine. The software was designed using a hierarchical state machine system, which easily changed between different experimental conditions depending on the proposed design. In **Chapter 3**, we present in detail the experimental methodology of the three experiments described in the main text.

Our first aim was to understand the role of congruent visuomotor information for the senses of ownership and agency over a virtual limb. While some studies report that active control over the fake hand movements enhances the sense of ownership (Kalckert and Ehrsson, 2012; Tsakiris, Prabhu, and Haggard, 2006), others fail to see the same effect (Kalckert and Ehrsson, 2014; Longo and Haggard, 2009). Thus, the impact of visuomotor information on the sense of ownership is yet to be fully understood.

We propose that the differences observed between studies could arise from the interplay of the available sensory information in favor of feeling ownership over the virtual hand, such as congruent visual appearance or proprioceptive information. In **Chapter 4**, we report our findings of two separate studies that assessed whether active control enhanced and maintained the reported sense of ownership over a limb that appeared detached from the body. Previous studies reported a decrease in the senses of ownership and agency over a virtual moving arm that was presented as discontinuous from the virtual body (Tieri et al., 2015a). However, their experimental setup consisted of passively observing the moving virtual limb without any movements being performed by the participant. We propose that, under active control, the senses of ownership and agency should be resistant to seeing the virtual limb as discontinuous (i.e., missing the forearm). In **Experiment 1**, we tested this hypothesis by manipulating the proprioceptive information and the visual appearance of the virtual limb. In **Experiment 2**, we built upon this hypothesis by examining whether active control could enhance the reported sense of ownership compared to observing a static arm without attempting to move it. To this end, we manipulated the absence or presence of visuomotor information, the visual appearance, and the movement congruence. The results in this chapter show that active control enhances and maintains a sense of ownership over a virtual hand, only when it appears in a discontinuous form.

The sense of agency relies on both external and internal cues (Haggard, 2017). In our experimental setup, these two components could be dissociated. We defined as action agency the feeling of authorship over the movements of the virtual arm and as outcome agency, the feeling of being the cause of the changes in the virtual environment. We hypothesized that both movement and outcome congruence was necessary to maintain a sense of ownership and agency over the virtual hand. To test this hypothesis, in **Experiment 3**, we manipulated the consequence of the action in the virtual environment, as well as the movement congruence and the visual appearance of the virtual limb and assessed the sense of ownership, action agency, and outcome. In **Chapter 5**, we found that incongruent outcome decreases outcome agency, action agency, and the sense of ownership.

In **Chapter 6**, we discuss the results reported in the thesis compared to previously published studies. Additionally, we extend the Bayesian framework for the sense of ownership (Samad, Chung, and Shams, 2015; Kilteni et al., 2015) to incorporate our findings on the role of visuomotor information. Finally, we consider some of the limitations and future directions from the current work.

Finally, this thesis contains five appendices. In **Appendix A**, we extend on the relevant parts of the code for the virtual environment. **Appendix B** presents the mathematical formulation for the Bayesian model proposed in the **Chapter 6**. In **Appendix C**, we show our results from implicit measures, such as the proprioceptive drift and GSR. **Appendix D** shows an analysis on the sociodemographic data from the participants. We analyzed the individual ownership scores in **Experiment 2** and **Experiment 3** according on the participants age, gender, gaming habits, and previous experience with VR systems. **Appendix E** collects the peer-reviewed publications that resulted from the thesis.

2 | A Virtual Reality system to study the role of visuomotor information in embodiment

“Reality is frequently inaccurate.”

Douglas Adams, The Restaurant at
the End of the Universe

2.1 Introduction

The term Virtual Reality (VR) refers to a computer-generated simulation of a three-dimensional image or environment. By the means of special electronic equipment, the user is able to interact with the virtual environment in a seemingly realistic way. To the extent that the virtual environment can be perceived by the user as it was the physical reality, generating a feeling of presence (Slater et al., 2009; Sanchez-Vives and Slater, 2005).

In the early stages, virtual scenarios were displayed by a desktop VR. The participants saw the environment in a 2D screen and interacted with it via a mouse or a joystick. A caveat of this system is that it did not allow for a naturalistic interaction with the environment and failed to provide an immersive experience, as the participants lacked body-related information, (Ruddle and Lessels, 2009), such as vestibular or proprioceptive information (Sanchez-Vives and Slater, 2005).

Later, VR environments were presented in large front-mounted projections, allowing for an increased visual field. Additionally, by the means of head tracking, the movements of the head of the participants were used to update the environment providing a more naturalistic experience. However, the range of motion in these systems was still somewhat limited. In a front-mounted projected virtual environment, Slater and colleagues replicated the results reported in the RHI (Botvinick and Cohen, 1998), by applying synchronous tactile stimulation to the physical and virtual arm (Slater et al., 2008).

The Cave Automatic Virtual Environment (CAVE) (Cruz-Neira, Sandin, and DeFanti, 1993) allowed to update the environment according to the information collected through the head- and hand-trackers (Steptoe, Steed, and Slater, 2013). It consists of a four-walled enclosure in which the virtual environment is projected onto the walls and floor. Even though, the CAVE presented an improvement over the previous systems, the range of movements was still limited to head and hand motions (Tarr and Warren, 2002).

The appearance of Immersive Virtual Reality (IVR) systems opened new possibilities in the study of embodiment and presence. In IVR, the users are presented with a more vivid experience of the environments. By the means of a head-mounted display (HMD), a stereo visualization of the environment is possible with two 2D images displayed one to each eye. IVR environments are updated according to the position and orientation of the participant's head. As a result, sensorimotor contingencies are met and provide the participant with the illusion of being and acting in an alternate reality (Sanchez-Vives et al., 2010; Slater, 2009), to which the participants could react (Sanchez-Vives and Slater, 2005). IVR environments offer maximal control over experimental variables, while maintaining a high degree of ecological validity (Bohil, Alicea, and Biocca, 2011). Simultaneously, IVR environments allow to measure behavioral (e.g. proprioceptive drift) and physiological responses (e.g. changes in body temperature, skin conductance) to changes in the environment (Armel and Ramachandran, 2003; Macauda et al., 2015; Salomon et al., 2013; Slater et al., 2006), as well as using brain recording techniques (Tremmel et al., 2019).

Thus, the concept of VR is not new; however, the recent technological improvements in computers and the quality of the HMDs and tracking systems have made this tool increasingly interesting in the field of Neuroscience. Especially, in the study of self-representation (Sanchez-Vives and Slater, 2005; Bohil, Alicea, and Biocca, 2011), which is our interest in this thesis.

To understand the role of multisensory integration in self-representation, the experiments require to independently manipulate the sensory signals presented to the participants. Since the representation of the self is strongly linked to the presence of our physical body, it requires the use of illusions of body ownership. By generating sensory conflicts, such as in the RHI paradigm (Botvinick and Cohen, 1998), it is possible to elicit ownership over a fake arm. Similar misattributions of a fake limb can be achieved by synchronously stimulating the physical hand using a system of mirrors (Nielsen, 1963; Ramachandran, Rogers-Ramachandran, and Cobb, 1995), and by the means of VR (Perez-Marcos, Slater, and Sanchez-Vives, 2009; Slater et al., 2010).

VR systems become particularly interesting, as they offer the possibility to distinctly manipulate and dissociate sensory information that is generally integrated simultaneously in the experience of our body (Tarr and Warren, 2002). The use of IVR opened a new door to manipulations on the virtual body that would have been near to impossible to achieve over the physical body or with other display systems, such as embodying full bodies with changing perspective (Slater et al., 2010; Kokkinara et al., 2016) or embodying bodies of different sizes (Banakou, Groten, and Slater, 2013; Tajadura-Jiménez et al., 2017). Also, it allows for manipulations that would not otherwise be feasible, for example rotating the virtual arm to investigate if the movement elicits electrical activity from the muscles (Slater et al., 2008). These illusions of ownership do not only work using visuotactile stimulation but also by the means of visuomotor correlation (Sanchez-Vives et al., 2010) or by controlling the limb through a brain-computer interface (Perez-Marcos, Slater, and Sanchez-Vives, 2009).

Furthermore, the use of VR in the study of self-representation allows for the manipulation of the bodily structure, morphology, and size (Kilteni, Groten, and Slater, 2012). Some of these manipulations include changes in skin color (Peck et al., 2013), breaks in the body continuity (Tieri et al., 2015a), uncommon morphologies (Kilteni et al., 2012) adding different degrees of transparency (Martini et al., 2015), or adding unconventional elements, such as extra fingers (Hoyet et al., 2016), owning an extra arm (Ehrsson, 2009), controlling a tail (Steptoe, Steed, and Slater, 2013), or even a full animal body (Krekhov, Cmentowski, and Krüger, 2019).

In this thesis, we took advantage of VR systems to study the integration of visuomotor information and morphological appearance to enhance the sense of ownership and the sense of agency over a virtual limb in healthy participants. Using a virtual system offered several advantages over a physical. We manipulated characteristics of the virtual body (i.e., body discontinuity), information related to visuomotor inputs (i.e., movement and task performance feedback) and other sensory inputs (i.e., the congruence of proprioceptive information), that would have otherwise been impossible. We have designed a virtual environment in which participants controlled the virtual limb during a goal-directed task and we measured the senses of ownership and agency by:

1. **Explicit measures**, in the form of questionnaires, to assess the subjective experience of the illusion. This measure has been constant during the whole project. We have worked on improving the acquisition of this data. At first, the responses from the participant were recorded manually. Later, they were logged onto a response file using the Matlab Likert.m function, which was modified to present the questions

in a randomized order for each condition and participant. Finally, we implemented a system to log the responses in the Unity environment. The questions appeared on a screen one by one in a randomized order and waited for the experimenter to input of the response give by the participants.

2. **Behavioral changes**. We measured the proprioceptive re-calibration of the position of the hand of the participant as a result of the illusion, i.e., proprioceptive drift. Given the characteristics of our experimental setup, we needed to adapt the classical paradigm (Botvinick and Cohen, 1998). After performing the task, the virtual hand would disappear and the participants had to stop a virtual marker when they thought that the marker had reached the perceived position of their real hand.
3. **Physiological reactions** to a change in the environment. In some of our experiments, we implemented a threatening stimulus towards the virtual hand and we measured physiological changes, such as Galvanic Skin Response (GSR) (Armel and Ramachandran, 2003).

In the following sections, we discuss in detail the apparatus and software used for the experiments presented in the next chapters. First, in **Section 2.2**, we describe the apparatus used during the experiments presented here. Following this overall structure, we discuss each component. We used the Oculus Rift DK2 to present the participants with the virtual environment. To interact with the environment, we used the Leap Motion Controller, which online translates the movements of the participants' hand to the virtual hand. We also used the Arduino board to interact with a specific component of the virtual environment and the BiTalino board to record physiological signals.

In **Section 2.3**, we shortly describe the graphical elements that are contained in the experimental environment. which was developed using the Unity 3D GameEngine.

Finally, **Section 2.4** explains the scripts to control the behavior of the elements of the room and the experimental conditions. We were interested in designing a software that would easily allow us to trade between different experimental designs. Therefore, we organized the software using a hierarchical State Machines (SMs) that allows exchanging between specific trials that include different tasks and implicit measures for easy modification of the experimental design.

2.2 Apparatus and Software

2.2.1 Oculus Rift DK2

We used the Oculus Rift DK2 (Oculus VR, LLC) to present the participants with the virtual environment. The Oculus Rift DK2 is an HMD that presents the virtual environment through two OLED displays with a total resolution of 1920 x 1080, with a field of view of 100°. Additionally, the position and rotation of the headset are tracked by an external camera (Near Infrared CMOS Sensor), which are used to update the view of the environment according to the movement of the participants' head. This feature allows the sensorimotor contingencies required for an enhanced illusion of presence in the environment (Sanchez-Vives and Slater, 2005).

The small tracking volume of the camera presents a caveat from this system, as it constraints the task to small movements. However, in our setup, the participant was required to sit down, thus, minimizing the effects of this constraint.

The current version of the project is compatible with Unity Runtime 1.3.0.

2.2.2 Unity 3D Engine

We implemented the virtual environment using the Unity 3D Engine (Unity Technologies, SF). Unity 3D allows for easy control of the components in the virtual environment through the Unity Editor [**Figure 2.1**]. The components of the room in our experiments were designed by using the shapes in Unity or designed using 3DS Max 2015 (Autodesk, Inc). Thus, a scene in Unity is composed of these GameObjects (e.g., characters, objects, cameras,...) and the components attached to them that define their functionality (e.g., scripts).

The Unity Editor is composed of several windows. First, the scene view shows all the active GameObjects in their 2D/3D representation and allows for the navigation of the virtual environment. Each GameObject (active or inactive) can be found in the hierarchy window, which is a hierarchical text representation of every object in a scene and shows in which manner the objects are connected. Finally, in the Inspector window, the properties of the objects can be manipulated, such as the transform (position, rotation, and scale), and the components attached to the currently selected GameObject or prefab. Furthermore, to the components in the environment, we can add elements such as collision detection or scripts to implement a specific behavior (i.e., user-defined components in C# programming language). In the example shown in **Figure 2.1**, the **TableLights1** GameObject is selected and it has the MaterialChanger script is attached to it, which controls the changes in the color of this element.

To avoid compatibility problems, we settled with Unity 5.3.4p1.

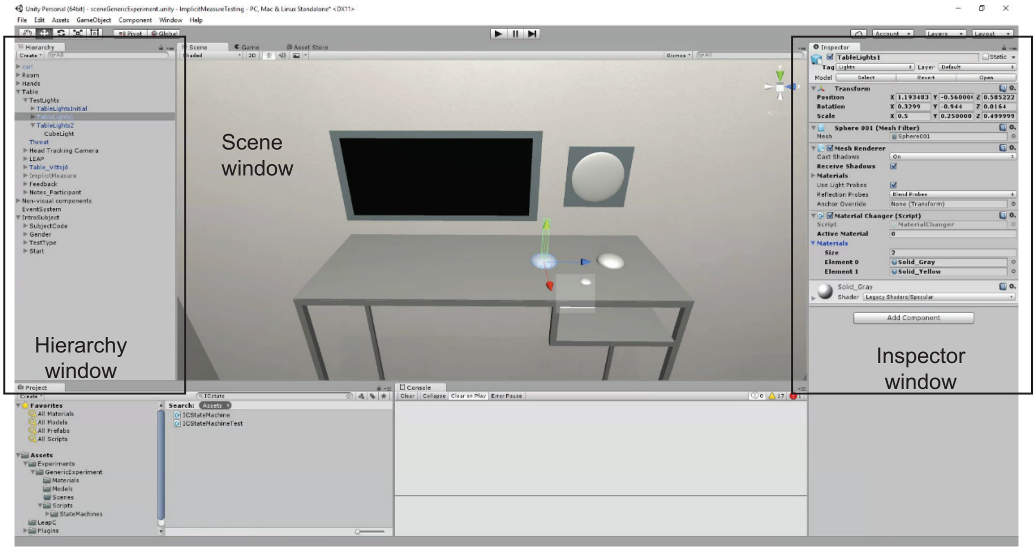

Figure 2.1: **Screenshot of the Unity 3D Game Engine showing the Experiment scene**. The Unity Editor is composed by several elements: the scene view (shows the GameObjects and their position in the virtual environment), Hierarchy window (a list of all the GameObjects), the Project window (a display of all the folders, scripts, and assets), the console, and the Inspector window.

2.2.3 Leap Motion

The Leap Motion Controller (UltraLeap,Inc - former Leap Motion, Inc) is a small USB device that detects hand and finger positions. These measurements are translated into the position of the virtual hand, which allows the user to interact with the objects in a virtual environment. The Leap Motion Controller uses an infrared scanner and sensor to map and track the human hand, by using two monochromatic infrared (IR) cameras and three infrared LEDs. The LEDs generate pattern-less IR light, while the cameras acquire the reflected light at 200 frames per second. It proceeds to synthesize 3D position data by comparing the 2D frames collected by the two cameras.

The Interaction Area (IA) of the Leap Motion Controller ranges to 80 cm above the device, 60 cm wide on each side (150^{o} angle), and 60 cm deep on each side (120^{o} angle) [**Figure 2.2**]. The overall average accuracy of the controller has shown to be 0.7 millimeters (Weichert et al., 2013). The Leap Motion SDK provided the models for the hands shown in the virtual environment.

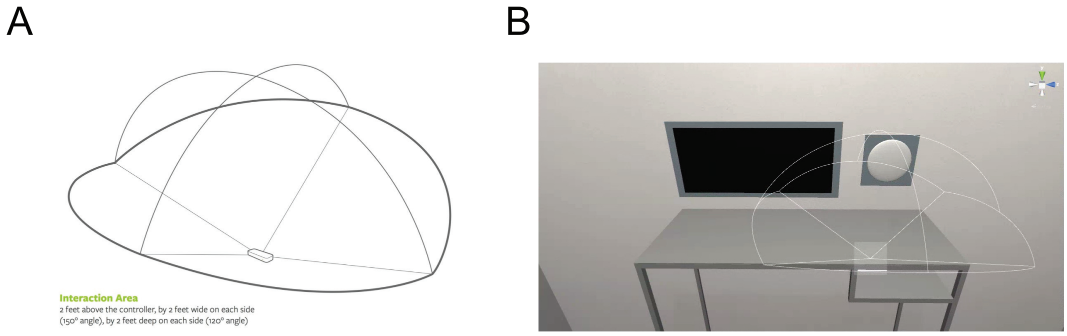

Figure 2.2: **Leap Motion Controller IA**. (A) IA area of the Leap Motion Controller (image credit: Leap Motion's former website leapmotion.com). (B) Position of the Leap Motion Controller, represented with a white cube in the virtual environment and of its interaction area in the environment.

In this project, we used the Leap Motion Controller to control the virtual arm and interact with the virtual environment without the need for sensors in contact with the participant. We also used the Leap Motion to store the position of the center of the hand during the whole experiment. To optimize the logging of the hand position, we placed the device on top of the table instead of mounted in the HMD. This was somewhat of a caveat since we needed to optimize the physical table to take maximal advantage of the Leap Motion IA. We decided on a table that presented a lower second shelf under a glass cover (VITTSJÖ model from IKEA, **Figure 2.3**), which allowed us to exploit a larger volume of the IA. We replaced the glass cover for an acrylic plastic layer to avoid artifacts of reflection.

2.2.4 BiTalino

BiTalino (plux | wireless biosignals) is a single-board device that acquires several physiological signals at the same time, such as electromyogram (EMG), electrocardiogram (ECG), electroencephalogram (EEG), and GSR. The BiTalino board offers accurate physiological signals with continuous acquisition (Kutt et al., 2018). The BiTalino operates wirelessly, as it connects to the computer via Bluetooth. Even though the connection can be done using their software, OpenSignals, we used it connected to Bonsai (Lopes et al., 2015) to acquire and store data.

Specifically, we used the BiTalino to acquire GSR signals from the participants in the trials that we used a physiological reaction to a threat to the virtual hand as an implicit measure of sense of ownership (Armel and Ramachandran, 2003).

2.2.5 Arduino

The Arduino board (arduino.cc) is an open-source hardware and software platform used to build electronic projects. It consists of a programmable microcontroller circuit board, programmed using the Integrated Development Environment (IDE). The Arduino can control other devices and send the data for later processing through serial communication with the PC.

In our project, we used the Arduino Uno board to detect when the participants pressed an analog button attached to their finger, which stopped a marker in the virtual environment. The participant was requested to stop the marker when it reached the perceived position of their unseen right hand, to calculate the proprioceptive drift.

2.3 Graphical Elements

The virtual room consisted of a replica of the experimental room, with the same size, and close appearance. The virtual environment also contains important elements that were used in the context of the experiment [**Figure 2.3**]. All these GameObjects are detailed in the list below.

- **Room**: This GameObject contains several child-GameObjects that represent the walls, floor, ceiling, and lighting of the virtual room (i.e., nine point lights). These components are controlled to be set to *inactive* at a certain point in the experiment to darken the room.

- **Table**: The room contained a table, which was a 1:1 replica of the table in the physical room, with the same shape, size (100 cm x 36 cm x 77 cm) and position. It contains important children objects
  - **Test Lights**: Semicircular GameObjets that act as lights for the goal-directed task. They are defined in the Unity Game Editor through an array that contains the number of lights in the environment [**Figure 2.1**], which allows to easily change the number of lights present in the environment. For all our tasks, we used one **initialLight** and two **targetLigths**.
  - **Screens**: The virtual environment contains two additional GameObjects that serve as screens to present the participants with (1) feedback on the performance of the task, and (2) the questions that are used as a subjective measure of the experience of the illusion.
  - **LeapHandController**: The origin of the hand tracking, which is equivalent to the position of the Leap Motion Controller in the physical environment.
  - **Marker**: The group of elements that are used to measure the proprioceptive drift measure in the trials where is required.
  - **Threat**: The threat was used as an implicit measure of the sense of ownership in some studies. When present, the threat is represented as a knife [**Figure 2.9B**].
- **Tracking camera** Origin of the VR headset. It contains the **VRCameraRig** that connects to the image in the Virtual Reality Headset.
- **Hands** These elements represent all the hand models that are used (male/female, with/without a forearm,...) during the experiment. The hands are controlled through RiggedHandEx script, which is a modified version of the Leap Motion Controller **RiggedHand** script to add noise to the trajectory of the virtual hand and stop the hand from moving in the required experimental conditions [see **Section A.5**].

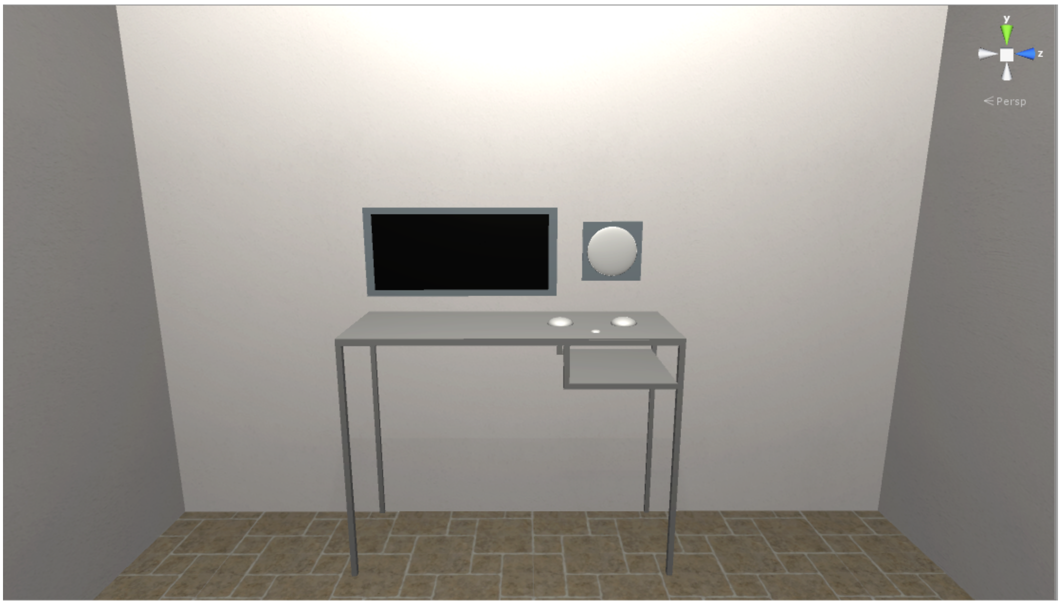

Figure 2.3: **Virtual Reality Room**. The virtual setup consisted of a simple room that imitated the physical experimental room in size and characteristics

2.4 Scripts

The behaviour of the objects, such as the detection of the collisions, or the selection of the appropriate hand model, is controlled by scripts. While there are no fundamental difference between them, we have grouped the scripts in four categories:

1. **State Machines** that control the main logic of the experiment, organized in a hierarchical manner (described in **Section 2.4.1**).
2. **Event providers** that trigger the transitions between states in a State Machine (described in **Section 2.4.2**).
3. **Action providers** are scripts that change the behaviors of the elements in the virtual environment (described in **Section 2.4.3**).
4. Scripts that **load** the parameters of the trials and **log** the events and results (described in **Section 2.4.4**).

In the following sections, we discuss in more detail each of these scripts and their roles in the project.

2.4.1 Hierarchical State Machines

A state machine (SM) is an abstract machine that contains a finite number of states and events that control the transitions between these states. The states and the events are fixed for a given SM. In our implementation, the transitions between two states are triggered either by an event (e.g., the experiment has started) or when a timer expires (e.g., after 5 seconds in the same state). The ICStateMachine[1] class is described in detail in **Appendix A.1**. This class is the basis for implement all the SMs.

The flow of our experiment is implemented using a hierarchical structure of the SM classes. Each SM has parent and child SMs and can trigger events between them, such as starting them or cause a transition of the states [**Figure 2.4**]). In our project, the ExperimentController is the main SM and it invokes the TrialController. In turn, the TrialController invokes the Controller for the specific trial, which is different for every experimental design, and the QuestionnaireController. Normally, the trials require that the participant performs a reaching task towards some targets. This behavior is controlled by the WaveController. Other SMs invoked by the Controller of each specific trial are the ThreatController (when the task required the physiological reaction as an implicit measure or the DriftController (a variation of the Proprioceptive Drift measure).

Experiment Controller

The ExperimentController SM is the main class of the experiment and is the parent to all SMs. It controls when the trials are started, whether there are any additional trials to be run, and when the experiment is finished. It also calls the methods to load the trials and logs the output files for each trial (hand positions, results, ...) (see **Section 2.4.4**).

The ExperimentController is composed of five states (Idle, Start, Interval, Trial, and End) and three events (ProtocolLoaded and NextTrial, and TrialFinished) [**Figure 2.5**].

In the initial state of the ExperimentController, Idle, the actual experiment has not yet started, but the logging component has been started (see ICLogger), and the getInformation class is active. This class is attached to a Graphical User Interface (GUI),

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[1] IC stands for Ivar Clemens, who worked as a postdoc at the *Collective Behaviour* lab during 2015. He was crucial in the implementation of the classes for this project. Among other classes, he designed a generic state SM class that can be easily implemented in any new state machine needed. We thank Ivar for his contributions to the initial states of this project. *Dank u zeer.*

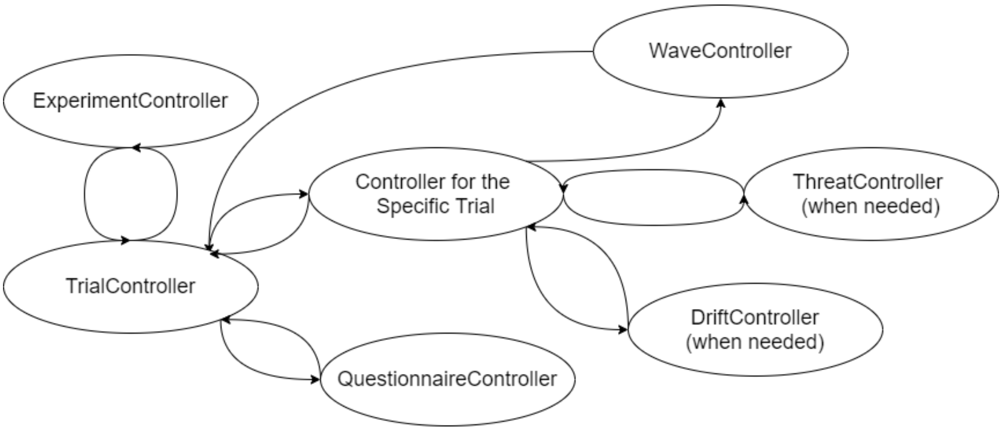


Figure 2.4: **Hierarchical relationship of the SMs classes**. The SMs are organized in a hierarchical manner. The ExperimentController is the main class and controls the rest of SMs. The TrialController controls two important components of the project: the Controller for the specific trial and QuestionnaireController.

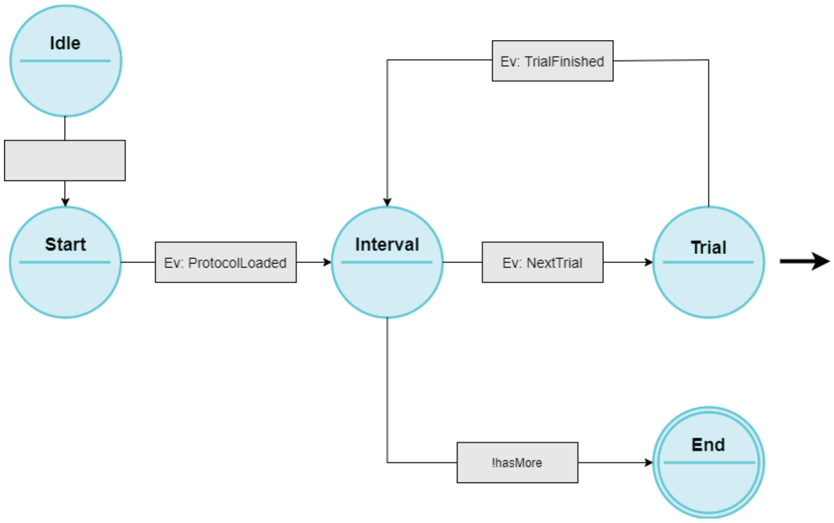


Figure 2.5: **ExperimentController SM diagram**. The ExperimentController consists of five states (in blue) and three events (in gray).

where the experimenter enters the subject code, selects the experiment type (which selects the specific trial type), and the appearance of the hand (male or female model). When the Start button is clicked on the GUI, the ExperimentController transitions to the Start state and the experiment starts. In this state, the **ProtocolFile** is loaded from the directory for the selected type of experiment **Section 2.4.4**, and the ProtocolLoaded event is fired. The ICTrialList checks whether **TrialList** contains any trials. If so, it triggers the NextTrial event, and the ExperimentController enters the Trial state, from which the TrialController is started. When the trial finishes, the TrialFinished event is triggered, and causes a transition back to the Interval state. In this transition, the **SaveTrialResult()** method logs all the information in the corresponding folder. If the **TrialList** contains additional trials to be run, the SM returns to the Trial state. If the **TrialList** has no more trials, (**!hasMore**) the ExperimentController changes to the End state and the experiment finishes.

Trial Controller

The TrialController SM controls the behaviour of every individual trial, which includes the specific type of trial trial and the questionnaires. It is started from the ExperimentController for every trial contained in the **TrialList**.

The TrialController consists of four states that run in a linear way (Idle, SpecificTrial, Questionnaire, and End) and two events (SpTrialFinished and QuestionFinished) [**Figure 2.6**].

The TrialController is started from the ExperimentController SM on its initial state, Idle. After a timeout of 2.0 seconds, it transitions to the SpecificTrial state. In this state, the Controller for the specific trial type is started, depending on the selected experiment type in the getInformation class. When the Controller for the specific trial finishes, the SpTrialFinished is triggered, and the TrialController transitions to the Questionnaire state. The QuestionnaireController is started and the questions are displayed through a screen that appears in the virtual environment. When the questionnaire is finished, the QuestionnaireFinished event is triggered. In the End state, the TrialController SM stops and it sets the TrialFinished event in the ExperimentController.

Controllers for the Specific Trials

The different experiments required different types of trials that present some substantial differences in their design. In the initial stages, this required making changes in the TrialController, making it difficult to swap between different experimental designs. For this reason, we resolved that we would create a specific Controller for each type of trial

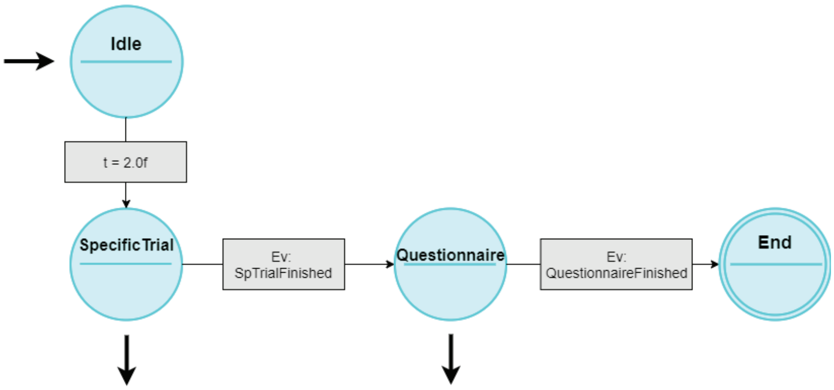


Figure 2.6: **TrialController SM diagram**. The TrialController consists of four states (in blue) and two events (in gray).

that would be invoked from the TrialController. This approach allowed us to change easily between experimental designs, while the other SMs of the project remained unchanged. In this type of design, we include four trial types:

activeTrialController : This type of trial was used to for the data collected in the *movement* conditions presented in **Chapter 4**. The position of the hand was controlled by the movements of the physical hand. In this type of trial, the visual appearance of the hand and the visuomotor correlations can be manipulated from the **ProtocolFile**.

inactiveTrialController : In this type of trial, the **ignoreUpdate** property is set to *active* and the virtual hand does not move. We used this type of trial for the *no movement* conditions presented in **Chapter 4**.

visuomotorInformation This type of trial was used to collect the data for **Block A** presented in **Chapter 5** and included modifications related to the visuomotor information presented to the participant (i.e., outcome of the action and trajectories of the virtual hand).

outcomeOwnership This type of trial was used to collect the data for **Block B** presented in **Chapter 5** and included manipulations related to the outcome of the action and the morphological appearance of the limb.

These Controllers invoke the respective child classes for specific functions. For instance, activeTrialController trials require the participant to perform a reaching task towards a target. These types of trials use the WaveController, which controls the behavior of the waving events towards the target. Additionally, a trial can include measuring the physiological reactions to a threat to the virtual hand, which requires the ThreatController, or the DriftController if the trial includes a behavioral measure.

Additional differences between trials in the same experimental design are defined by the **ProtocolFile**.

Wave Controller

In some trials, the participants executed a task that consisted of reaching movements towards target lights in the virtual environment [**Figure 2.3**]. The WaveController controls the behaviors related to this task, such as the lights turning on/off, counting the outcome results, or give the feedback of the task.

The WaveController SM consists of seven states (Idle, Initial, Delay, Target, Feedback, Interval, and End) and three events (Wave_Initial, Wave_0, and Wave_1).

The WaveController is initiated on the Idle state from the Controller of each specific trial class. After 0.25 seconds, the SM transitions to the Initial state and the **initialLight** changes color to dark blue while the collider attached to this light is set to *active*. When the virtual hand reaches the collider, the Wave_Inital event is fired from the SimpleCollision class (see **section 2.4.2**), resulting in the light changing back to its original color. The SM transitions to the Delay state and, after a **timeout** of 0.5 seconds, it changes to the Target state. A random number between 0 and the total amount of target lights defines the **currentLight**, which changes color to yellow. At the same time, the colliders for all the **targetLights** are set to *active*. When the collider of one of the **targetLights** is triggered, the corresponding event for that light is fired. If the event is triggered from the **currentLight**, it is counted as correct wave and added to the correct counter in the TrialController; otherwise, it is counted as incorrect. Additionally, if the participants failed to reach any of the target lights before the defined **timeout**, the wave is counted as a late wave. After any of these events, the state changes to the Feedback state and the **feedbackScreen** changes color depending on the outcome. After 1.5 seconds, the

feedbackScreen screen turns off and the SM returns to the Interval state. We have labelled as **wave** each of the movements encompassed between the Initial and the Interval state.

For as long as the number of the **currentWave** is lower than the **requiredWaves** (defined in the **ProtocolFile**, the WaveController transitions back to the Initial state and the whole process is repeated. When the SM reaches the Initial state and the number of the **currentWave** matches the number of **wavesRequired**, the SM enters the End state, the WaveController SM stops and the TaskFinished event is triggered in the TrialController.

Questionnaire Controller

The participants reported their subjective experience of the illusion by answering a questionnaire at the end of each condition. These questionnaires are controlled by the QuestionnaireController. The list of statements is defined within the QuestionnaireController class and presented to the participant by the **display** GameObject (black screen in **Figure 2.3**).

The QuestionnaireController consists of six states (Idle, Start, ShowQuestion, WaitingforResponse, Delay, and End) and three events (StartQuestionnaire, QuestionDisplayed, and QuestionAnswered) [**Figure 2.8**].

When QuestionnaireController is started from the TrialController in the initial state, Idle, the **display** GameObject is set to *active* and it is shown in the virtual environment. The StartQuestionnaire event is triggered and the SM changes to the QuestionnaireStarted state. After a 1.0 seconds **timeout**, the SM changes to the ShowQuestion state. The QuestionDisplayed event is triggered, which changes the state to the WaitingforAnswer state. Here, while the question is displayed, the program waits for the input from the experimenter (i.e. response). The answer is recorded in the output file and the QuestionAnswered event is triggered. As a result, the QuestionnaireController changes to the Delay state.

The statements are presented in a randomized order using the **GetRandomNumber()** method implemented in this class. This method takes the total number of statements and creates a numerical array of equal length to the number of elements that are

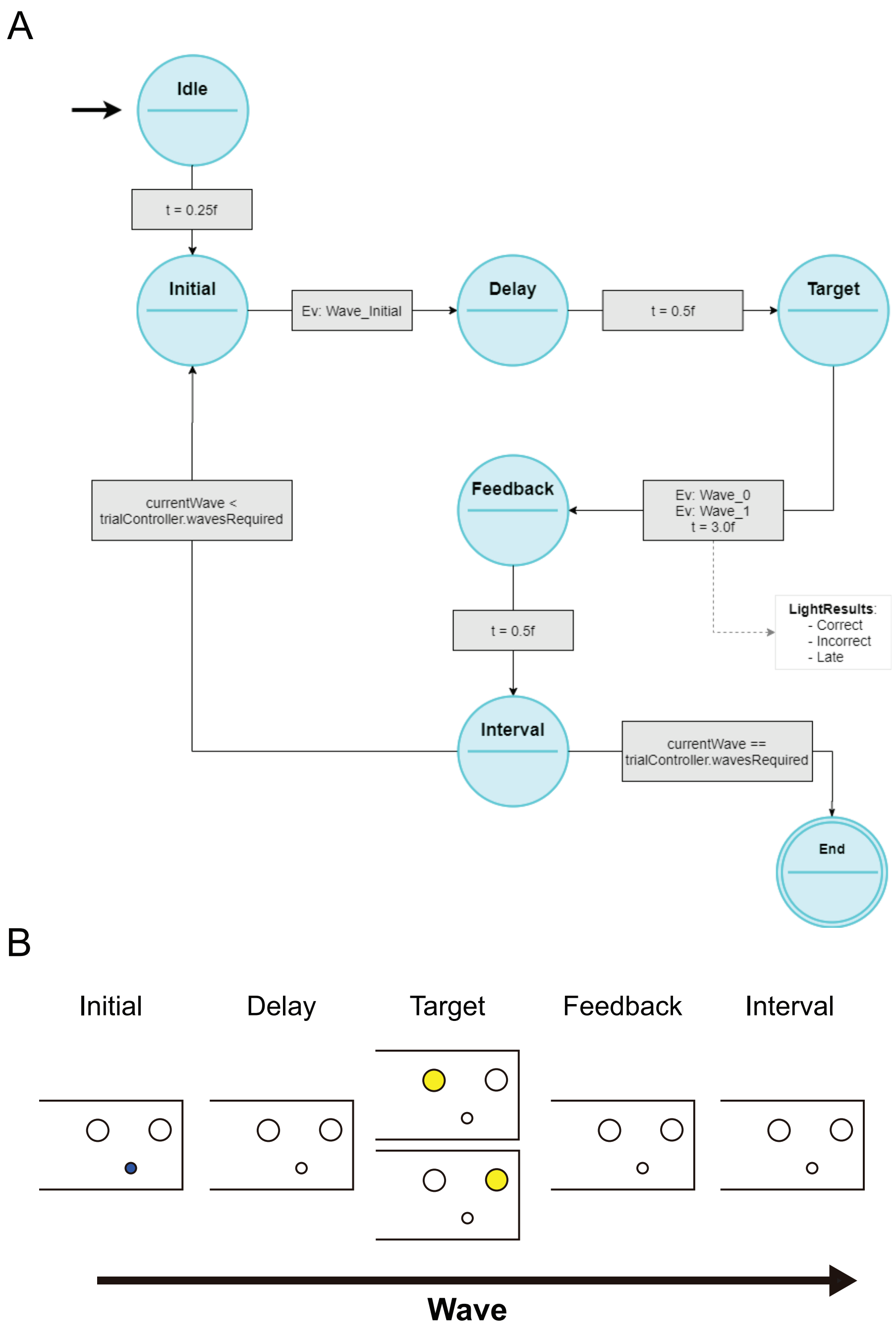


Figure 2.7: **WaveController SM diagram and schematic of a wave**. (A) The WaveController consists of six states (in blue) and three events (in gray). (B) Schematics of the behavior of the lights during a single wave event.

contained in the **statements** string. Every time a question is displayed, a random number is selected from this array, the statement is presented, and the number is eliminated from the array. In Delay state, if the numerical array contains additional elements, it returns to the ShowQuestion state and a new question is selected; otherwise, if the array is *null*, the SM transitions to the End state and QuestionnaireController is stopped.

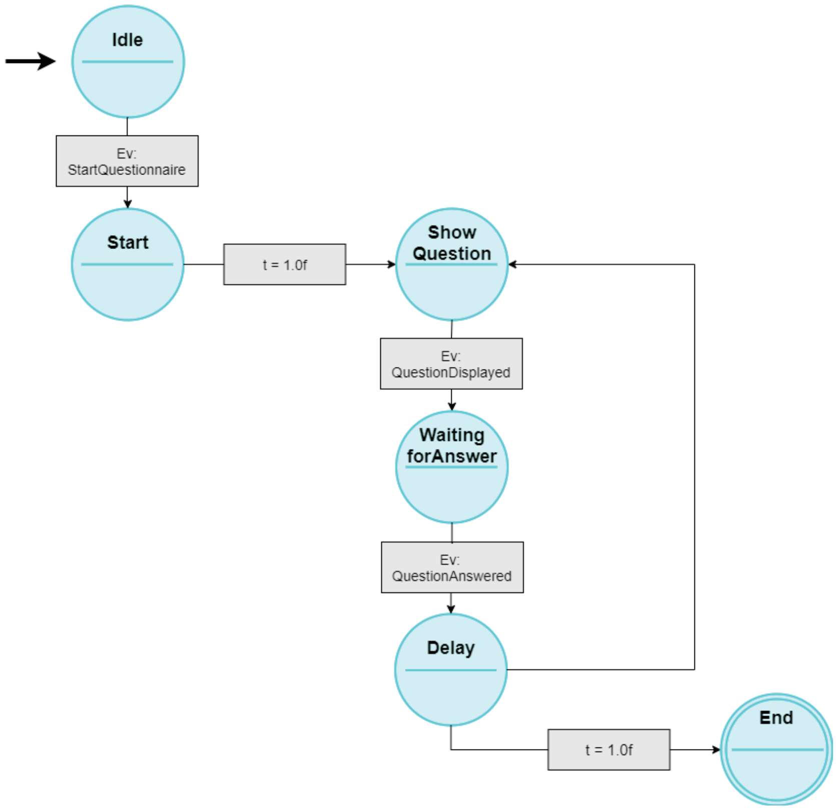


Figure 2.8: **QuestionnaireController SM diagram**. The QuestionnaireController consists of six states (in blue) and three events (in gray).

Threat Controller

In a subset of the studies, we measured the physiological reaction to a threat directed to the virtual hand as an implicit measure of the sense of ownership. The threat is controlled by the ThreatController SM. The **threat** GameObject is set *active* at the end of a specific trial and falls onto the specified position in the virtual environment (e.g., the center of the virtual hand). The threat was presented in the form of a knife (*knife_5p* from the Melee Pack package from the Unity Asset store, **Figure 2.9**).

The presence or absence of the threat is defined in the **ProtocolFile**, which also defines the target position of the threat using the **knifeOffset** parameter.

The ThreatController SM consists of four states (Initial, Falling, Following, and End) and two events (ReleaseThreat and TargetReached) [**Figure 2.9**].

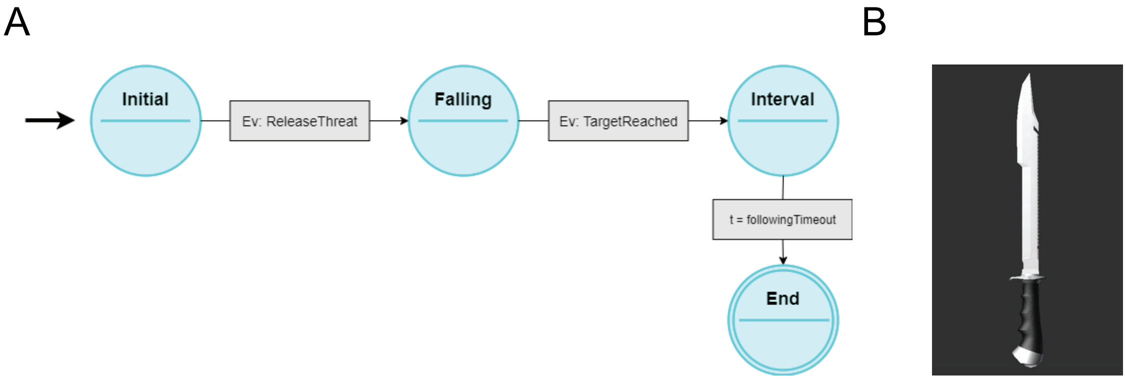


Figure 2.9: **ThreatController SM diagram and threat knife model**. (A) The ThreatController consists of four states (in blue) and two events (in gray). (B) Knife model from the Melee Pack package the Unity Asset.

The ThreatController SM is started on the Initial state, and the threat component is set to *active*. Once the ReleaseThreat event is triggered from the Controller for a specific trial, the SM changes to the Falling state, in which the threat moves towards the target position. Once it has been reached, the TargetReached event is triggered and the SM changes to the Following state. The knife is kept in the position during the specified time (defined in the followingTimeout), during which it matches the rotation of the hand. At the end the followingTimeout time, the ThreatController transitions to the End state and the SM stops.

Proprioceptive Drift Controller

In some of the experiments, the participants needed to report the perceived position of their real hand at the end of each condition by the means of a visual marker. The DriftController is responsible for controlling the visual marker and logging the response. When active, it shows a marker that moves from left to right and back [**Figure 2.10**].

The participants are required to press a button when the marker is in the perceived location of their unseen physical right hand.

The DriftController SM consists of four states (Idle, Moving, Measured, and Finished) and three events (Start, ButtonPressed, and Stopped) [**Figure 2.10**].

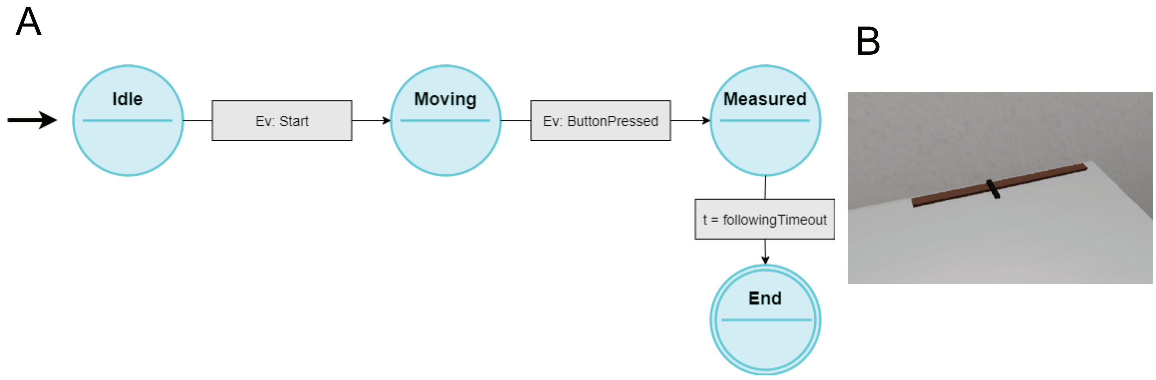


Figure 2.10: **DriftController SM diagram and marker**. (A) The DriftController consists of four states (in blue) and three events (in gray). (B) The marker GameObject.

The DriftController SM is initiated on the Idle state. After a 1.5 seconds timeout, the Start event is triggered and the SM transitions to the Moving state. At this point, the marker starts moving from -0.28 to 0.28 units with a velocity of 0.04 units/s. The visual marker moves until the participant presses the button, which fires the ButtonPressed event and the SM transitions to the Measured state. After one second, the Stopped event is triggered and the SM transitions to the Finished state and an event is fired to the TrialController signalling the end of the measurement.

2.4.2 Event providers

Simple Collision

The SimpleCollision script is used to detect when the virtual hand has reached a **targetLight**. The colliders attached to the lights are invisible and are set to *active* by the WaveController SM. The SimpleCollision class waits for a collision between the light collider and an object named HandContainer (which covers the palm of the virtual hand) [**Figure 2.11B**] and then fires the selected **triggerEvent** on WaveController. It is important that the **HandContainer** contains both a **RigidBody** and **BoxCollider** component. Additionally, th SimpleCollision script is used in the manipulated the outcome of the task by changing the *probability* property.

Figure 2.11: **Colliders and HandContainer**. (A) The rectangular prisms depicted in green contain the area that detects the collision with the **HandContainer** (B) The **HandContainer** covers the palm of the virtual hand and interacts with the colliders to trigger a **SimpleCollision** event

2.4.3 Action providers

getInformation

This class collects all the relevant information for the experiment to start. The getInformation class is related to the GUI [**Figure 2.12**], which requires to input the code of the subject, the gender of the hand, and the type of experiment.

The code of the subject is used for logging purposes, specifically, to name the **outputFolder** that contains the text files (log, handposition, and questionnaire responses). Second, the gender of the hand is selected to match the gender of the participant, by the means of the HandSwitcher [see **Section 2.4.3**]. Finally, the type of experiment selects the trial type by selecting the Controller for the specific trial. The StartExperiment button changes the state of the ExperimentController and the experiment starts.

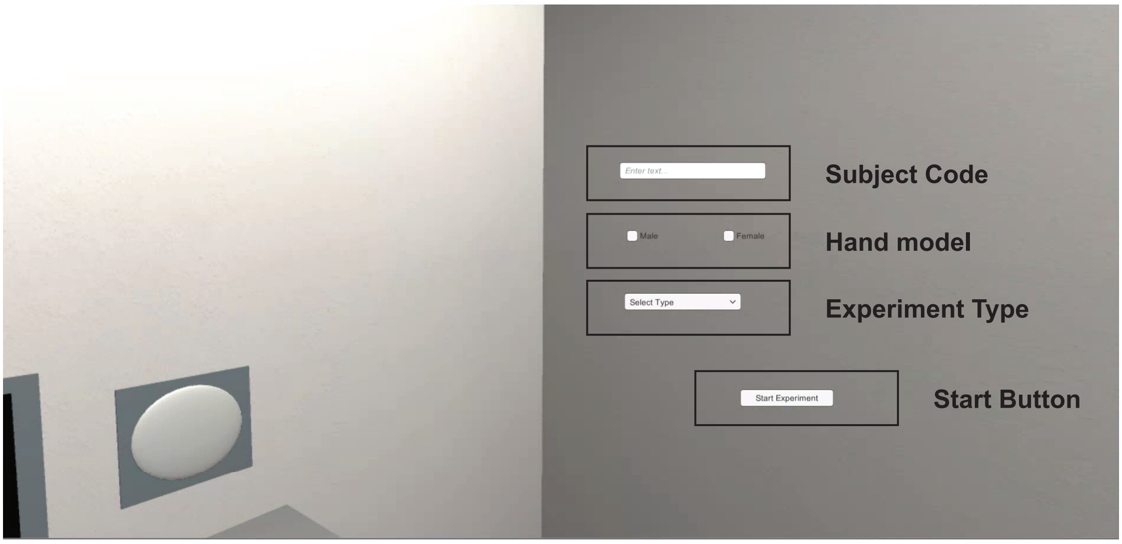


Figure 2.12: **Graphical User Interface (GUI)**. The GUI appears at the beginning of each experiment and is used to introduce relevant information regarding the characteristics of the experiment, such as the code for the participant, the type of the experiment and the gender of the hand model

Material Changer

The MaterialChanger allows us to easily change the material of an object. We used this script to change the color of the target lights and the feedback screens. When this script is added to a GameObject (e.g., target light), it allows to add a list of materials (colors) that are set by events or by entering a specific state of the SM, using the **activeMaterial** property.

Hand Switcher

The HandSwitcher script changes between the different hand models. During the experiments presented in this dissertation, we used this class to change between the two hand models: continuous and discontinuous (with and without forearm).

The model of the hand used for a determined condition is defined by the **GapStatus** property of the **ProtocolFile**, which can be defined as *inactive* when the arm has to be in a continuous form or *active* when it has to appear in the discontinuous form.

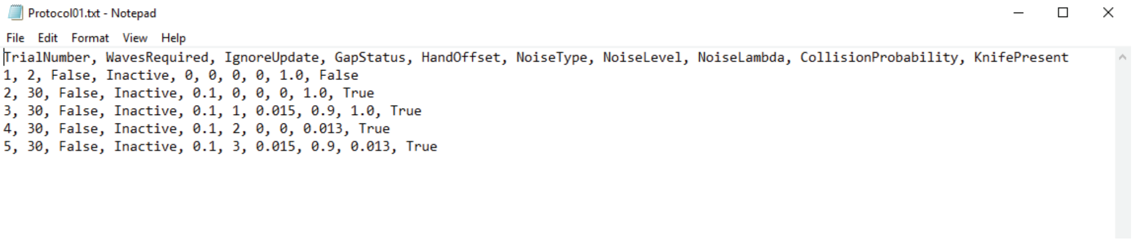
Offset Switcher

The OffsetSwitcher is a simple script that takes the initial position of the **HandController** GameObject, and updates its transform (i.e., position and orientation). Thus, the origin of the virtual hand is displaced by a specified distance to the left. The offset is determined by the **ProtocolFile** in centimeters in the **HandOffset** property. A non-zero offset causes displacement between the position of the center of the virtual and physical hand equivalent to the displacement of the **HandController**. If the **ProtocolFile** does not define an offset, the default offset is set to be 0 cm (i.e., both hands in the same position).

2.4.4 Trial loading and logging

ICTrialList

The ICTrialList class loads and reads the **ProtocolFile**, which is a .txt file that contains all the information regarding all the trials included in an experiment [**Figure 2.13**]. The ICTrialList is called from the ExperimentController, at the beginning of an experiment and passes the information to the respective child classes.



```
TrialNumber, WavesRequired, IgnoreUpdate, GapStatus, HandOffset, NoiseType, NoiseLevel, NoiseLambda, CollisionProbability, KnifePresent
1, 2, False, Inactive, 0, 0, 0, 0, 1.0, False
2, 30, False, Inactive, 0.1, 0, 0, 0, 1.0, True
3, 30, False, Inactive, 0.1, 1, 0.015, 0.9, 1.0, True
4, 30, False, Inactive, 0.1, 2, 0, 0, 0.013, True
5, 30, False, Inactive, 0.1, 3, 0.015, 0.9, 0.013, True
```

Figure 2.13: **Protocol File example**. The Protocol Files are text files specific to each type of experiment. The columns correspond to the properties of the experiment, while each row corresponds to an individual trial.

The **ProtocolFile** is specific for each experiment type. To counterbalance the order of the conditions between the participants, we prepared a protocol file for each possible combination of trial types. Then, the ICTrialList randomly selects a file from the folder and loads it. In a **ProtocolFile**, each row represents a single trial and the columns correspond to the trial properties. The properties defined by this file are: **TrialNumber** (numbering of the trials), **WavesRequired** (number of waves that are needed to finish a trial), **IgnoreUpdate** (whether the virtual hand moves or not), **GapStatus** (define the hand model used, full arm or detached hand), **HandOffset** (difference in the position between the real and the virtual hand), **NoiseType** (identifier of the noise added to the virtual hand movement), **NoiseLevel** (amount of noise added to the movement of the virtual hand), **NoiseLambda** (also used in the addition of noise to the virtual hand movement), **CollisionProbability** (defines the probability of the collider being active), and **KnifePresent** (whether the threat is present or not). If the **ProtocolFile** does not define any of these parameters, a default value is defined from the ExperimentController.

The ICTrialList component loads the file, passing the file name to the constructor. It has three main functions: **HasMore()** returns a boolean indicating whether or not there are more trials in the list, **Count()** returns the total number of trials, and **Pop()** returns the next trial as a Dictionary<string, string> which maps header identifiers to field values for the current trial (see **Appendix A.2**).

ICLogger

The ICLogger component logs the events that happen during an experiment and the respective timestamps onto a .txt file. The ICLogger is attached to every SM to be able to log when the events are triggered and the transitions are happening.

The ICLogger has three main functions: the **Write(message)** writes the entries to the log. Also, the functions **OpenLog(string filename)** and **CloseLog()** are called to open the file and close it at the beginning and end of the experiment, respectively (see **Appendix A.3**).

2.5 Output files

Experiment File : A .txt file where all the events of a single experiment are logged in order, with their corresponding timestamp, the SM that triggered it, and the event.

Trial File : A Trial File is saved containing all the properties of the trial.

Response File : A .csv file for every trial that records the questionnaire responses (in the order they were collected for every question displayed to the participant).

Hand Position File : A .csv file that contains a list of the x, y, and z positions of the center of the virtual hand, with the corresponding timestamp.

2.6 Discussion

VR environments have been extensively used in behavioral human studies. They offer many advantages to research in naturalistic interactive settings while ensuring a high degree of control and standardization (Tarr and Warren, 2002; Bohil, Alicea, and Biocca, 2011; Slater and Sanchez-Vives, 2016). VR environments have proven instrumental in the study of self-representation (Slater et al., 2010; Sanchez-Vives and Slater, 2005) and in navigation in humans (Warren et al., 2001; Diersch and Wolbers, 2019). Additionally, VR has not only proven useful in humans, but also in animal models (Stowers et al., 2017) in studies ranging from motor adaptation in zebrafish (Ahrens et al., 2012) to visual cues in fruit flies (Schuster, Strauss, and Götz, 2002; Haberkern et al., 2019) and rodents (Thurley and Ayaz, 2017).

During this project, we aimed to understand how different sources of information (namely, proprioception, visual appearance, and motor information) interact to induce a sense of ownership and agency over a virtual limb. To achieve this goal, we needed a system that would allow us to modify the appearance of the hand and visuomotor information about the movement in an effective manner.

In this chapter, we present the virtual environment that we have developed for our studies in self-representation in healthy human participants. By using a hierarchical SMs, we have created a modular project that requires minimal modifications to change the experimental designs. Each design is defined by the Controller for the specific trial and the properties defined externally by the **ProtocolFile**.

Overall, VR systems have proven themselves useful in the study of multisensory integration in the field of self-representation (Slater et al., 2010; Kilteni, Groten, and Slater, 2012). Additionally, these systems have also been helpful in the study of body image disorders, treatment of disorders such as anorexia (Riva, Wiederhold, and Mantovani, 2019), and also in pain management (Matamala-Gomez et al., 2019),

Nevertheless, our system presents some limitations. First of all, our current setup presented a very limited range of movements as a result of the devices that we were using. Using the Leap Motion Controller, we achieved a good degree of hand tracking; however, it limited the movement to a small interaction area. This would not be the case in other types of systems, such as tracking gloves (Sanchez-Vives et al., 2010). When the hand was taken beyond the interaction area, tracking errors would occur, creating mismatches between the movement of the participant and the movement of the virtual hand. Such errors would potentially break the illusion (Sanchez-Vives and Slater, 2005; Slater and Steed, 2000) and render the data unusable (and subsequently, discarded).

Other types of hardware could allow us for control over a full body (i.e., full-body motion capture systems) (Peck et al., 2013) or haptic devices that could deliver further sensory stimulation (tactile, auditory) (Desantis et al., 2012; Burin et al., 2017). However, for this thesis we decided to focus on sitting participants, while only using their right hand, to understand the role of visuomotor information on the senses of ownership and agency over a virtual limb.

Finally, it is worth noting that, due to technical limitations, we did not show a virtual body in the environment. However, the participants were always requested to look at the hand, which minimized the effect of this constraint. Additionally, the sense of ownership and agency over a virtual limb has been reported in the absence of a body (Kondo et al., 2018).

Overall, the unrestricted interaction (using the Leap Motion Controller) with an immersive environment presented through a HMD allowed us to finely manipulate distinct sources of information to study the senses of ownership and agency over a virtual hand. Thus, providing advantages compared to screen systems and rubber hands. Moreover, our hierarchical SM architecture provides the flexibility to tackle different experimental hypothesis regarding self-representation.

2.7 Conclusions

- Virtual Reality systems offer new tools to tackle questions in the field of self-representation, as it allows for the dissociation of sensory information, which is crucial to study the integration of how multiple sources of information build up the representation of the self.
- The implementation using State Machines (SM) offers easy control of the behaviors used in the project.
- We provide a framework to study the role of visuomotor information in the senses of ownership and agency in a virtual reality environment. This environment allows for an easy interchange of the type of experiment, making it adaptable to different experimental questions.
- We also provide an environment in which the addition of new behavioral and physiological measures can be easily integrated into the existing hierarchical system of classes.

2.8 Conclusões

- Os sistemas de Realidade Virtual (RV) conferem novas ferramentas que permitem investigar questões relacionadas com a representação do próprio. Estes sistemas permitem a separação e manipulação de diferentes fontes de informação sensorial, o que é de vital importância para investigar a integração de multiples fontes de informação para a construção da representacão do próprio.
- A implementação do nosso sistema de RV usa *State Machines* permitindo um controlo fácil dos comportamentos necessários neste projecto.
- Com este sistema, fornecemos uma estrutura de trabalho para estudar a importância da informação visuomotora nos sentidos de propriedade e agência. Esta estrutura permite uma alterção rápida e fácil entre differentes metodologias experimentais, garantindo uma flexível adaptação a questão experimental em estudo.
- Fornecemos tambêm uma estrutura em que a adição ou remoção de novas medidas implícitas pode ser integrada no sistema de uma forma fácil.

3 | Experimental methodology

"[...] que tot està per fer i tot és possible."
"[...] that all is to be done and all is possible"

Miquel Martí i Pol, Ara mateix

3.1 Overview

In this chapter, we describe the experimental methodology for the three studies presented in **Chapters 4** and **5**. These experiments were carried out during 2015 and 2019 and included a total of 116 human volunteers. The data were collected at the Champalimaud Research by the author of this dissertation.

The data obtained from **Experiment 1** and **2** are presented in **Chapter 4**. These experiments aimed to assess whether congruent active control enhanced and maintained the reported senses of ownership and agency over a virtual limb that appeared in a discontinuous form. In **Chapter 5**, we present the results collected in **Experiment 3**, in which we manipulated the consequence of the task in the environment to assess the importance of the outcome congruence in the reported senses of ownership and agency.

3.2 Description of the Experiments

3.2.1 Experiment 1

Motivation

Previous studies have reported a decrease in the senses of ownership and agency over a virtual limb as a result of seeing the arm in a discontinuous form. These studies include visuotactile stimulation (Perez-Marcos, Sanchez-Vives, and Slater, 2012) and passive observation of movement (Tieri et al., 2015a). However, whether body discontinuity decreases the sense of agency under active control over the virtual hand movements remains unclear.

We hypothesized that visuomotor information resulting from active control should maintain a sense of agency and, subsequently, a sense of ownership over the virtual hand that appears detached from the body. To test for this hypothesis, the participants controlled the virtual hand in a goal-directed task. We compared the reported agency and ownership scores over a virtual hand that could appear connected or in a discontinuous form (i.e., seeing the hand with the missing forearm). Additionally, we tested whether the proprioceptive displacement of the hand affected the reported senses of agency and ownership in the conditions mentioned above.

Experimental design

In a custom-made VR environment, the participants controlled a gender-matched virtual arm. The task consisted of reaching the lights on top of the virtual table to turn them off without touching them, to avoid tactile information.

We manipulated the physical appearance and the relative position of the virtual arm to the physical arm. We used two hand models, one that appeared attached to the body and one that appeared as discontinuous from the body (i.e., missing forearm). These conditions were labeled *full arm* and *detached hand*, respectively. Additionally, the hands could either appear in the same position or displaced ten centimeters from each other. These conditions were labeled as *no displacement* and *displacement*, respectively. **Table 3.1** provides a description of the conditions for **Experiment 1**.

Condition	Hand appearance	Hand position
Full arm - no displacement	Continuous	The virtual and the physical hand appeared in the **same** position.
Full arm - displacement	Continuous	The hands were **10 cm** apart.
Detached hand - no displacement	Discontinuous (missing forearm)	The virtual and the physical hand appeared in the **same** position.
Detached hand - displacement	Discontinuous (missing forearm)	The hands were **10 cm** apart.

Table 3.1: **Description of the experimental conditions for Experiment 1**. Experiment 1 consisted of four conditions, in which either the appearance of hand (i.e. *full arm* vs *detached hand*) or the relative position of the virtual and the physical hand was manipulated (i.e. *no displacement* or *displacement* conditions).

Procedure

Upon arrival, the participants were seated and the experimenter verbally explained the instructions to them. The experimenter fitted the HMD and the experiment started.

All participants underwent two blocks of conditions, one that included two *full arm* conditions and another that included two *detached hand* conditions. Each block consisted of a *no displacement* and a *displacement* condition. Thus, resulting in a total of four conditions: *full arm* - *no displacement*, *full arm* - *displacement*, *detached hand* - *no displacement*, and *detached hand* - *displacement*. The blocks were counterbalanced across the participants: half of the participants experienced first the *full arm* conditions and half the *detached hand* conditions [**Figure 3.1**]. Within the blocks, *no displacement* always preceded the *displacement* condition. The participants underwent the two blocks without any period of rest between them. A detailed explanation of the procedure of each condition can be found in an upcoming section [see **Section 3.4**].

After each condition, the participants were required to report their hand's perceived position. The virtual hand would disappear while the participants were asked to maintain their hand still without resting it on the table. Then, a ruler with a marker appeared at the end of the table and started moving. Using an analogical button attached to their physical left hand, the participants stopped the marker when they thought it reached their right hand's perceived position. After this, the marker would disappear and the participant verbally replied to the questionnaires [see **Section 3.7**] without removing the headset.

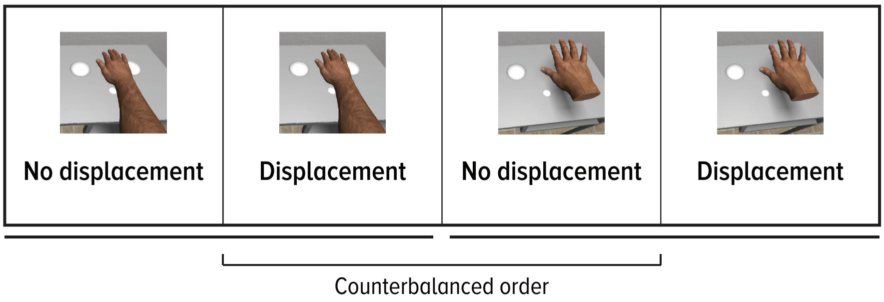


Figure 3.1: **Experimental design for Experiment 1**. The participants underwent four conditions, two with the arm that appeared attached to the body (i.e., *full arm* conditions) and two with the hand that appeared in the discontinuous form (i.e., *detached hand* conditions). Additionally, the hands could either be collocated or displaced ten centimeters of each other. The conditions with the same hand appearance were presented together, but the order in which they appeared was counterbalanced. Thus, the *no displacement* conditions always was presented before the *displacement* conditions.

3.2.2 Experiment 2

Motivation

The results obtained in **Experiment 1** suggest that visuomotor information maintained a sense of agency and ownership over a virtual hand when it appeared as detached from the body.

We further hypothesized that visuomotor information resulting from voluntary active control would enhance the reported sense of ownership over an actively controlled virtual hand compared to observing a static limb. Using the same experimental setup, we compared the reported sense of ownership and agency in conditions where the participants actively controlled the virtual hand or without visuomotor information. Additionally, we assessed the effect of body discontinuity in the absence of movement to understand the interplay between visual appearance and motor information. Conversely, we hypothesized that, when the movement of the virtual hand was incongruent to the movement performed by the participant, both the senses of ownership and agency would decrease. Thus, we assessed the reported ownership and agency in a condition where noise was added to the trajectory of the virtual hand.

Experimental design

The experiment was divided into four blocks [**Figure 3.2**]. The first block consisted of two *no movement* conditions, one in which the arm appeared to be attached to the body and one in which the forearm was missing. These conditions were labeled *full arm* - *no movement* and *detached hand* - *no movement*, respectively. These conditions were counterbalanced within the block across participants. The second block was a *movement* block in which the participants performed the goal-directed task. As in the first block, it also consisted of two counterbalanced conditions, *full arm* - *movement* and *detached hand* - *movement*. The third block consisted of the repetition of a single *full arm* - *no movement* condition, which we labeled *full arm* - *post*. This condition was used to retest the reported sense of ownership and sense of agency after participants were allowed to control the virtual hand. Finally, a fourth block consisted of a *movement* condition, in which the movement was manipulated to appear incongruent to the actual movement of the participants, labeled as *full arm - incongruent movement*. **Table 3.2** provides a description of the conditions for **Experiment 2**.

Condition	**Type**	**Hand appearance**	**Movement**
Full arm - no movement	No movement	Continuous	Passive observation of the static limb.
Detached hand - no movement	No movement	Discontinuous (missing forearm)	Passive observation of the static limb.
Full arm - movement	Movement	Continuous	Participants controlled the virtual arm in a goal-directed task.
Detached hand - movement	Movement	Discontinuous (missing forearm)	Participants controlled the virtual arm in a goal-directed task.
Full arm - post	No movement	Continuous	Passive observation of the static limb.
Full arm - incongruent movement	Movement	Continuous	Participants controlled the virtual arm in a goal-directed task. There is added noise to the trajectory of the movement.

Table 3.2: **Experimental conditions for Experiment 2**. Experiment 2 consisted of six conditions. The conditions could either consist of passively observing the static virtual arm (*no movement* conditions) or performing a goal-directed task (*movement* conditions). Additionally, the participants were presented with two hand appearances (i.e., *full arm* and *detached hand*). Finally, the trajectory of the movement of the virtual hand was manipulated by the addition of noise in the *incongruent movement* condition.

Procedure

Upon arrival, the participants were seated in front of the physical table. Then, the experimenter verbally explained the instructions to them. The participants were requested to place the right hand on top of the table. They were instructed not to move it since the start of the experiment until the end of the first, *no movement* block.

The experimenter then fitted the HDM, and the experiment started. All participants underwent all six conditions. In each condition, the participants could either perform a goal-directed task or observe a static limb without attempting to movement. At the end of each condition, the virtual hand would disappear and the participants would report the subjective experience of the illusion. The participants verbally responded to the questionnaires without removing the headset [see **Table 3.5**]. After this, the next condition would start. A more detailed explanation of the procedure of each condition can be found in an upcoming section [see **Section 3.4**].

At the end of the experiment, the participants were paid €15 in a voucher and were debriefed. The whole experiment lasted approximately 30 minutes.

The participants underwent the four blocks without any period of rest between them. The first block of two *no movement* conditions always appeared before the first block of *movement* conditions to avoid artifacts coming from the participants having controlled the virtual arm [**Figure 3.2**].

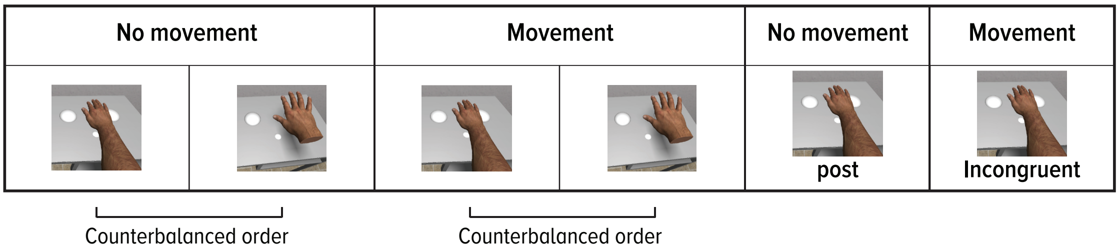


Figure 3.2: **Design for Experiment 2**. The participants underwent four blocks of conditions for a total of six conditions. The first block was a *no movement* block, which consisted of two conditions, *full arm* and *detached hand*. The second block consisted of two *movement* conditions, *full arm* and *detached hand* condition. The third block consisted of a single *no movement* condition (*full arm - no movement*). Finally, a fourth block, with a single condition, in which there was added noise to the trajectory of the virtual hand, labelled as *incongruent movement* condition. The order of the blocks was fixed, but the conditions in the first and second blocks were counterbalanced within each block.

3.2.3 Experiment 3

Motivation

In our previous experiments, we manipulated the visual appearance of the hand or the movement congruence with respect to the physical movements. In all *movement* conditions, the expected outcome of the task was always met. That is, the lights turned off without any delay when reached by the virtual hand. The sense of agency has been shown to depend on the motor control (i.e., movement) and the contextual cues (i.e., outcome). Thus, the sense of agency comprises both the feeling of authorship over action and the changes caused in the environment (Haggard, 2017).

The perturbations in both the movement and the consequence of the action have been shown to affect the reported sense of agency negatively (Villa et al., 2018). We hypothesized that manipulating the task's outcome would negatively affect the reported sense of agency and, subsequently, the sense of ownership. If a congruent outcome is necessary for the sense of ownership, we expect a significant decrease in both reported senses of agency and ownership. To test this hypothesis, we manipulated the outcome by making the lights responsive to the virtual hand at only random intervals.

Experimental design

The experiment consisted of two blocks of conditions (arbitrarily named **A** and **B**), each containing four conditions.

Condition	**Block**	**Hand appearance**	**Movement**	**Task outcome**
Full arm - movement	A and B	Continuous	Participants controlled the virtual arm in a goal-directed task.	The outcome of the task was congruent to the expected result.
Full arm - incongruent outcome	A and B	Continuous	Participants controlled the virtual arm in a goal-directed task.	The outcome of the task was manipulated.
Full arm - incongruent movement	A	Continuous	There is added noise to the trajectory of the movement.	The outcome of the task was congruent to the expected result.
Full arm - incongruent	A	Continuous	There is added noise to the trajectory of the movement.	The outcome of the task was manipulated.
Detached hand - movement	B	Discontinuous (missing forearm)	Participants controlled the virtual arm in a goal-directed task.	The outcome of the task was congruent to the expected result.
Detached hand - incongruent movement	B	Discontinuous (missing forearm)	Participants controlled the virtual arm in a goal-directed task.	The outcome of the task was manipulated.

Table 3.3: **Experimental conditions for Experiment 3**. Experiment 3 consisted in two consecutive blocks, A and B, of four conditions each. Two conditions were common in both blocks, *full arm - movement* and *full arm - incongruent outcome* . In **Block A**, we also manipulated the movement of the virtual, *full arm - incongruent movement* and *full arm - incongruent*, in which both the movement and the outcome were manipulated. In **Block B**, we also manipulated the appearance of the virtual hand to appear in a discontinuous form, *detached hand - movement* and *detached hand - incongruent outcome*.

In **Block A**, we either added noise to the trajectory of the virtual hand or manipulated the consequence in the environment (i.e., the lights not responding to the participant's movements). We labeled these conditions as *incongruent movement* and *incongruent* *outcome*, respectively. The *incongruent movement* condition was the same as in **Experiment 2**. In all conditions, the participants saw the arm as attached to the body (i.e., *full arm*). The participants underwent four conditions in **Block A**, *full arm* - *movement* (no manipulation), *full arm* - *incongruent movement* (added noise to the trajectory of the virtual hand), *full arm* - *incongruent outcome* (manipulated outcome), and *full arm* - *incongruent* (both manipulations present).

In **Block B**, we assessed the interaction between the outcome of the task and the appearance of the limb. Thus, we manipulated the appearance of the hand or manipulated the consequence of the action in the environment (i.e., the lights not responding to the participant's movements). We labeled these conditions as *detached hand* and *incongruent outcome*, respectively. The *detached hand* condition was the same as in **Experiment 1** and **2**. In all conditions, the movement that the participants saw in the virtual hand was congruent to the participant's physical movement. Thus, the participants underwent four conditions *full arm* - *movement* (no manipulations added), *detached hand* - *movement* (the hand appeared with the missing forearm), *full arm* - *incongruent outcome* (manipulated outcome), and *detached hand* - *incongruent outcome* (both manipulations present) [see **Table 3.3** for a description of the conditions].

The order of the conditions was randomized within each block. The order of the blocks was counterbalanced across participants (half of them were presented with Block A first followed by Block B, while for the other half Block B preceded Block A). Note that the *full arm* - *movement* and the *full arm* - *incongruent outcome* were present in both **Block A** and **Block B**.

Procedure

Upon arrival, the participants were seated in front of the physical table and the experimenter verbally read the instructions of the experiment.

The participants underwent both blocks in a single session, with a short break between both blocks. At the end of each block, we requested the participants to describe their experience in the preceding session. Doing so required them to look at their hand and move it. Each condition consisted of performing a goal-directed task [see **Section 3.4** for a detailed explanation of the procedure for each condition]. When a condition was finished, the lights in the virtual room would turn off, and a screen would appear. This screen showed the statements, and the participants verbally reported their answers.

At the end of the experiment, the participants were paid €15 in a voucher and were debriefed. The whole experiment lasted approximately 50 minutes.

3.3 Hand models

For all the experiments, we used a gender-matched right arm in a congruent anatomical position. The virtual arm was controlled using a Leap Motion controller (Leap Motion,

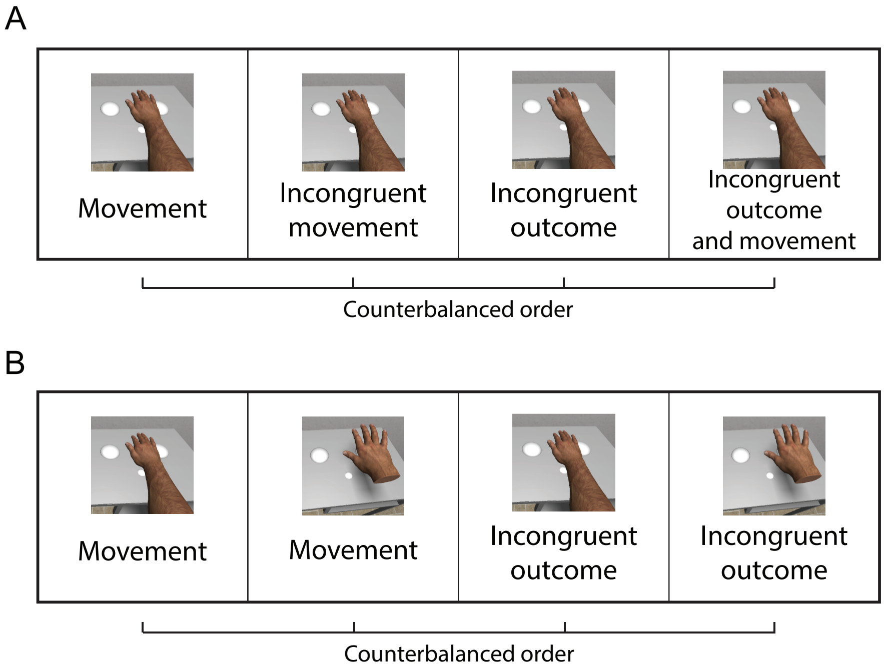


Figure 3.3: **Design for Experiment 3**. The participants underwent two blocks of conditions, A and B. (A) In Block A, we manipulated the movement of the virtual hand and the outcome of the task, resulting in four conditions *full arm - movement* (no manipulation), *full arm - incongruent movement* (the movement of the virtual hand was manipulated), *full arm - incongruent outcome* (the outcome of the task was manipulated), and *full arm - incongruent* (both manipulations presented). The conditions were counterbalanced across participants. (B) In Block B, we manipulated the appearance of the virtual hand and the outcome of the task, resulting in four conditions *full arm - movement* (no manipulation), *detached hand - movement* (the hand appeared in a discontinuous form), *full arm - incongruent outcome* (the outcome of the task was manipulated), and *detached hand - incongruent outcome* (both manipulations presented). The conditions were counterbalanced across participants.

Inc). The virtual and the physical hands were carefully aligned by measuring the location of the LEAP Motion controller in the physical room and using the same location in the virtual world as the origin for the hand models [see **Section 2.2.3**]. The relative positions of the arms could be displaced using the OffsetSwitcher [see **Section 2.4.3**].

These hand models were provided by the LEAP motion SDK. We presented the participants with two different hand models, one that appeared attached to the body and one detached without a forearm [**Figure 3.4**]. Throughout the experiment, the participants' physical hand trajectories were logged using the LEAP Motion coordinate system.

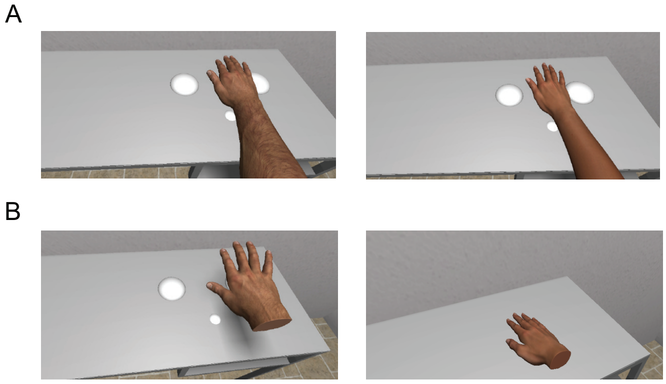


Figure 3.4: **Hand models**. The hands in the virtual environment were gender-matched right hands. The hands could appear in two forms, (A) appeared attached to the body or (B) detached, with the forearm removed.

3.4 Details of the conditions

3.4.1 *Full arm* conditions

In the *full arm* conditions, the virtual arm presented a forearm and appeared connected to the body [**Figure 3.4A**].

3.4.2 *Detached hand* conditions

The *detached hand* conditions were motivated by previous reports of a negative effect of body discontinuity in the senses of ownership and agency over an arm at rest (Perez-Marcos, Sanchez-Vives, and Slater, 2012) or when passively observing an arm move

(Tieri et al., 2015a; Tieri et al., 2015b; Tieri et al., 2017).

In the *detached hand* conditions, we used a hand with a missing forearm, creating a discontinuity from the body. The hand appeared with a clean cut at the wrist [**Figure 3.4B**].

3.4.3 *Displacement* conditions

We labeled as *displacement* the conditions those in which we displaced the center of the virtual hand ten centimeters to the left from the participant's physical hand. We used the OffsetSwitcher class to move the position of the virtual hand with respect to the position of the physical hand. The distance between the hands was defined from the **ProtocolFile** [**Figure 2.13**]. As a result, the participants corrected for the displacement by moving their physical hand ten centimeters to the right of the center tracking origin (Leap Motion Controller).

3.4.4 *No movement* conditions

In the *no movement* conditions, the participants were required to rest the hand on the table and not move it for 60 seconds while looking at it. The virtual hand position was not updated to ensure that the virtual hand would remain static until the trial's completion. The participants were carefully monitored by the experimenter during the whole task to control that they did not move their physical hand.

3.4.5 *Movement* conditions

In the *movement* conditions, the participants controlled the virtual hand while performing a goal-directed task. The task consisted of reaching movements towards target lights on top of the virtual table.

At the beginning of the task, the participants were asked to lift their right hand from the table and not place it back on the table until they were told otherwise. First, the small central blue light turned on. The participants had to turn it off by placing the virtual hand on top of it without touching it, to avoid tactile information from the physical arm. As a result, one of the large lights turned yellow, which of the two target lights turned on was determined at random. The subject had to reach towards the newly illuminated light and to turn it off within the specified timeout. We labeled each of these movements as a *wave* [**Figure 3.5B**]. If performed correctly, the target light would change to green. Conversely, the target light would turn red if the wave was performed incorrectly. In **Experiment 3**, the feedback was provided by a separate virtual screen. After 0.5 seconds, the central blue light turned on again, and a new wave would start. The **ProtocolFile** determined the required amount of waves for each condition. Each *movement* task lasted approximately three minutes.

3.4.6 *Incongruent movement* conditions

We used the *incongruent movement* conditions to test the importance of movement congruence on the sense of agency and sense of ownership. To this purpose, we added noise to the trajectory of the virtual hand, so that it would appear incongruent to the participant's hand while maintaining the mean trajectory constant.

The resulting virtual arm position ($\hat{p}_i$) resulted from the combination of the actual hand location (p_i) and the previous virtual hand location ($\hat{p}_{i-1}$) plus Gaussian random noise (r) of mean 0 and standard deviation σ from the Gaussian, given by the equation:

$$\hat{p}_i = \lambda p_i + (1-\lambda)(\hat{p}_{i-1} + (p_i - p_{i-1}) + r). \tag{3.1}$$

The parameter λ determines the amount of the actual location used in favor of the noisy virtual location. In our experiment, $\sigma = 0.015$ meters and $\lambda = 0.9$. This means that 90% of the virtual hand movement was based on the current sample (i.e., no latency was added there). For the remaining 10%, we added the delta movement (previous vs. present frame) and random noise to the old virtual hand location.

As a result of this manipulation, the trajectory of the virtual hand appeared shaky around the trajectory performed by the participant.

3.4.7 *Incongruent outcome* conditions

In the *incongruent outcome* conditions, we manipulated the consequence of the action not to match the expected result (i.e., the light turning off). To achieve this effect, we manipulated the **CollisionDetection** in the lights so that they might not respond consistently to the participant's movements [see **Section 2.11A**]. In conditions without the manipulated outcome (e.g., *movement* conditions), the collider would be set to *active* at the same time that the light changed color. In the *incongruent outcome* conditions, the collider would be active only in certain frames.

We maximized the randomness of the consequence to ensure that the participants could not learn how to perform the task optimally. To this end, we used two delays that would determine when the light collider would be set to *active*. The first delay was fixed to 500 ms. Thus, the light would never respond in this window of time. Secondly, in every frame that the collider was triggered, a second delay was determined by a random number between 0 and 1 and compared to a threshold that was set to 0.013 [**Figure 3.5C**]. If the number were below the threshold, the collider would be set to *active*, and the light would turn off and would count as a correct wave; otherwise, it would remain inactive. After a timeout of 3 seconds, the light would turn off by itself, return red feedback to the participant [**Figure 2.3**], and would be counted as an incorrect wave.

3.5 Participants

All participants provided written informed consent before their participation. The experimental protocol was approved by the Institutional Review Board at the Champalimaud Foundation and was carried out following the ethical standards of the Declaration of Helsinki.

Experiment 1

A total of 19 volunteers (5 females) took part in the study. The participants were recruited from within the Champalimaud Research and were naive to the purposes of the study. We collected no additional sociodemographic data.

Experiment 2

A total of 44 volunteers (29 females; age range=18-45; mean age=28.2 ± SD=7.5 years) took part in the study. The participants signed up through a public online form. Those that declared having no neurological conditions and being right-handed were contacted to participate. All subjects were naive to the purposes of the study. Seven participants were excluded from the analysis; four participants were excluded due to technical issues (e.g., the tracking of the virtual hand failed during a *movement* trial), and another three as they failed to follow the provided instructions (e.g., moved their hand before or during the *no movement* trials). In all the cases, the participants completed the experiment, but the data was not used for those excluded.

All analyses were performed on a sample of 37 participants (23 females, age range=18-45; mean age=27.6 ± SD=6.7 years). The participants were tested for handedness using the Edinburgh Handedness Inventory (Oldfield, 1971) (mean=75.86 ± SD=24.83). 73% had no previous contact with VR and 55% declared not to be regular video game players.

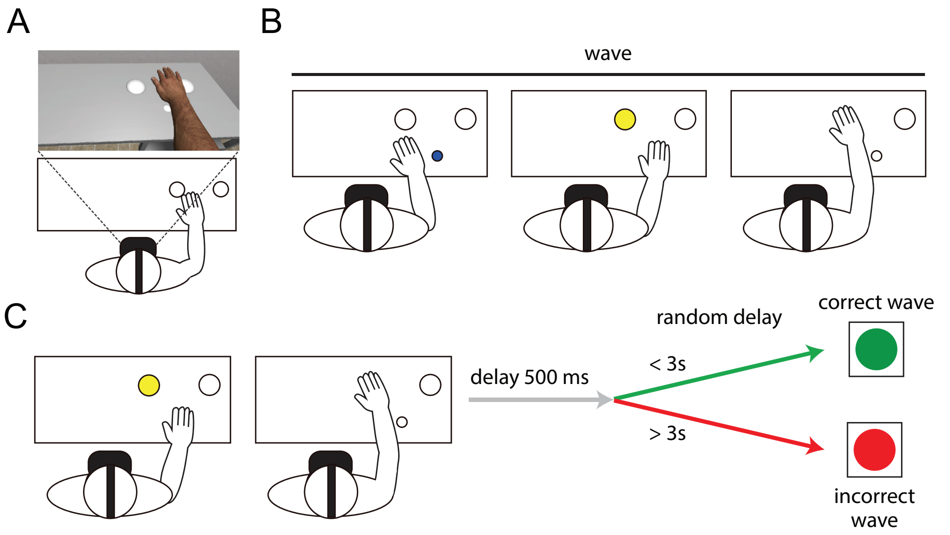


Figure 3.5: **Description of the *no movement* and *movement* tasks and the *incongruent outcome* manipulation**. (A) The *no movement* task consisted of looking at the static virtual hand without attempting to move their physical hand. (B) The *movement* task consisted of controlling the hand in a goal-directed task. The task consisted of turning off the lights that turn on in the virtual environment. First, the initial light (small central light) would change from gray to blue, indicating that it turned on. The participant turned off the light by placing the hand on top of it, without touching. After this, one of the two target lights (big lights) would change from gray to yellow. The participant would turn off the light within the three-second timeout by placing the hand on top of it without touching it. Each of these actions was labeled as a wave. (C) The *incongruent outcome* manipulation consisted of altering the response of the collision detection attached to the **activeLight**. A fixed 500ms delay and a random delay up to 3 seconds in total were added. If the combined delay were above 3 seconds, the light would not respond and return as an incorrect wave. Otherwise, the **collisionDetection** would be set to active, and when the participants reached the light it would count as a correct wave.

Experiment 3

A total of 53 volunteers (28 females; age range=21-42; mean age=29.1 ± SD=5.1 years) took part in this study. The participants signed up through a public online form. Those that declared having no neurological conditions and being right-handed were contacted to participate. Out of these participants, ten were excluded from the analysis, eight as a result of the hand tracking failures, and two because they had already been part of one of our previous studies. Thus, the included participants were naive to the purpose of the experiment. In all cases, the participants completed the experiment, but the data was not used for further analysis.

All analyses were performed on a sample of 43 participants (24 females, age range=21-42; mean age=28.8 ± SD=5.3 years). The participants were tested for handedness using the Edinburgh Handedness Inventory (EHI) (Oldfield, 1971) (mean=71.9 ± SD=27.5). 44.2% had no previous contact with VR, and 60.5% declared not to be regular video game players.

Of the final 43 that underwent further analyses, 18 were presented first with **Block A**, and 25 were presented first with **Block B**.

3.6 Sociodemographic Data

The participants recruited for **Experiments 2** and **3** completed a sociodemographic form with data to be used for later analysis. An example of the file used to collect this data and a summary can be found in **Appendix D**.

3.7 Questionnaires

We used a set of questionnaires to assess the subjective experience of the illusion. All questionnaires included statements to assess the senses of ownership, agency, outcome agency, and location. Additionally, when appropriate, they contained control statements for these categories. These questionnaires were adapted from previous studies (Botvinick and Cohen, 1998; Kalckert and Ehrsson, 2012; Kalckert and Ehrsson, 2014).

In all cases, the participants verbally reported their subjective experience on a 7-point Likert scale (1=totally disagree, 4=neutral, 7=totally agree). The responses were always recorded digitally (either using the Likert.m Matlab function or the custom-made recording in Unity) and manually on paper. The statements would always appear in a counterbalanced order across participants and conditions.

3.7.1 Experiment 1

In **Experiment 1**, we used a 14-item questionnaire. It contained four questions to assess the sense of ownership (statements 1 to 4), one for similarity (statement 5), three for the sense of agency (statements 7 to 9), and two for the sense of location (statement 13 and 14). Additionally, the questionnaires contained a control statement for the sense of ownership (statement 6) and three for the sense of agency (statement 10 to 12) [see **Table 3.4**].

3.7.2 Experiment 2

In **Experiment 2**, we used two different questionnaires depending on the type of condition, *no movement* and *movement*.

For the *no movement* conditions, we used an 11-item questionnaire that targeted the sense of ownership (statements 1 to 4), sense of agency (statements 8 and 9), and the sense of location (statement 22); and the respective control statements for the sense of ownership (statements 5 to 6) and agency (statement 10). Similarly, the questionnaire for the *movement* conditions consisted of a 19-item questionnaire to assess the sense of ownership (statements 1 to 4), the sense of agency (statements 11 to 14), and the sense of location (statements 22 and 23); and the respective control statements of ownership (statements 5 and 6) and agency (17 to 20). Additionally, we assessed the perceived agency over the consequences of the action (hereafter, outcome agency) (statements 15 and 16) [see **Table 3.5**].

3.7.3 Experiment 3

For **Experiment 3**, we used a 20-item questionnaire to assess the sense of ownership (statements 1 to 4), the sense of agency (statements 8 to 11), outcome agency (statements 15 and 16), and the sense of location (statements 19 and 20); and the respective control statements for the sense of ownership (statements 5 and 6), agency (statements 14 and 15), and outcome agency (statements 17 and 18). Furthermore, we assessed perceived similarity towards the real hand (statement 7) [see **Table 3.6**]. Before starting the experiment, the participants were explicitly instructed to reply to the questionnaires taking into account the last condition experienced and disregarding the other conditions.

	Category	**Statement**
1	**Ownership**	. . . in which I felt as if I were looking at my own hand, rather than a virtual hand.
2	**Ownership**	. . . that I felt as if the virtual hand was my hand.
3	**Ownership**	. . . when it seemed like the virtual hand belonged to me.
4	**Ownership**	. . . when it seemed that the virtual hand was part of my body.
5	**Similarity**	. . . I felt as if the virtual hand was physically resembling my real hand.
6	**Ownership***	. . . when I felt like my real hand were turning virtual.
7	**Agency**	. . . that I felt I could control the virtual hand.
8	**Agency**	. . . that I felt that the movements of the virtual hand were caused by me.
9	**Agency**	. . . that I felt that the movement of my hand was turning off the lights on the table.
10	**Agency***	. . . when I had the feeling of forgetting my own hand, focusing only on the movements of the virtual hand.
11	**Agency***	. . . that I felt as if the virtual hand were controlling my hand.
12	**Agency***	. . . that it felt as if the virtual hand caused the movement of my hand.
13	**Sense of location**	. . . when it seemed like my hand was in the location the virtual hand.
14	**Sense of location**	. . . when it seemed as if the movement of my hand was located where the virtual was moving.

Table 3.4: **Questionnaires for Experiment 1**. Statements to assess the sense of ownership, the sense of agency, and the sense of location, with their respective control statements (marked with *). The statements were presented in a random order for each participant and condition. The participants replied verbally in a 7-point Likert scale. All questions start with "During the experiment there were moments. . . ".

	Category	Condition	Statement
1	**Ownership**	Both	I felt as if I were looking at my own hand, rather than a virtual hand.
2	**Ownership**	Both	I felt as if the virtual hand was my hand.
3	**Ownership**	Both	It seemed like the virtual hand belonged to me.
4	**Ownership**	Both	It seemed that the virtual hand was part of my body.
5	**Ownership***	Both	I felt as if I had more than one right hand.
6	**Ownership***	Both	I felt like my real hand was turning virtual.
7	**Similarity**	Both	I felt as if the virtual hand physically resembled my real hand in terms of shape, freckles, and other features
8	**Agency**	No movement	I felt that I could control the virtual hand if I wanted to.
9	**Agency**	No movement	I felt that if I started to move my hand, the virtual hand would obey my will.
10	**Agency***	No movement	I had the feeling of forgetting my own hand focusing only on the movements of the virtual hand.
11	**Agency**	Movement	I felt that I could control the virtual hand.
12	**Agency**	Movement	I felt that the movements of the virtual hand were caused by me.
13	**Agency**	Movement	I felt as if the virtual hand was obeying my will.
14	**Agency**	Movement	I felt that I controlled the virtual hand as if it was part of my body.
15	**Agency***	Movement	I felt as if the virtual hand was controlling my hand.
16	**Agency***	Movement	I had the feeling of forgetting my own hand, focusing only on the movement of the virtual hand
17	**Agency***	Movement	I felt as if the virtual hand caused the movement of my hand.
18	**Outcome agency**	Movement	I felt as if the lights were obeying my will.
19	**Outcome agency**	Movement	I felt that the movement of my hand was turning off the lights on the table.
20	**Outcome agency***	Movement	I felt as if the lights changed at random.
21	**Location**	Both	It seemed like my hand was in the location of the virtual hand
22	**Location**	Movement	It seemed as if the movement of my hand was located where the virtual hand was moving.

Table 3.5: **Questionnaires for Experiment 2**. Statements were used to assess the sense of ownership, the sense of agency, outcome agency, and the sense of location, with their respective control statements (marked with *). We used two questionnaires depending on the type of conditions, *no movement* and *movement*. Some statements were common to both types of conditions (*both*). The statements were presented in a random order for each participant and condition. The participants replied verbally in a 7-point Likert scale.

	Category	Statement
1	**Ownership**	I felt as if I were looking at my hand, rather than a virtual hand.
2	**Ownership**	I felt as if the virtual hand was my hand.
3	**Ownership**	It seemed like the virtual hand belonged to me.
4	**Ownership**	It seemed that the virtual hand was part of my body.
5	**Ownership***	I felt as if I had more than one right hand.
6	**Ownership***	I felt like my real hand was turning virtual.
7	**Similarity**	I felt as if the virtual hand physically resembled my real hand in terms of shape, freckles, and other features.
8	**Agency**	I felt that I could control the virtual hand.
9	**Agency**	I felt that the movements of the virtual hand were caused by me.
10	**Agency**	I felt as if the virtual hand was obeying my will.
11	**Agency**	I felt that I controlled the virtual hand as if it was part of my body.
12	**Agency***	I felt as if the virtual hand was controlling my hand.
13	**Agency***	I had the feeling of forgetting my own hand, focusing only on the movement of the virtual hand.
14	**Agency***	I felt as if the virtual hand caused the movement of my hand.
15	**Outcome agency**	I felt that the lights were obeying my will.
16	**Outcome agency**	I felt that the movement of my hand was turning off the lights on the table.
17	**Outcome agency***	I felt as if the lights turned off randomly.
18	**Outcome agency***	I felt as if I had no control over the target lights.
19	**Location**	It seemed like my hand was in the location of the virtual hand.
20	**Location**	It seemed as if the movement of my hand was located where the virtual hand was moving.

Table 3.6: **Questionnaires for Experiment 3**. Statements to assess sense of ownership, sense of agency, outcome agency, and sense of location, with their respective control statements (marked with *). The statements were presented in a random order for each participant and condition. The participants replied verbally in a 7-point Likert scale.

4 | Active control over the movements of the virtual hand as evidence for the sense of ownership

“What is more important for us, at an elemental level, that the control, the owning and operation, of our own physical selves? And yet it is so automatic, so familiar, we never give it a thought.”

Oliver Sacks, The Man Who Mistook His Wife for a Hat

4.1 Introduction

In the classical RHI paradigm, the synchronous stroking and spatial congruence of the participant's physical arm and the rubber arm results in an illusion of ownership over the rubber arm (Botvinick and Cohen, 1998). Similarly, in a virtual reality environment, synchronous visuotactile stimulation resulted in feelings of ownership over the virtual hand (Slater et al., 2008). Conversely, asynchronous visuotactile stimulation between the physical and the rubber arm does not result in the illusion of ownership (Botvinick and Cohen, 1998; Armel and Ramachandran, 2003; Slater et al., 2008). These results highlight the importance of spatial and temporal congruence of the seen and felt touch to elicit ownership over the virtual hand. While the role of synchronous visuotactile stimulation has been widely studied in the RHI and VHI, the effect of visuomotor information as a trigger of body ownership is still contested.

Synchornous, but not asynchronous, control over the movements of the index finger of a rubber hand elicits a sense of ownership (Kalckert and Ehrsson, 2012; Tsakiris, Prabhu, and Haggard, 2006). Active synchronous control using a mechanical setup also resulted in a stronger reported sense of ownership than the passive observation of movement or active asynchronous control (Dummer et al., 2009). This effect has also been reported in virtual environments (Sanchez-Vives et al., 2010; Slater et al., 2010), and it is not restricted to upper body limbs (Kokkinara and Slater, 2014). Moreover, the participants reported a stronger sense of ownership over the virtual legs when both visuomotor and visuotactile stimulation was combined (Kokkinara and Slater, 2014).

On the other hand, some studies have failed to find that voluntary control enhances the sense of ownership over a fake limb. In a setup where participants controlled an artificial hand index finger, active control did not increase the ownership scores compared to externally generated passive movement (Kalckert and Ehrsson, 2014; Longo and Haggard, 2009; Walsh et al., 2011), or compared to visuotactile stimulation (Dummer et al., 2009; Kalckert and Ehrsson, 2014; Longo and Haggard, 2009). Furthermore, active control failed to elicit a sense of ownership when controlling hands with an unusual appearance such as hands with supernumerary fingers (Hoyet et al., 2016) or on non-hand objects (Yuan and Steed, 2010).

We propose that the lack of agreement on the role of active control in eliciting a sense of ownership might be due to differences in the experimental setups. For instance, some studies used a rubber hand (Kalckert and Ehrsson, 2014), while others used virtual environments (Sanchez-Vives et al., 2010). The tasks were also different, ranging from single finger movements (Kalckert and Ehrsson, 2014), performing circular motions with the hand (Shibuya, Unenaka, and Ohki, 2018), to full arm movements in a cognitive task (Padrao et al., 2016). Specifically, we propose that the limb's visual appearance can play a differential effect on the role of active control on eliciting a sense of ownership over a virtual arm.

The morphological appearance of the hand needs to be congruent to a pre-existing model of a hand induce embodiment over a fake limb (Tsakiris, 2010). Thus, the illusion is abolished over non-hand shaped objects (Haans, Ijsselsteijn, and Kort, 2008; Tsakiris and Haggard, 2005a) and decreased over limbs with increasing degrees of transparency (Martini et al., 2015), or when the limb has been stretched beyond a certain length (Kilteni et al., 2012). A break in body continuity has also been shown to decrease the sense of ownership over a moving hand (Tieri et al., 2015a; Tieri et al., 2017; Tieri et al., 2015b; Perez-Marcos, Sanchez-Vives, and Slater, 2012). Specifically, seeing the hand detached from the virtual body decreased the sense of ownership over a static limb (Tieri et al., 2017; Tieri et al., 2015b; Perez-Marcos, Sanchez-Vives, and Slater, 2012) and when passively observing the moving arm (Tieri et al., 2015a).

The sense of agency, the subjective experience of being the author of the action (Haggard, 2017) is affected by changes in the visual appearance of the hand in the absence of active control. In the absence of visuomotor information, the sense of ownership elicits a weak sense of agency (Kalckert and Ehrsson, 2014), as a result of congruent morphological, proprioceptive, and visuotactile information. When the body continuity appears to be broken, the vicarious agency significantly decreased in the absence of voluntary motor commands (Tieri et al., 2015a; Tieri et al., 2017; Tieri et al., 2015b). Previous studies also report a significant decrease in the reported vicarious agency when participants passively observe the virtual arm moving with a missing forearm (Tieri et al., 2015b). However, no study reported the effect of body discontinuity in an arm actively controlled by the participant in the senses of ownership and agency.

First, we aimed to study whether active control over the movements of a virtual arm maintains and enhances the senses of ownership and agency over a virtual hand that appears detached from the body. We tested whether if seeing the hand detached from the body decreased the sense of ownership and the sense of agency while controlling the arm in a variation of the mVHI that consisted of a goal-directed task. Furthermore, we assessed the effect of introducing a displacement between the virtual and the physical hand positions.

Secondly, we tested the interplay between the visual appearance of the hand and the visuomotor information that arises from active control in the reported sense of ownership over a virtual hand. Therefore, we assessed if active control added evidence in favor of a sense of ownership. Additionally, we tested the importance of the congruence between the virtual hand and the participants' movement in the sense of ownership by adding noise to the movement of the virtual hand. Overall, we aim to understand the role of congruent active control in the senses of ownership and agency over a virtual hand.

4.2 Results Experiment 1

Experiment 1 aims to assess whether active control over the movements of the virtual hand maintains the senses of agency and ownership over a hand that appeared detached from the body.

The participants controlled a virtual arm that could appear either attached to the body or in a discontinuous form (i.e., forearm missing). We named these conditions *full arm* and *detached hand*, respectively [**Figure 3.4**]. Additionally, we manipulated the physical hand position with respect to the position of the virtual hand, creating a displacement between both hands. Thus, the hands could either appear in the same position or with a lateral displacement of the physical hand ten centimeters to the right relative to the position of the virtual hand. We named these conditions *no displacement* and *displacement*, respectively. In these conditions, we did not add any manipulations to the virtual hand movement.

We hypothesized that the visuomotor information related to the voluntary movement of the virtual hand would maintain the senses of agency and ownership over the discontinuous virtual limb (i.e., missing forearm) compared to the *full arm* conditions, regardless of the proprioceptive conflicts.

Table 4.1 shows the median scores and IQR for **Experiment 1**

	Full arm no displacement	**Full arm displacement**	**Detached hand no displacement**	**Detached hand displacement**
Ownership	4.00 (2.18)	2.50 (2.93)	3.25 (2.56)	3.00 (3.37)
Ownership*	2.00 (2.75)	2.00 (2.75)	2.00 (2.50)	1.00 (1.75)
Agency	6.50 (1.00)	6.00 (1.37)	6.50 (1.00)	7.00 (1.37)
Agency*	2.66 (1.58)	2.66 (0.91)	2.66 (1.00)	2.66 (0.91)
Outcome agency	7.00 (1.00)	6.00 (1.00)	7.00 (1.00)	7.00 (0.91)
Similarity	6.00 (2.75)	5.00 (3.00)	5.00 (3.00)	5.00 (3.00)
Location	6.00 (1.62)	6.00 (1.00)	6.00 (1.25)	6.00 (1.37)

Table 4.1: **Reported median scores and IQR for the senses of ownership, agency, outcome agency, and location for Experiment 1**, and their respective control statements (marked with a *) for *full arm - no displacement*, *full arm - displacement*, *detached hand - no displacement*, and *detached hand - displacement*.

4.2.1 The reported sense of agency over the virtual hand

First, we compared the agency scores to their respective control statements in each condition to test for task compliance and suggestibility.

The participants reported a sense of agency in the *full arm - no displacement* (median=6.33, IQR=1.00) and the *full arm - displacement* (median=6.00, IQR=1.00) conditions. The reported sense of agency was higher than the respective control statements in both conditions (Wilcoxon signed-rank; Z=3.82, p<0.001, and Z=3.78, p<0.001, respectively). In the *detached hand* conditions, the participants also reported a sense of agency in the *detached hand - no displacement* (median=6.50, IQR=0.91) and *detached hand - displacement* (median=7.00, IQR=1.33) conditions. In both conditions, the reported sense of agency was higher to the respective control statements (Wilcoxon signed-rank; Z=3.83, p<0.001, and Z=3.82, p<0.001, respectively) [**Figure 4.1**].

4.2.2 The reported sense of agency was resistant to the body discontinuity and proprioceptive displacement

The following analyses aim to assess whether manipulating the visual appearance or the proprioceptive displacement affected the reported agency scores.

We found no main effect for the reported sense of agency across conditions (Friedman test; χ^2=5.71 (df=3, n=19), p=0.12). We performed pairwise comparisons to assess whether each manipulation changed the reported agency scores. Pairwise analysis did not yield a significant difference between any pair of compared conditions (i.e. *full arm* - *no displacement* vs. *full arm* - *displacement*, *full arm* - *no displacement* vs. *detached hand* - *no displacement*, *detached hand* - *no displacement* vs. *detached hand* - *displacement*, and *full arm* - *displacement* - *detached hand* - *displacement*; p>0.06) [**Figure 4.1**].

These results suggest that, under active control, the reported sense of agency is resistant to body discontinuity (i.e., seeing the hand detached from the body in the *detached hand* condition) and the proprioceptive displacement of the physical hand.

4.2.3 The reported sense of ownership over the virtual hand

We compared the ownership scores to their respective control statements in each condition to test for task compliance and suggestibility.

The participants reported a weak sense of ownership in the *full arm* - *no displacement* condition (median=4.00, IQR=2.18). In this condition, the reported sense of ownership was higher than the respective control statements (Wilcoxon signed-rank; Z=3.62, p<0.001). The ownership scores in the *full arm* - *displacement* condition were below the neutral point (median=2.50, IQR=1.61) and did not yield a significant differences when compared to the respective control statements (Wilcoxon signed-rank; Z=1.82, p=0.07).

In the *detached hand* - *no displacement*, the reported ownership scores (median=3.25, IQR=2.56) were also below the neutral point. The reported ownership scores were still higher than the respective control statements (Wilcoxon signed-rank; Z=2.82, p=0.004)

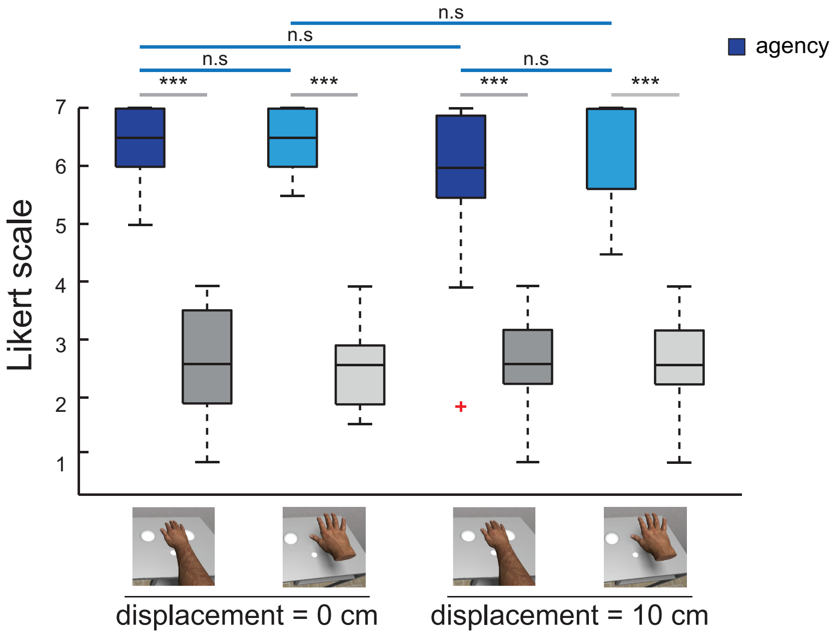


Figure 4.1: **The reported sense of agency was resistant to body discontinuity and proprioceptive displacement**. The agency scores (in blue) and the respective control statements (in gray). Darker colors represent the *full arm* conditions, while lighter shades represent the *detached hand* conditions. In all conditions, the agency scores were higher than the control statements in the respective conditions (p<0.001). In pairwise comparisons, the agency scores did not yield any significant difference (p>0.06). The middle quartile indicates the median value, and the whiskers indicate the most extreme values that are not considered outliers. n.s. p>0.05, *** p<0.001.

[**Figure 4.2**]. The reported sense of ownership in *detached hand* - *displacement* (median=3.00, IQR=3.37) were higher than the respective control conditions (p<0.001) [**Figure 4.2**].

4.2.4 The reported sense of ownership was resistant to the body discontinuity but decreased as a result of proprioceptive displacement

The following analyses aim to assess whether manipulating the visual appearance or the proprioceptive displacement affected the reported sense of ownership.

The reported sense of ownership was significantly different across all four conditions (Friedman test; χ^2=11.51 (df=3, n=19), p=0.009). We proceeded to perform pairwise comparisons between all of the pairs of conditions.

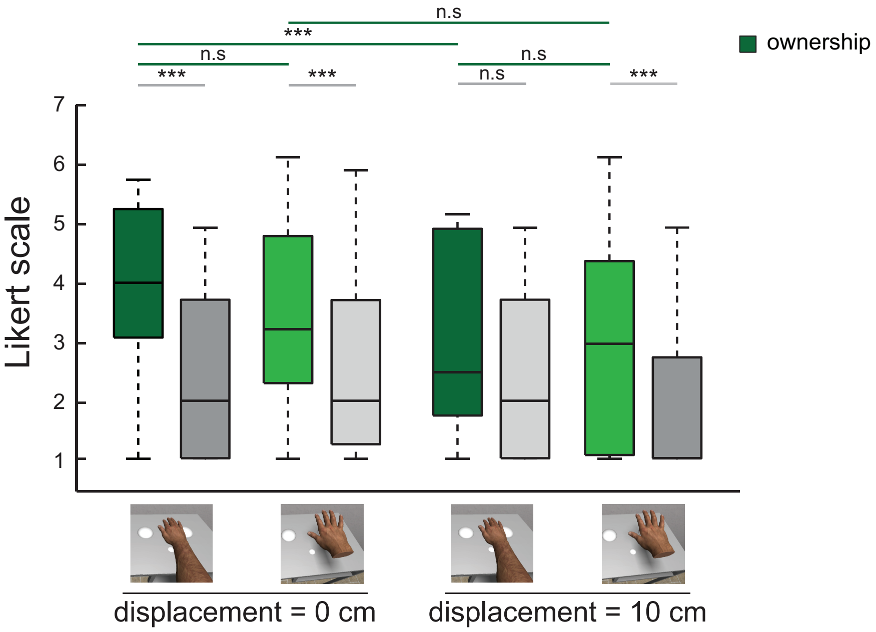


Figure 4.2: **The reported sense of ownership was resistant to body discontinuity but was decreased due to proprioceptive displacement**. Ownership scores (in green) and the respective control statements (in gray). Darker colors represent the *full arm* conditions, while lighter shades represent the *detached hand* conditions. The ownership scores were higher than the control statements in the respective conditions ($p<0.001$), except the *detached hand* - *displacement* conditions ($p=0.07$). The ownership scores in the *full arm* - *no displacement* were significantly higher than in the *full arm* - *displacement* ($p=0.002$). The rest comparisons did not yield a significant difference ($p>0.17$). The middle quartile indicates the median value, and the whiskers indicate the most extreme values that are not considered outliers. n.s. $p>0.05$, *** $p<0.001$.

In the *displacement* conditions, the reported sense of ownership did not differ when participants saw the hand with forearm missing (*detached hand* - *no displacement*) compared the *full arm* - *no displacement* condition (Wilcoxon signed-rank; Z=1.35, p=0.17). Also, we found no significant difference between the *detached hand* - *displacement* condition compared to the *full arm* - *displacement* condition (Wilcoxon signed-rank; Z=0.28, p=0.77) [**Figure 4.2**].

In the *full arm* conditions, displacing the position of the virtual hand significantly decreased the sense of ownership in the *full arm* - *displacement* condition compared to the *full arm* - *no displacement* condition (Wilcoxon signed-rank; Z=3.03, p=0.002). However, this was not the case in the conditions where the arm was presented in the discontinuous form when comparing the *detached hand* - *displacement* to the *detached hand* - *no displacement* condition (Wilcoxon signed-rank; Z=0.92, p=0.35) [**Figure 4.2**].

Taken together, the results from this first study suggest that, under active control, the senses of agency and ownership are resistant to seeing the hand in a discontinuous form (i.e., missing forearm). However, the sense of ownership was negatively affected by a proprioceptive displacement, only when the hand appeared attached to the body.

4.3 Results Experiment 2

The results from **Experiment** [**Section 4.2**] suggest a strong effect of visuomotor information generated from voluntary control in the senses of ownership and agency. Thus, under active control over the virtual hand movements, the reported senses of ownership and agency were resistant to body discontinuity. Contrary to the results reported by Tieri et al., 2015a, which found a decrease in the senses of ownership and agency after passively observing a discontinuous moving arm. Therefore, suggesting that active control is crucial in maintaining a sense of ownership over the virtual hand.

The present section intends to understand whether active control also plays a role in enhancing the reported sense of ownership compared to conditions where visuomotor information is absent. In this study, the participants controlled the virtual hand in a goal-directed task, as in the previous study, or stared at the static virtual arm without attempting to move it. These conditions were named *movement* and *no movement*, respectively. As in **Experiment 1**, the hand was presented in two different appearances, *full arm* and *detached hand*. Additionally, we tested whether the effect of active control is contingent on the movement of the virtual hand being congruent to the movement performed by the participant. Therefore, we introduced the *full arm* - *incongruent movement* condition, in which noise was added to the movement of the virtual hand.

The results reported in **Experiment 1** suggest that the sense of ownership is susceptible to proprioceptive displacement. In **Experiment 2**, we maintained the physical and virtual hands in the same position (i.e., *no displacement*) to avoid introducing additional interference. See **Section 3.2.2** for a detailed description of the experimental methodology.

We hypothesized that visuomotor information could add evidence in favor of a sense of ownership. Therefore, active control would enhance the reported sense of ownership over the virtual arm compared to passively observing a static arm. On the other hand, we expected that in the absence of active control, the senses of ownership and agency would be negatively affected by seeing the arm in the discontinuous form.

Table 4.2 shows all median scores and IQR for **Experiment 2**.

	Full arm - no movement	**Detached hand - no movement**	**Full arm - post**	**Full arm - movement**	**Detached hand - movement**	**Full arm - incongruent movement**
Ownership	4.50 (2.25)	3.25 (2.81)	4.25 (2.62)	4.75 (2.31)	4.25 (1.56)	3.50 (2.25)
Ownership*	3.00 (1.50)	2.50 (1.75)	2.50 (2.00)	2.50 (2.50)	2.50 (1.50)	2.50 (2.00)
Similarity	4.00 (4.00)	5.00 (4.00)	5.00 (3.00)	5.00 (3.25)	5.00 (2.25)	5.00 (3.00)
Agency	6.00 (2.25)	5.00 (2.50)	6.00 (1.50)	n/a	n/a	n/a
Agency*	5.00 (3.25)	4.00 (4.00)	5.00 (3.00)	n/a	n/a	n/a
Agency	n/a	n/a	n/a	6.25 (1.00)	6.25 (1.06)	5.50 (1.25)
Agency*	n/a	n/a	n/a	3.00 (1.08)	3.00 (2.33)	3.00 (2.00)
Outcome agency	n/a	n/a	n/a	6.00 (2.50)	6.00 (2.00)	6.00 (2.12)
Outcome agency*	n/a	n/a	n/a	2.00 (3.00)	2.00 (3.00)	2.00 (3.00)
Location	7.00 (1.00)	6.00 (3.00)	7.00 (1.00)	6.50 (1.50)	6.00 (1.12)	6.00 (1.62)

Table 4.2: **The reported median scores and IQR for the senses of ownership, agency, outcome agency, and location in Experiment 2**, and their respective control statements (marked with a *) for *full arm - no movement*, *detached hand - no movement*, *detached hand - post*, *full arm - movement*, *detached hand - movement*, *full arm - incongruent movement*. The statements for the sense of agency differed in the *no movement* and *movement* conditions, and were not applicable to all conditions (marked with n/a). The outcome agency statements were only applicable in the *movement* conditions.

4.3.1 The reported senses of agency and ownership over the virtual hand

First, to test for task compliance and suggestibility, we compared the ownership and agency scores to their respective control scores for each experimental condition.

The participants reported a sense of agency in the *full arm* - *no movement* condition (median=6.00, IQR=2.25). The agency scores were higher than the respective control statements (Wilcoxon signed-rank; Z=3.12, p<0.001). In the *detached hand* - *no movement* condition, the agency scores (median=5.00, IQR=2.50) showed no significant difference compared to the control statements (Wilcoxon signed-rank; Z=1.14, p=0.15). Finally, in the *full arm* - *post* condition, the reported agency scores (median=6.00, IQR=1.50) were significantly higher from their respective control statements (Wilcoxon signed-rank; Z=3.66, p<0.001) [**Figure 4.3**].

In *movement* conditions, the participants also reported feeling a sense of agency over the movements of the virtual in the *full arm* - *movement* (median=6.25, IQR=1.00) and *detached hand* - *movement* (median=6.25, IQR=1.06) conditions. In both conditions the scores were higher than their respective control statements (Wilcoxon signed-rank; Z=5.30, p<0.001; and Z=5.28, p<0.001, respectively). Finally, in the *full arm* - *incongruent movement*, the reported sense of agency scores (median=5.50, IQR=1.25) were also significantly higher than the control statements (Wilcoxon signed-rank; Z=5.18, p<0.001) [**Figure 4.3**].

The participants reported a sense of ownership after seeing the arm at rest connected to the body (*full arm* - *no movement* condition) (median=4.50, IQR=2.25). The ownership scores were higher than the respective control statements (Wilcoxon signed-rank; Z=4.56, p<0.001). In the *detached hand* - *no movement* condition, the median reported sense of ownership in the neutral score (score=4.00) (median=3.25, IQR=2.81) and the ownership scores were higher that in their respective control statements (Wilcoxon signed-rank; Z=3.02, p=0.002). The *full arm* - *post* (median=4.25, IQR=2.62) was also significantly higher from the control statements (Wilcoxon signed-rank; Z=5.15, p<0.001) [**Figure 4.3**].

In the *movement* conditions, the participants reported a feeling ownership over the virtual hand in the *full arm* - *movement* (median=4.75, IQR=2.31) and in the *detached hand* - *movement* (median=4.25, IQR=1.56) conditions. In both conditions, the ownership scores were higher than in the respective control statements (Wilcoxon signed-rank; Z=4.65, p<0.001, and Z=4.92, p<0.001). In the *full arm* - *incongruent movement*, the median ownership score in the neutral score (score=4.00) (median=3.50, IQR=2.25), but still higher than in the respective control statements (Wilcoxon signed-rank; Z=3.73, p<0.001) [**Figure 4.3**].

4.3.2 The reported sense of agency was resistant to body discontinuity under active control, but not in the *no movement* conditions

We assessed whether seeing the hand detached from the body affected the reported sense of ownership in both *no movement* and *movement* conditions.

The agency scores were different across the three *no movement* conditions (Friedman test; χ^2=25.29 (df=2, n=37), p<0.001) and across the three *movement* conditions (Friedman test; χ^2=21.53 (df=2, n=37), p<0.001). We tested for differences in the agency scores according to the planned pairwise comparisons [see **Section 4.7**]. In the absence of movement, the agency scores in the *detached hand* - *no movement* condition were lower than in the *full arm* - *no movement* condition (Wilcoxon signed-rank; Z=3.03, p=0.002). In contrast, under congruent active control, the reported agency scores in the *full arm* - *movement* condition did not yield a significant difference compared to the *detached hand* - *movement* (Wilcoxon signed-rank; Z=0.77, p=0.44) [**Figure 4.4**].

Similar to the results reported in the **Section 4.2**, these findings indicate that active control of the movements of the virtual hand plays a differential role in the reported sense of agency when there is a break in body continuity.

4.3.3 The reported sense of ownership was resistant to body discontinuity under active control, but not in the *no movement* conditions

Similar to the agency scores, we assessed whether seeing the hand detached from the body affected the reported sense of ownership in both *no movement* and *movement* conditions.

In the absence of movement (*no movement* conditions), the ownership scores in the *detached hand* were lower than the scores in the *full arm* - *no movement* condition (Wilcoxon signed-rank; Z=4.21, p<0.001). However, we found no significant difference between the ownership scores in the *full arm* - *movement* and the *detached hand* -

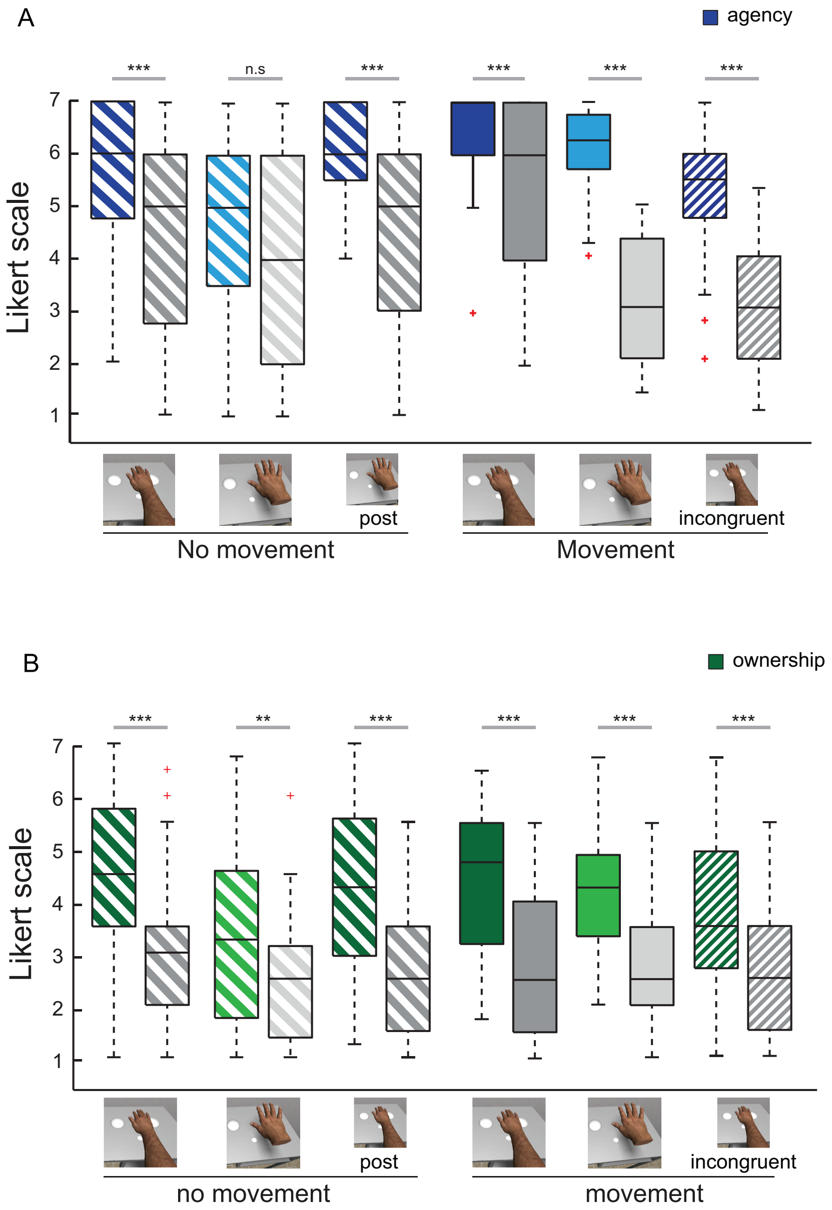


Figure 4.3: **The reported sense of agency and sense of ownership over the virtual hand and the respective control statements**. The agency (in blue) and ownership scores (in green) with their respective control statements (in gray) in all experimental conditions. Darker colors represent the *full arm* conditions, while lighter shades represent the *detached hand* conditions. Descending thick lines represent the *no movement* conditions, full colors represents *movement* and ascending thin lines the *incongruent movement* conditions. (A) The agency scores were significantly higher than their respective control statements in all conditions (p<0.001), except in the *detached hand* - *no movement* condition (p=0.15). (B) The ownership scores were significantly higher than their respective control statements in all conditions (p<0.002). The middle quartile indicates the median value and the whiskers indicate the most extreme values that are not considered outliers. ** p<0.01, *** p<0.001.

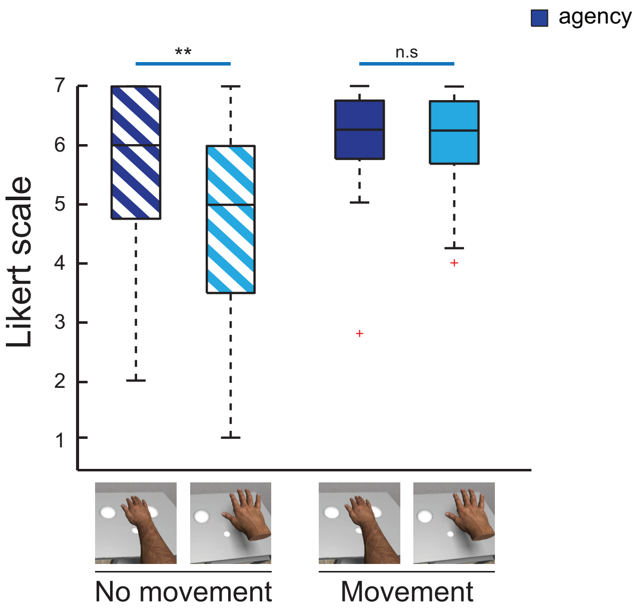


Figure 4.4: **The reported sense of agency was resistant to body discontinuity under active control, but not in the *no movement* conditions**. Agency scores in the *full arm* (in dark blue) and in the *detached hand* (in light blue) conditions for the *no movement* (descending thick lines) and *movement* (full color) conditions. In the *no movement* conditions, seeing the hand that appeared detached from the body (*full arm - no movement* vs. *detached hand - no movement*) resulted in a decrease in reported agency (p=0.002). The reported agency scores yielded no significant difference in the *movement* conditions (p=0.44). n.s. p>0.004 (Bonferroni corrected p-value), The middle quartile indicates the median value and the whiskers indicate the most extreme values that are not considered outliers. n.s p>0.05, ** p<0.004 (Bonferroni corrected p-value).

movement (Wilcoxon signed-rank; Z=2.02, p=0.04, not significant with Bonferroni correction) [**Figure 4.5**].

Similar to the results seen in **Experiment 1**, these findings are consistent with the idea that active control over the virtual hand movement plays a differential role in maintaining a sense of ownership when the hand appears in a discontinuous form (i.e., missing forearm).

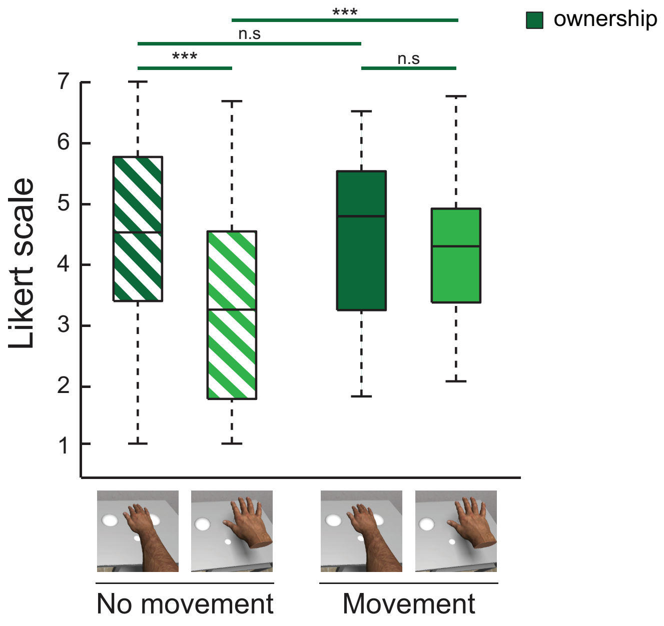


Figure 4.5: **The reported sense of ownership is resistant to body discontinuity under active control, but not in the *no movement* conditions**. The ownership scores in the *full arm* (in dark green) and in the *detached hand* (in light green) conditions for the *no movement* (descending thick lines) and *movement* (full color) conditions. Active control did not change reported ownership when comparing the *full arm* - *no movement* and the *full arm* - *movement* conditions (p=0.51). Seeing the hand detached caused a decrease in reported ownership scores in the *no movement* conditions (p<0.001), but not in the *movement* conditions (p=0.04, not significant with Bonferroni correction). Active control increases reported ownership scores in *detached hand* conditions (p<0.001). The middle quartile indicates the median value and the whiskers indicate the most extreme values that are not considered outliers. n.s p>0.05, *** p<0.001

4.3.4 Congruent active control did not enhance the reported sense of ownership in *full arm*, but it did in *detached hand* conditions

To assess the role of active control on the reported sense of ownership, we compared the ownership scores between the *no movement* and *movement* conditions. We hypothesized that, under active control over the virtual hand movements, the ownership scores would increase compared to the *no movement* conditions.

Contrary to our expectations, we found no significant differences in the reported sense of ownership when comparing *full arm* - *no movement* and *full arm* - *movement*

(Wilcoxon signed-rank; Z=0.66, p=0.51). However, active control resulted in a significant increase in the ownership scores over the limb in the discontinuous form (*detached hand* - *no movement* vs. *detached hand* - *movement*) (Wilcoxon signed-rank; Z=-3.38, p<0.001) [**Figure 4.5**].

These results show that active control can increase the reported sense of ownership, but only when the hand appears detached from the body. Thus, suggesting that the effect of visuomotor information might be contingent on the already available evidence for the sense of ownership (e.g., the visual appearance of the virtual arm).

4.3.5 Incongruent virtual hand movement hand decreased both the reported agency and ownership scores

Up to this point, our results suggest that active control over the virtual hand movements influences the senses of agency and ownership. We further hypothesized that the movement should be congruent with the participant's physical movements. Thus, we used the *full arm* - *incongruent movement*, in which noise was added to the trajectory of the virtual hand to test for this effect. See **Section 3.4** for a description of the *full arm* - *incongruent movement* condition.

The reported agency and ownership scores in the *full arm* - *incongruent movement* condition were significantly reduced when compared to the *full arm* - *movement* condition (Wilcoxon signed-rank; Z=4.09, p<0.001, and Z=3.64, p<0.001, respectively) [**Figure 4.6**].

These results suggest that incongruent movement of the virtual hand decreases the reported senses of ownership and agency.

4.3.6 Active control did not change the reported sense of ownership nor sense of agency scores in a subsequent *no movement* condition

Before the *movement* conditions, the participants did not experience control over the virtual hand. Only after the first *movement* block, they were aware that they could control the virtual arm. We wanted to assess whether the effect of active control had a lasting effect on the reported ownership and agency. We used an additional *no movement* condition after the first *movement* block [**Figure 3.2**]. In the *full arm* - *post*

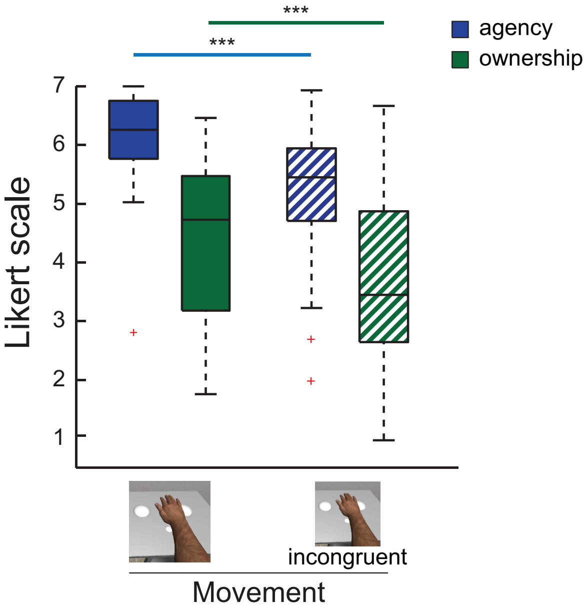


Figure 4.6: **Incongruent hand movement of the virtual hand decreased both the reported senses of agency and ownership**. The ownership (in green) and agency scores (in blue) for the *full arm - movement* (full colors) and *full arm - incongruent movement* (ascending thin lines). The reported ownership scores significantly decreased in the *full arm - incongruent movement* condition compared to the *full arm - movement* condition (p<0.001). The reported agency scores also significantly decreased in the *full arm - incongruent movement* (p<0.001). The middle quartile indicated the median value and the whiskers indicate the most extreme values that are not considered outliers. *** p<0.001

condition, as in the *full arm - no movement* conditions, the participants observed the static virtual arm without attempting to move it.

We found no significant difference in the ownership scores, nor in the agency scores in the *full arm - post* compared to the *full arm - no movement* condition (Wilcoxon signed-rank; Z=1.30, p=0.19 and Z=-1.58, p=0.11, respectively) [**Figure 4.7**].

From these results, we do not see evidence for a long-lasting influence of active control on the senses of ownership and agency.

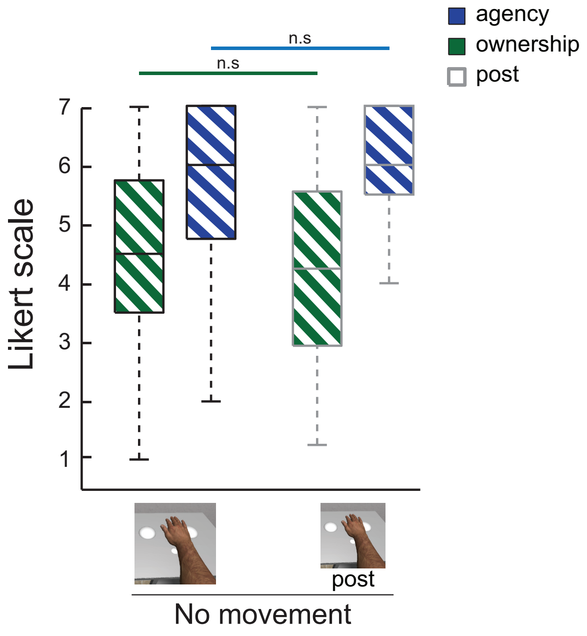


Figure 4.7: **The reported ownership and agency scores did not increase in a subsequent *no movement* condition**. Ownership scores (green) and agency scores (blue) in the *full arm - no movement* (descending thick lines, black outline) and *full arm - post* (descending thick lines, grey outline). Neither the ownership or agency scores yielded a significance (p=0.84 and p=0.11, respectively). The middle quartiles indicate the median value and the whiskers indicate the most extreme values that are not considered outlier. p>0.004 (Bonferroni corrected p-value)

4.3.7 Incongruent movement and body discontinuity differently affected the senses of ownership and agency

To get an insight into the relationship between the senses of ownership and agency, we measured the correlation of the change in individual ownership scores and the change in individual agency scores between different pairs of conditions (e.g., *full arm - no movement* and *full arm - movement*). Refer to **Section 4.7** for a detailed explanation of the data handling.

The individual changes in the ownership scores and the changes in agency scores between the *full arm - no movement* and the *detached hand - no movement* conditions showed a weak correlation (Spearman ρ=0.37, p=0.002) [**Figure 4.8A**]. For the *full arm - movement* compared to the *detached hand - movement* conditions, the individual changes in ownership scores and agency scores were more correlated (Spearman

ρ=0.50, p=0.002) [**Figure 4.8B**]. When comparing the *full arm - no movement* to the *full arm - post* conditions, the individual changes in the reported ownership scores and agency showed a weak correlation (Spearman ρ=0.42, p=0.009) [**Figure 4.8C**]. The stronger correlation was found between the individual changes in the ownership scores and the individual changes in the agency scores between the *full arm - movement* and *full arm - incongruent movement* conditions (Spearman ρ=0.61, p<0.001) [**Figure 4.8D**].

These results suggest that body discontinuity and incongruent movement differently affect the participants. While incongruent movement appears to have a similar disturbing effect in both the senses of ownership and agency, body discontinuity has a less consistent effect.

It is worth noting that the position of the dots in the quadrants provides additional information on the relationship between the reported ownership and agency scores, indicating the direction of the change. On the top-right quadrant, both the reported sense of ownership and agency decrease due to the manipulation. Conversely, the bottom-left quadrant represents an individual were both the ownership and the agency scores increase due to the manipulation. The top-left quadrant shows individuals who report a higher sense of agency but a lower sense of ownership and the opposite in the bottom-right quadrant.

When comparing the *full arm - no movement* and the *detached hand - no movement* conditions, we can observe that the individuals are scattered across the plot, but most are found on the top-right quadrant (21 out of 37). Indicating that most participants reported lower values of both ownership and agency scores when seeing the hand detached from the body in the *no movement* conditions [**Figure 4.8A**].

In **Figure 4.8B**, *full arm - movement* compared to the *detached hand - movement*, the dots appear to be less scattered. In this comparison, a mere nine participants decreased both in the reported ownership and the agency scores, while eleven participants reported an increase in both components. The effect of body discontinuity in *movement* conditions resulted in a more variable response from the participants than in [**Figure 4.8A**].

When comparing the *full arm - no movement* to the *full arm - post* conditions, we observe that eleven individuals decreased their values in both components, while six increased their values in both. In this comparison, most individuals maintained either their ownership or agency scores.

Incongruent movement caused a decreased in both components in 24 out of 37 individuals when comparing *full arm* - *incongruent movement* to the *full arm* - *movement*. In this comparison, the dots are more condensed than in the other comparisons. Therefore, suggesting that the participants decreased by similar values in the ownership and agency scores.

4.3.8 The reported sense of ownership was differently affected depending on the manipulations

Up to this point, our results suggest that active control plays a role in the sense of ownership over the virtual hand. The results shown in the previous section suggest that the effect of active control depends on the pre-existing evidence of ownership. Thus, we tested whether participants responded differently to the manipulations depending on their basal ownership levels. For this purpose, we divided the participants into three groups according to a different baseline in each pairwise comparison [see **Section 4.7**], and tested for differences within each group.

In the *no movement* conditions, the reported ownership was significantly reduced in the *detached hand* compared to the *full arm* condition [**Figure 4.5**]. The individual ownership scores between the *full arm* - *no movement* and *detached hand* - *no movement* conditions showed a positive correlation (Spearman ρ=0.51, p<0.001). The reported ownership scores in the *detached hand* condition were lower in the high ownership individuals (ownership scores $\geq$ 5) (Wilcoxon signed-rank: Z=3.41, p<0.001, n=16), but they were not different in the medium and low ownership groups (ownership scores < 5) (Wilcoxon signed-rank; p=0.04, not significant under Bonferroni, n=15 and 0.53, n=6, respectively) [**Figure 4.9A**].

Under active control (i.e., *movement* conditions), the ownership scores in the *full arm* - *movement* and *detached hand* - *movement* conditions were correlated (Spearman ρ=0.63, p<0.001). None of the subgroup comparison showed a significant difference (p=0.022 (not significant under Bonferroni correction), n=17, p=0.09, n=11, and

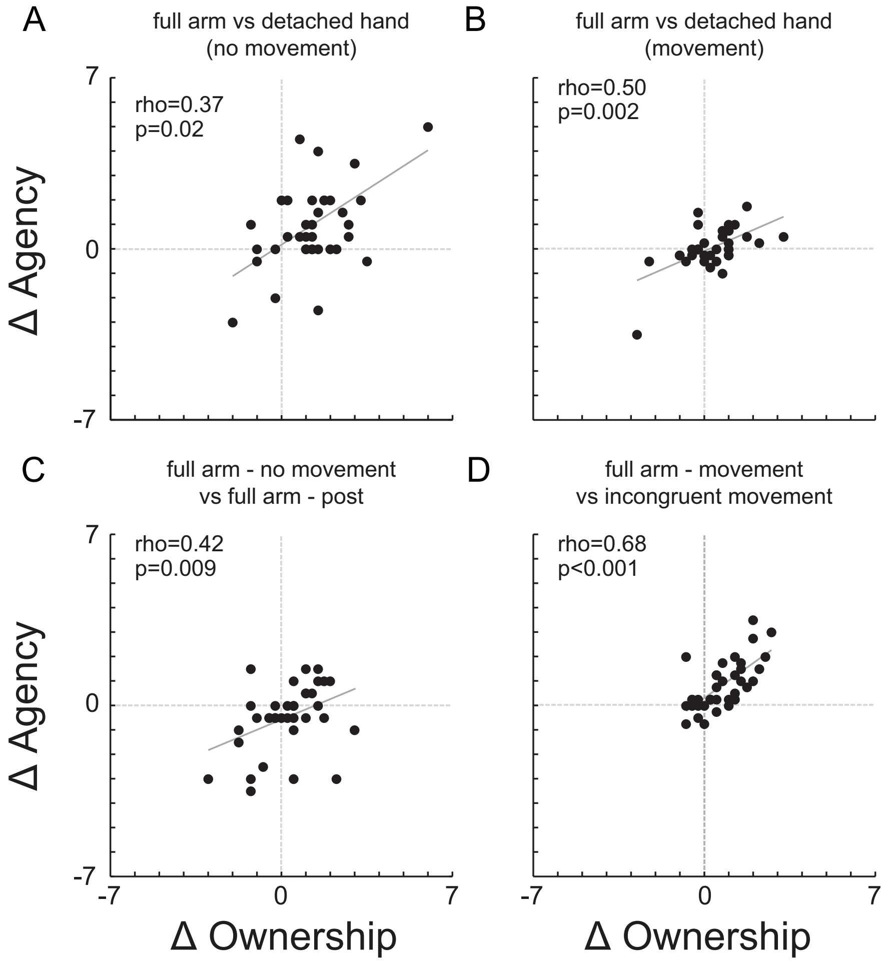


Figure 4.8: **The reported ownership and agency scores changed differently depending on the manipulations**. The x-axis shows the difference in the reported ownership between the two compared conditions, while the y-axis shows the difference in the reported sense of agency between the same conditions. Thus, each dot represents these two differences for an individual. (A) Comparison of the *full arm - no movement* and *detached hand - no movement*. The change in the ownership scores and the change in agency scores were weakly correlated (Spearman ρ=0.37, p=0.002). (B) Comparison of the *full arm - movement* and *detached hand - movement*. The change in the ownership scores and the change in agency scores were correlated (Spearman ρ=0.50, p=0.002) (C) Comparison in the *full arm - no movement* and *full arm - post* conditions. The change in the ownership scores and the change in agency scores were weakly correlated (Spearman ρ=0.42, p=0.009). (D) Comparison in the *full arm - movement* and *full arm - incongruent movement* conditions. The change in the ownership scores and the change in the agency scores were highly correlated (Spearman ρ=0.68, p<0.001).

p=0.48, n=9, for high, medium and low ownership score, respectively) [**Figure 4.9B**].

Active control enhanced the reported sense of ownership only in discontinuous limb conditions (*detached hand* - *no movement* compared to *detached hand* - *movement*) [**Figure 4.5**]. The individual reports for these conditions were positively correlated (Spearman ρ=0.48, p=0.002). The analysis of the subgroups revealed that active control caused a significant increase in low (Wilcoxon signed-rank; Z=-3.37, p<0.001, n=18), but not in medium or high ownership groups (Wilcoxon signed-rank; p=0.03, not significant under Bonferroni correction, n=13 and p=0.49, n=6, respectively) [**Figure 4.9C**].

In the *full arm* conditions, the individual ownership scores were correlated between the *full arm* - *no movement* and *full arm* - *movement* conditions (Spearman ρ=0.47, p=0.003). In the subgroup comparison, the high ownership showed a significant decrease (Wilcoxon signed rank; p<0.001, n=16), but not in medium (Wilcoxon signed rank; p=0.91, n=15) nor low ownership groups (p=0.03 (not significant under Bonferroni correction), n=6) [**Figure 4.9D**].

Comparison of the *full arm* - *movement* and *full arm* - *incongruent movement* conditions showed a strong correlation in the responses (Spearman ρ=0.76, p<0.001). In the analysis of the subgroups, only the medium ownership group showed a significant decrease in the ownership scores group (p=0.002, n=15), but not in high (p=0.03 (not significant under Bonferroni correction), n=17), or low (p=0.14, n=6) [**Figure 4.9E**].

These results show that active control and the hand's appearance have different effects depending on the basal level of reported sense of ownership.

4.4 Discussion

In this chapter, we report our findings regarding the interplay between visual appearance and active control over the virtual hand movements to maintain and enhance the senses of ownership and agency over a virtual hand. First, we show in **Experiment 1** (**Section 4.2**) that, under the active control of the movements of the virtual hand, both the reported sense of agency and ownership were resistant to body discontinuity. These findings are replicated in the data shown in **Experiment 2** (**Section 4.3**).

The results in **Experiment 2** further show that visuomotor information acts as evidence in favor of the sense of ownership. Body discontinuity did not affect the senses of ownership and agency when the participants could control the virtual hand; however,

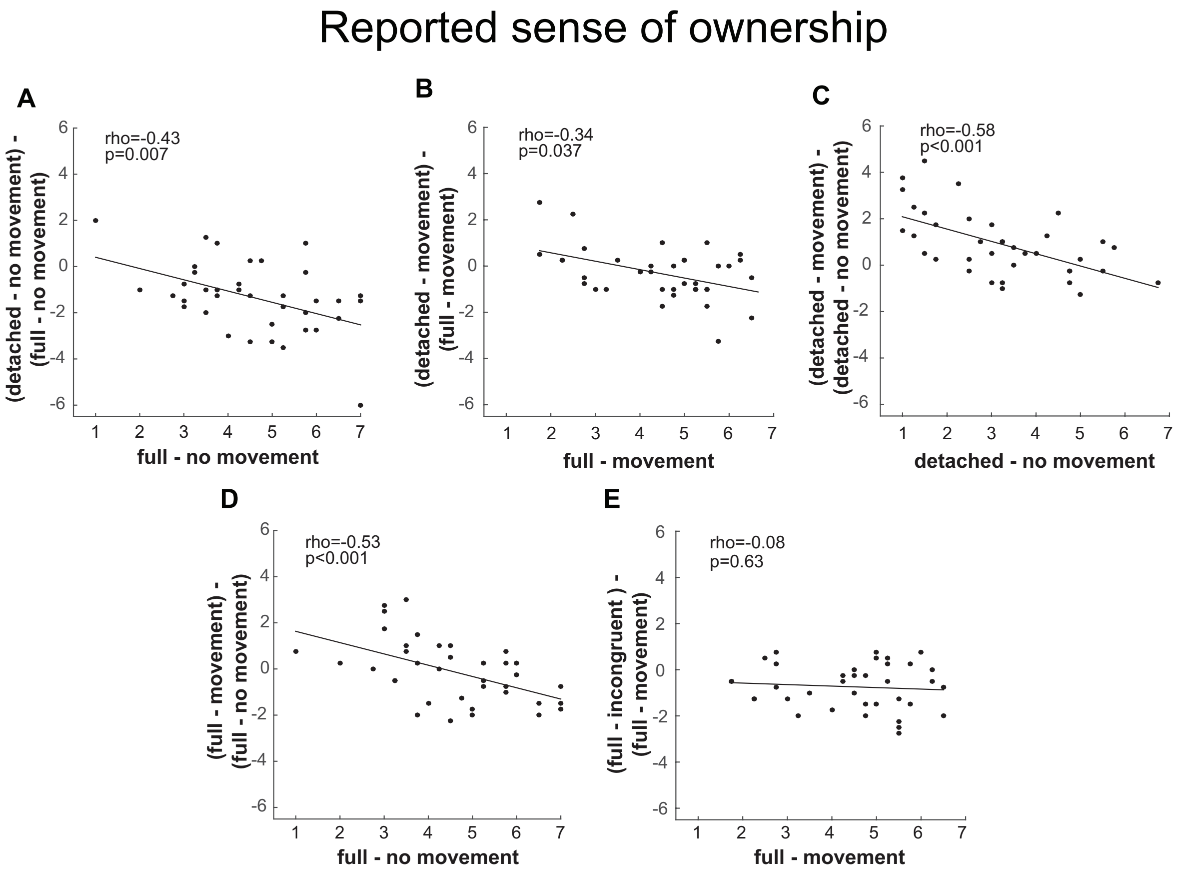


Figure 4.9: **Correlation of the individual ownership scores in different pairwise comparisons**. Reported ownership scores in the pairwise comparisons divided into three groups, low ($\leq$3), medium (>3 and <5), and high ($\geq$5) ownership. (A) The ownership scores in the *full arm* - *no movement* and *detached hand* - *no movement* were correlated (ρ=0.48, p=0.002). Only the high ownership group ($\geq$5) showed a significant decrease (p<0.001) in the reported ownership scores. (B) The ownership scores in the *full arm* - *movement* and *detached hand* - *movement* were correlated (ρ=0.63, p<0.001). No subgroup showed a significant difference between these two conditions. (C) The ownership scores in the *detached hand* - *no movement* and *detached hand* - *movement* were correlated (ρ=0.48, p=0.002). The low ownership group showed an increase in the ownership scores (p<0.001). (D) The ownership scores in the *full arm* - *no movement* and the *full arm* - *movement* were correlated (ρ=0.47, p=0.003). The high ownership group showed a significant difference (p<0.001). (E) The ownership scores in the *full arm* - *movement* and *full arm* - *incongruent movement* conditions were correlated (ρ=0.76, p<0.001). Ownership scores in the medium ownership decreased significantly (p=0.002). y-axis shows the subtraction between both compared conditions.

body discontinuity caused a decrease in the reported sense of ownership and agency when observing a static virtual arm. These results suggest a strong effect of visuomotor information in the sense of ownership. Secondly, we found that active control over the virtual hand enhances the reported ownership only when the evidence of ownership is lowered by a break in body continuity (i.e., *detached hand* conditions). Thus, suggesting that the effect of active control could be contingent on the visual appearance of the limb. Furthermore, we found that body discontinuity and incongruent movement had a differential effect in the reported senses of ownership and agency. Thus, suggesting an interaction between the sensory modalities (i.e., visuomotor information and visual appearance of the virtual limb) acting as evidence for the sense of ownership. Moreover, when comparing the participants according to their ownership levels, we found that active control significantly affected individuals with lower ownership scores.

The morphological appearance of the fake limb plays a crucial role in the RHI paradigm (Kilteni et al., 2015). For the illusion to occur, the top-down modulation requires the limb to be hand-shaped (Tsakiris, 2010; Haans, Ijsselsteijn, and Kort, 2008; Tsakiris and Haggard, 2005a). Additionally, the RHI is sensitive to manipulations in body morphology, such as size and transparency (Martini et al., 2015; Kilteni et al., 2012). Among all the features, body continuity seems to be a requirement. When passively observing a static hand, body discontinuity has shown to negatively affect the reported sense of ownership (Tieri et al., 2015a; Tieri et al., 2015b; Tieri et al., 2017), during visuotactile stimulation (Perez-Marcos, Sanchez-Vives, and Slater, 2012), or when passively observing a virtual moving arm without actual movement from the participants (Tieri et al., 2015a). In this chapter, we report a similar decrease in the sense of ownership when participants saw the arm with the missing forearm in the absence of any additional information (i.e., *no movement* conditions).

To elicit a sense of body ownership, all the sensory information, including visuomotor information, needs to be integrated (Kalckert and Ehrsson, 2012; Synofzik, Vosgerau, and Newen, 2008b). We hypothesized that, if participants actively controlled the virtual limb, the reported sense of ownership should be resistant to body discontinuity. Our results from the *movement* conditions in both **Experiment 1** and **Experiment 2** agree with this hypothesis. We found no significant difference in the ownership scores between the *full arm* and the *detached hand* conditions when participants controlled the virtual arm (*movement* conditions). Thus, active control circumvents the decrease in reported ownership caused by seeing a limb in the discontinuous form. We conclude that visuomotor information, when available, plays a critical role in maintaining a sense of ownership over a limb that appears detached from the body.

Recognizing our actions is critical to the sense of ownership (Jeannerod, 2003). However, the role of visuomotor information, as a result of active control, for the sense of ownership over a fake limb is still a matter of debate. While some studies have reported that active control increased the sense of ownership (Dummer et al., 2009; Kalckert and Ehrsson, 2012; Hamasaki et al., 2019), others failed to see this effect (Kalckert and Ehrsson, 2014; Walsh et al., 2011). We used the discontinuous form of the arm (i.e., *detached hand*) to test for this hypothesis. In our setup, the information provided to the participants in *full arm* - *no movement* condition (i.e., first-person perspective, anatomical plausibility, and a realistic virtual hand appearance) was sufficient to drive the illusion of ownership (Costantini and Haggard, 2007; Ehrsson, Spence, and Passingham, 2004; Haans, Ijsselsteijn, and Kort, 2008; Maselli and Slater, 2013; Slater et al., 2010). The illusion of ownership can arise from the sole effect of seeing a realistic virtual body in the same location and posture as the physical body (Maselli and Slater, 2013). In this scenario active control did not further enhance the sense of ownership (*full arm* - *no movement* compared to *full arm* - *movement*). However, in the *detached hand* - *no movement*, where the evidence of the sense of ownership was lowered, active control provided evidence in favor of ownership in the *detached hand* - *movement* condition. The analysis of the subgroups further strengthens this idea. The participants with low individual ownership scores (≤ 3) in the *detached hand* - *no movement* condition reported significantly higher scores in the *detached hand* - *movement* condition. The reported presence or absence of an effect of active control on the sense of ownership over the fake limb could depend on the experimental design or the hand's visual appearance. These results could help reconcile the differences found in the literature.

A reported sense of agency can be present without any actual movement when passively observing a moving limb (Tieri et al., 2015a; Wegner, Sparrow, and Winerman, 2004; Pezzetta et al., 2018), and after inducing a sense of ownership through visuotactile stimulation (Burin et al., 2017). In our setup, the participants reported a perceived sense of agency in the *full arm - no movement* condition (e.g., 'I could control the virtual hand if I wanted to'), which was decreased by body discontinuity. Therefore, the already existing sense of ownership created a weak sense of agency contingent on the hand's visual information. In the absence of visuomotor information (*no movement* conditions), feeling a sense of ownership elicits a weak sense of agency (Kalckert and Ehrsson, 2014), as a result of congruent morphological, proprioceptive, and visuotactile information, which can even result in involuntary movements in the participant's physical hand (Shibuya et al., 2018). However, when body continuity is broken, the vicarious agency significantly decreased in the absence of voluntary motor commands (Tieri et al., 2015b; Tieri et al., 2015a; Tieri et al., 2017). We here report a similar finding in the *no movement* conditions: the reported sense of agency was significantly lower in *detached hand* than the *full arm - no movement*.

This is not the case under the active control of the virtual hand movements, as we found that the reported sense of agency was not affected by seeing the arm detached from the body (i.e., *detached hand*) compared to the *full arm - movement* condition. Visuomotor signals resulting from voluntary action (Synofzik, Vosgerau, and Newen, 2008b) are crucial for the sense of agency, as the recognition of action is enhanced when the efference copy mechanisms are engaged (Tsakiris and Haggard, 2005a; Farrer et al., 2003). When the participants control the virtual hand movements, the intention to move generates a motor command and an efference copy used to predict future bodily states (Wolpert, 1997), which is then compared to the actual sensory feedback from the body and the environment (Farrer and Frith, 2002). When this efference copy matches the predicted sensory feedback from the movement, the sense of agency arises (Blakemore, Wolpert, and Frith, 1998; Miall and Wolpert, 1996). Conversely, a visual or temporal mismatch abolishes a sense of agency (Blakemore, Wolpert, and Frith, 2002). This comparator model highlights the importance of visuomotor effects of the movement for the sense of agency (Haggard, 2017). The presence of active control plays a differential role in the effect of incongruent morphological appearance in the reported sense of agency. Thus, active control could explain the difference between our findings and what has been previously reported using passive observation of the movement.

In a voluntary action, proprioceptive, motor, and visual information about the movement and the consequences of the action are available to the participant. The presence of these sensory signals adds information in favor of a sense of agency over the virtual limb. Unfortunately, as a result of the experimental design, we could not compare the reported sense of agency across *no movement* and *movement* conditions. The main focus of **Experiment 2** was the role of active control in shaping the sense of ownership over a virtual limb. Therefore, to avoid priming the participants in the *no movement* conditions, the statements to assess the sense of agency needed to be different between the *no movement* and the *movement* conditions. Thus, the statements agency statements could not be compared. This comparison could help us further understand the interplay between morphological and visuomotor congruence in the sense of agency.

Our results indicate that, when active control is present, visuomotor information is weighted more heavily than visual appearance. The data from our *full arm* - *incongruent movement* condition can further support this hypothesis. In this condition, the mismatch between the performed and observed action is accompanied by a decrease in the reported sense of agency and the sense of ownership compared to the *full arm* - *movement* condition, despite the appearance of the hand being congruent. These results are consistent with studies that have used an asynchronous movement of the virtual hand, which does not elicit a sense of ownership or agency over the virtual hand (Kalckert and Ehrsson, 2012; Kalckert and Ehrsson, 2014; Sanchez-Vives et al., 2010). Additionally, visuomotor delays decrease the reported feelings of ownership (Lesur et al., 2019). Interestingly, the difference in the individual ownership scores between the *full arm* - *movement* and the *full arm* - *incongruent movement* conditions strongly correlated with the difference in the individual agency scores between the same conditions [**Figure 4.8**]. The results shown in **Figure 4.8D** suggests that congruent movement is important to maintain both a sense of agency and a sense of ownership over the virtual limb. Overall, suggesting that in order for visuomotor information to influence the sense of ownership, the movement needs to be congruent to the performed movement by the participant.

Finally, in the first *no movement* block, the participants still had not performed the task and had no evidence that they could control the movement of the virtual hand. In the second *no movement* block, the participants had already controlled it. Contrary to our expectations, we found no differences in the reported agency scores [**Figure 4.7**] compared to the *full arm* - *movement* condition. These results suggest that the effects of our manipulations, such as allowing the participants to move the virtual hand, may be restricted to the condition in which they are used. Interestingly, when looking at the changes in responses [**Figure 4.8C**], the participants seem to be changing their responses, but there is no correlation in these changes. The sense of agency did not change after the participants were aware that they could control the virtual hand. However, the variability of the responses decreases, as can be seen in the IQR.

We found no significant difference in the reported sense of agency between the *detached hand* - *no displacement* and the *detached hand* - *displacement* or between the *full arm* - *no displacement* and the *full arm* - *displacement* conditions in **Experiment 1**. Indicating that the proprioceptive displacement does not affect the reported sense of agency. Due to physical limitations of the experimental setup (e.g., limited tracking area of the Leap Motion), the displacement was restricted to distances below 12 cm. Contrary to previous reports using visuomotor information (Yuan and Steed, 2010; Sanchez-Vives et al., 2010) or visuotactile stimulation (Zopf, Friedman, and Williams, 2015), we do find a small but significant decrease in the reported sense of ownership with a proprioceptive displacement of 10 cm (*full arm* - *no displacement* vs. *full arm* - *displacement*). However, we report no difference in the *detached hand* conditions.

While puzzling, the decrease in the reported ownership scores in the *full arm* - *displacement* seems to be unrelated to the subjective experience of the displacement. The participants did not report a significant change in the reported sense of location when comparing the *full arm* - *displacement* and the *full arm* - *movement* conditions, or the rest of the pairwise comparisons in **Experiment 1** (Wilcoxon-signed rank test; p>0.12, data not shown). The distance between the virtual and the physical hand in the *displacement* conditions was ten centimeters. Thus, a possible explanation could be that the displacement was not sufficient for the participant to notice. Further experiments and replication are necessary to understand these results fully. However, the relationship between body discontinuity and the proprioceptive displacement is beyond the scope of this dissertation.

A striking limitation of our experimental design is the lack of a condition where they passively observed the moving virtual hand without performing any movement themselves (Pezzetta et al., 2018; Tieri et al., 2015b). This condition would be useful for a more direct comparison with previous literature. In passive observation of movement, no internal motor information is available (Farrer et al., 2003), and participants are only susceptible to visual information. Thus, a break in body continuity, similar to our *detached hand* conditions, negatively affects vicarious agency and the sense of ownership in the absence of movement (Tieri et al., 2015b). We would expect that, in the absence of active control, the participants would report a decreased sense of ownership and agency when observing a discontinuous limb moving.

The results presented in this chapter suggest that the sensory information is weighted differently depending on the available information in each condition. In the absence of motor information, the participants relied on the visual appearance of the virtual hand and the proprioceptive information. When we introduce a mismatch in the expected appearance, i.e., missing forearm, the sense of ownership decreases. However, when the participants are required to control the virtual hand movements, visuomotor information is heavily weighted. In these conditions, introducing a break in body continuity did not affect the reported sense of ownership or agency. Conversely, a mismatch in the seen movement of the virtual hand resulted in a decrease in the reported ownership, regardless of the visual appearance of the virtual arm.

4.5 Conclusions

- The results reported in this chapter show that visuomotor information resulting from active control maintains the senses of agency and ownership when the virtual hand appears detached from the body. The opposite is observed in the absence of movement: observing a discontinuous limb decreases the reported sense of ownership and agency.
- We also report that active control over the virtual hand movements adds evidence in favor of the sense of ownership over a virtual hand when the evidence for ownership is low, in our case, over a hand that appears detached from the body. Thus, the effect of visuomotor information appears to be contingent on the available sensory information.
- By adding noise to the trajectory of the virtual hand movement, we show that the movement of the virtual hand needs to be congruent to the participant's movement for active control to add evidence in favor of ownership. The addition of perturbations to the virtual hand's observed trajectory resulted in a significant decrease in the reported sense of ownership and agency.
- We also show that the perturbations, incongruent movement and body discontinuity affect the individuals differently depending on their reported levels of ownership.
- Our results suggest that the reported sense of ownership over the virtual hand arises from the interplay of the visual appearance of the hand and the presence of visuomotor information.

4.6 Conclusões

- Os resultados apresentados neste capítulo mostram que a informação visuomotora resultante do controlo ativo dos movimentos observados na mão virtual mantêm os sentidos de propriedade e agência sobre uma mão virtual, mesmo que esta pareça desanexada do corpo. O oposto acontece na ausência de movimento, situação em que a observação passiva de uma mão desconectada diminui os sentidos de propriedade e agência.
- Também reportamos que o controlo ativo sobre os movimentos da mão virtual adiciona evidência a favor do sentido de propriedade sobre a mão, quando a evidência para o sentido de propriedade é baixa. Portanto, o efeito da informação visuomotora é contingente à restante informação sensorial disponível.
- Com a adição de perturbações na trajetória dos movimentos da mão virtual, mostramos que o movimento da mão virtual tem de ser congruente com o movimento realizado pelo participante para que o controlo ativo funcione como evidência a favor do sentido de propriedade. Adicionar perturbações na trajetória observada na mão virtual diminui os sentidos de propriedade e agência.
- Demonstramos ainda que as perturbações realizadas, movimento incongruente e descontinuidade no corpo, afecta os participantes de forma diferente dependendo dos seus níveis individuais de sentido de propriedade.
- Os nossos resultados sugerem que o sentido de propriedade sobre a mão virtual decorre da interação entre a aparência visual da mão é da presença de informação visuomotora.

4.7 Data Handling

All data were analyzed using Matlab 2014b.

Data preprocessing

The questionnaires used in both studies in this chapter included more than one statement for assessing the sense of ownership, sense of agency (for *no movement* conditions), sense of agency (for *movement* conditions), outcome agency (for *movement* conditions), and their respective control statements [see **Section 3.5 and 3.4**]. To avoid the artifacts related to pseudoreplication, for each participant we calculated the individual mean score for each category (e.g. sense of ownership) in each condition (e.g. *full arm* - *no movement*). Thus, we obtained a total of 37 individual scores for each category and condition.

Normality

Using the Shapiro-Wilk test, the individual ownership scores were not found to follow a normal distribution, while the individual agency scores did. Therefore, we used non-parametric tests for the remaining analysis. We used a Friedman ANOVA to compare across all the conditions and the Wilcoxon signed-rank test for pairwise comparisons.

Pairwise comparison

Experiment 1

First, we compared the sense of ownership and the sense of agency statements to their respective control statements in each condition to test for task compliance and suggestibility effects.

We compared the ownership and agency scores between all pairs of conditions (i.e., *full arm* - *no displacement* vs. *full arm* - *displacement*, *full arm* - *no displacement* vs. *detached hand* - *no displacement*, *detached hand* - *no displacement* vs. *detached hand* - *displacement*, and *full arm* - *displacement* - *detached hand* - *displacement*)

Thus, in total, we performed eight pairwise comparisons, each with a Bonferroni corrected p-value of 0.00625.

Experiment 2

First, we compared the sense of ownership and the sense of agency statements to their respective control statements in each condition to test for task compliance and suggestibility effects.

In accordance to our hypotheses, we compared the ownership scores in the following pairs of conditions: *full arm - no movement* against *detached hand - no movement* and *full arm - movement* against *detached hand - movement*, to assess the effect of morphological congruence; *full arm - no movement* against *full arm - movement* and *detached hand - no movement* against *detached hand - movement*, to assess the effect of active control; *full arm - movement* against *full arm - incongruent movement* to assess the importance of movement congruence; and *full arm - no movement* against *full arm - post*.

We also compared agency scores in the following pairs of conditions: *full arm - no movement* against *detached hand - no movement* and *full arm - movement* against *detached hand - movement*, to assess the effect of morphological congruence; *full arm - movement* against *full arm - incongruent movement* to assess the importance of movement congruence; and *full arm - no movement* against *full arm - post*.

Finally, to assess the effects of morphological incongruence and movement incongruence on outcome agency, we compared *full arm - movement* against *detached hand - movement* and *full arm - movement* against *full arm - incongruent movement*.

Thus, in total, we performed twelve pairwise comparisons, each with a Bonferroni corrected p-value of 0.004.

Correlations

We reasoned that participants might be affected differently by the manipulations depending on their basal level of ownership. For this reason, we also made an analysis separating the participants into three groups according to their individual ownership score: low (i.e., individual ownership score $\leq$ 3), medium (i.e., individual ownership score > 3 and < 5), and high (i.e., individual ownership score $\geq$ 5), defining a different baseline condition in each pairwise comparison. We compared participants in the following pairs of conditions using the Wilcoxon signed-rank test: *full arm - no movement* against *full arm - movement* and *detached hand - no movement* against *detached hand - movement*, to assess the effect of active control movement; *full arm - no movement* against *detached hand - no movement* and *full arm - movement* against *detached hand - movement* to assess the effect of morphological congruence; and *full arm - movement* against *full arm - incongruent movement* to assess the importance effect of movement congruence. Each of these five pairs of conditions was tested for the three groups of different basal individual ownership scores, giving a total of 15 tests. Each with a Bonferroni corrected p-value threshold of 0.003.

Additionally, we assessed the correlation between the changes in the sense of agency and the changes in the sense of ownership between two conditions. For each pair of compared conditions, we calculated the individual changes in the sense of ownership and the sense of agency, which we labeled $\Delta Ownership$ and $\Delta Agency$, respectively.

$$\begin{aligned} \Delta Ownership_i &= Ownership_{i_A} - Ownership_{i_B} \\ \Delta Agency_i &= Agency_{i_A} - Agency_{i_B} \end{aligned} \tag{4.1}$$

where $\Delta Ownership$ and $\Delta Agency$ are the differences between condition A (e.g. *full arm - no movement*) and condition B (e.g. *detached hand - no movement*) for a given individual, i. Thus, we obtained 37 Δ values for both ownership and agency scores.

We calculated the correlation between the values obtained using the Spearman ρ correlation coefficient. We made the following comparisons: *full arm - no movement* against *detached hand - no movement*, *full arm - movement* against *detached hand - movement*, *full arm - post*, and *full arm - movement* against *full arm - incongruent movement*. This resulted in a total of four comparisons, each with a Bonferroni corrected p-value of 0.0125.

5 | The contribution of the outcome of the task to the senses of ownership and agency

> *"It's not worth doing something unless someone, somewhere, would much rather you weren't doing it."*
>
> Terry Pratchett

5.1 Introduction

The sense of agency relies both on internal and external cues. It refers to the subjective experience of being the source of an action and the source of the consequences that an action has in the environment (Haggard, 2017; Haggard and Chambon, 2012). Human agents can learn the associations between the actions they perform and their outcomes, thus, having a sense of agency over events external to the body (Kalckert and Ehrsson, 2012; Caspar, Cleeremans, and Haggard, 2015). Two layers can be defined in the sense of agency, which have been referred to as body or proximal agency (i.e., authorship over the own actions) and external or distal agency (i.e., control over the external events) (Kalckert and Ehrsson, 2012; Metcalfe, Eich, and Miele, 2013). If we consider a goal-directed action, such as turning on a light, reaching our arm towards the switch would be considered the proximal or body agency. Feeling that our action caused the light to turn on would be the distal or external agency. Body agency relies on sensory and motor feedback from the body, while the external agency relies mainly on the sensory consequences and intention.

Mismatches between the observed and the executed movement results in a decreased sense of agency in healthy participants (Farrer, Valentin, and Hupé, 2013). When this occurs, the participants can attribute the authorship of the movement to another agent (Farrer and Frith, 2002). For instance, increasing delays between the executed and observed movement resulted in a loss of self-agency for temporal delays larger than 300 ms (Shimada, Qi, and Hiraki, 2010) up to 1100 ms (Farrer et al., 2008; Farrer, Valentin, and Hupé, 2013). Furthermore, spatial perturbations on the movement of the virtual hand (without a temporal delay) also decrease the reported sense of agency. The sense of agency decreases due to incongruent movement to the one performed by the participant (Padrao et al., 2016) and when noise is added to the trajectory of the virtual hand (Brugada-Ramentol, Clemens, and Polavieja, 2019).

On the other hand, delays in the expected outcome of the task can also negatively affect the sense of agency (Wen, 2019). For instance, in a setup where the participants are required to control a square on a screen via keyboard input, the ratings of control decrease when delays are added (Wen, Yamashita, and Asama, 2015a). In a computerized test, where the participants controlled a moving dot towards a target, the feeling of control over the dot was influenced by goal-achievement expectation (Wen, Yamashita, and Asama, 2015b). Interestingly, the same authors found that improved performance, even when the participant did not perform the observed action, resulted in a stronger sense of agency (Wen, Yamashita, and Asama, 2015c). These results suggest that goal-achievement highly influences perceived control.

The aforementioned studies have manipulated either proximal or distal agency separately. To fully understand the contribution of movement and outcome to the sense of agency, it is necessary to study them simultaneously within the same paradigm. The SoA-GAME (Sense of Agency for Goal Achievement and Movement Execution) allowed the authors to manipulate the visual feedback with respect to the action and the outcome resulting from that action in the same experiment (Villa et al., 2020). Both the perturbations in either the execution of the movement and the goal's achievement result in reducing the sense of agency. Specifically, the authors find that movement monitoring may be a more constant source of information for the sense of agency than goal-achievement (Villa et al., 2018). Using a human-like robot hand, the experimenters manipulated either the action congruence, the outcome congruence, or the temporal congruence of the action. Their results showed that the congruent outcome is relevant for a sense of agency only when the outcome was also congruent (Caspar et al., 2016b).

In contrast, other studies suggest a more substantial effect of outcome-related information. Using a finger-tapping paradigm, the participants were found to be more sensitive to delays in the task's outcome than to delays in the action itself, which was independent of the type of sensory feedback of the outcome (auditory and visual outcome). Their results suggest that outcome-related information was more important for the sense of agency (David et al., 2016). In all, the contradictory results presented above suggest that it remains unclear whether the information regarding the action or the information regarding the consequence of the action is the most relevant to elicit a sense of agency.

The role of movement in the moving Rubber (or Virtual) Hand Illusion paradigm has been assessed previously; however, few studies aim to understand the role of the outcome of the action in the reported sense of ownership. Matching executed and observed outcome resulted in fewer errors in a self-recognition task (Bos and Jeannerod, 2002) and the subjects are more accurate in discriminating self-body movement from other's body movement in the active condition than in the passive condition (Tsakiris et al., 2005). Conversely, seeing a hand that does not belong to the self results in errors in self-recognition when the experimenter and the subject performed the same movement (Daprati et al., 1997), which might result in compensatory movements to correct for a wrong action (Nielsen, 1963; Fourneret and Jeannerod, 1998). In the previous chapter, we outline the importance of active control in eliciting and maintaining a sense of ownership over the virtual hand while performing a goal-directed action (Brugada-Ramentol, Clemens, and Polavieja, 2019). To the best of our knowledge, only one study investigated the difference in body ownership, depending on whether the movement consisted of a goal-directed or non-goal-directed action. Specifically, the authors found that goal-directed actions enhanced the sense of ownership over a fake limb compared to non-goal-directed actions (Wen et al., 2016).

In this chapter, we aim to test the effect of the outcome of continuous goal-directed action in the reported senses of ownership and agency. Similarly to previous studies (Kalckert and Ehrsson, 2012; Metcalfe, Eich, and Miele, 2013), we defined two types of sense of agency, which we labeled action agency and outcome agency. These two types of agency correspond to the authorship over the action (i.e., action agency) and the feeling of causing a change in the environment (i.e., outcome agency). We modified the task reported in **Chapter 4** in a way that the lights would not respond when the participant reached the light. In these *incongruent outcome* conditions, the light failed to respond to the participant's hand, while the movement was congruent to the participant's movement. Additionally, we emphasized the importance of the outcome of the task by adding a counter of successful and failed attempts to turn off the lights and strengthening the feedback. We reasoned that, if goal-achievement were relevant, then the uncertainty in the outcome of the action would decrease both the reported senses of ownership and action agency, in conditions where the consequence of the action did not match the expected result.

We have previously shown that the visual appearance of the virtual limb and congruent active control contribute as evidence for the reported sense of ownership. However, its effect depended on the available sensory information. Thus, we wanted to assess the interplay of the congruent outcome simultaneously with body discontinuity or incongruent movement. In the present study, the participants underwent two consecutive blocks of conditions. In addition to manipulating the outcome of the task, in each of the blocks, we either simultaneously manipulated the visuomotor information of the action congruence (i.e., *incongruent movement* condition) or the hand's visual appearance (i.e., *detached hand* condition). These conditions were the same as the ones reported in **Chapter 4**.

5.2 Results Experiment 2

5.2.1 Outcome agency was resistant to body discontinuity and incongruent movement

For **Experiment 2** (presented in the previous chapter), the questionnaires contained statements that assessed the outcome agency, the feeling of being the cause of the changes in the environment. We compared the outcome agency scores in the *full arm - incongruent movement* and *detached hand - movement* to the outcome agency scores in the *full arm - movement* condition.

The participants felt in control over the changes in the environment (i.e., the lights turning off when the subject reached them) (median=6.00, IQR=1.19). Refer to **Table 4.2** for the median scores and IQR for outcome agency. The outcome agency scores did not yield a significant difference across the three *movement* conditions (Friedman test; χ^2=0.25 (df=2, n=37), p=0.88). We further compared the outcome agency scores in the *detached hand - movement* (median=6.00, IQR=1.28) and the *full arm - incongruent movement* (median=6.00, IQR=1.36) conditions to the *full arm - movement* condition. We found that neither body discontinuity nor incongruent movement affected the outcome agency scores when compared to the *full arm - movement* condition (Wilcoxon signed-rank test; Z=-0.44, p=0.65 and Z=0.35, p=0.72, respectively) [**Figure 5.1**].

These results suggest that the feeling of authorship over the consequences of the action in the environment is resistant to manipulations in the visual appearance of the limb or when noise is added to the trajectory of the movement.

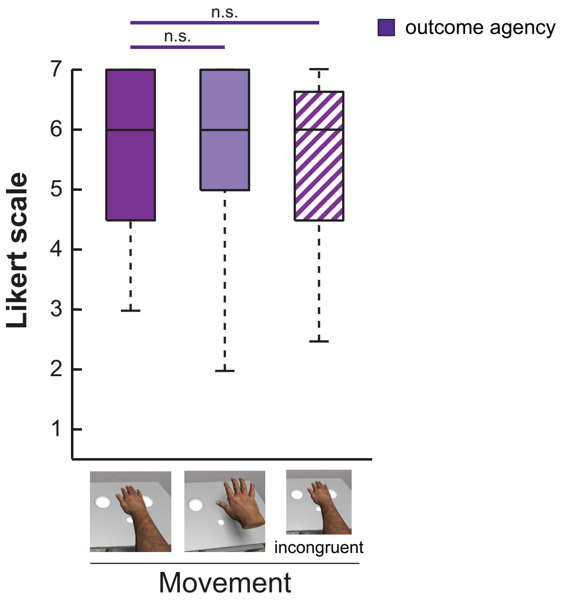


Figure 5.1: **The outcome agency is resistant to body discontinuity and incongruent movement**. The outcome agency scores (in purple) in the *full arm - movement* (full dark color), *detached hand - movement* (full light color), and *full arm - incongruent movement* (ascending thin lines). The participants felt being the cause of the lights turning off in the *full arm - movement*. The outcome agency scores did not decrease when seeing the hand detached from the body or the noise added to the movement of the virtual hand (p=0.65 and p=0.72, respectively). The middle quartiles indicate the median value and the whiskers indicate the most extreme values that are not considered an outlier. n.s. p>0.05.

5.3 Results Experiment 3

The overall aim of **Experiment 3** was to assess the effect of an unexpected outcome of the action in the reported senses of action agency and ownership. In the *incongruent outcome* condition, the consequence of that action of the virtual hand movement did not match the expected result of the action. To achieve this effect, we manipulated the virtual lights' response to the presence of the virtual hand. **Section 3.4.7** offers a detailed description of the manipulation of the outcome. Additionally, the results in our previous study suggest an interaction between all available sources of information to generate a sense of ownership. Thus, we also aimed to test for the interaction of the incongruent outcome with the *incongruent movement* and *detached hand* conditions.

The experiment was divided into two blocks of four conditions each, randomly labelled as **Block A** and **Block B**. Both **Block A** and **B** contained the *full arm - movement* and *full arm - incongruent outcome* conditions. In **Block A**, the trajectory of the virtual hand was manipulated, alone (i.e., *incongruent movement* condition) or simultaneously with the outcome (i.e., *full arm - incongruent*). In **Block B**, we also manipulated the body continuity alone (i.e., *detached hand* condition) or together with the outcome manipulation (i.e., *detached hand - incongruent outcome*). A detailed description of the methods for the results presented in this chapter can be found in **Section 3.2**.

Table 5.1 and **Table 5.2** show the median scores and IQR for **Block A** and **Block B**, respectively.

5.3.1 The reported senses of outcome agency, action agency, and ownership over the virtual hand for Block A and B

First, to test for task compliance and suggestibility, we compared the ownership, action agency, and outcome agency scores to their respective control scores for each experimental condition in **Block A** and **Block B**.

Block A

The participants reported a sense of ownership over the virtual arm in the *full arm - movement* condition (median=5.00, IQR=2.93). The ownership scores in the *full arm - movement* were higher than the respective control statements (Wilcoxon signed-rank; Z=5.55, p<0.001). The reported sense of ownership in *full arm - incongruent movement* (median=4.50, IQR=2.87), *full arm - incongruent outcome* (median=4.00, IQR=2.87), and *full arm - incongruent* (median=4.00, IQR=3.37) was also significantly higher than their respective control statements (Wilcoxon signed-rank, Z=4.84, p<0.001; Z=4.56, p<0.001; Z=4.74, p<0.001, respectively) [**Figure 5.2A**].

The participants reported feeling authorship over the movements of the virtual limb (i.e. action agency) in the *full arm - movement* condition (median=6.50, IQR=1.00).

	Full arm movement	**Full arm incongruent movement**	**Full arm incongruent outcome**	**Full arm incongruent**
Ownership	5.00 (2.93)	4.50 (2.87)	4.00 (2.87)	4.00 (3.37)
Ownership*	2.50 (3.00)	2.50 (3.00)	2.50 (2.50)	2.50 (2.87)
Action agency	6.50 (1.00)	6.50 (1.25)	5.75 (1.25)	5.50 (1.50)
Action agency*	3.00 (1.58)	2.66 (2.00)	3.00 (2.58)	2.67 (2.58)
Outcome agency	6.50 (1.00)	7.00 (1.00)	4.00 (2.50)	3.50 (2.37)
Outcome agency*	1.50 (1.00)	1.00 (1.00)	5.00 (2.00)	4.00 (2.00)
Similarity	6.00 (1.00)	5.00 (2.75)	5.00 (2.00)	6.00 (2.00)
Location	6.50 (1.37)	6.00 (1.50)	6.00 (2.00)	5.50 (1.50)

Table 5.1: **Median reported scores and interquartile ranges for sense of ownership, action agency, outcome agency, and location in Block A**, and their respective control statements (marked with a *) for *full arm - movement*, *full arm - incongruent movement*, *full arm - incongruent outcome*, *full arm - incongruent*.

The action agency scores were significantly higher than the respective control statements (Wilcoxon signed-rank; Z=5.64, p<0.001). The reported action agency scores in the *full arm - incongruent movement* (median=6.50, IQR=1.25), the *full arm - incongruent outcome* (median=5.75, IQR=1.25), and the *full arm - incongruent* (median=5.50, IQR=1.50) conditions were also higher than the respective control statements (Wilcoxon signed-rank; Z=5.59, p<0.0001; Z=5.39, p<0.001; Z=5.44, p<0.001, respectively) [**Figure 5.2B**].

In **Block A**, the participants reported feeling being the authors of the consequence of the task (i.e. outcome agency) in the *full arm - movement* condition (median=6.50, IQR=1.00). The reported outcome agency scores were higher than the respective control statements (Wilcoxon signed-rank; Z=5.57, p<0.001). The reported outcome agency scores in the *full arm - incongruent movement* condition (median=7.00, IQR=1.00) were also higher than their respective control statements (Wilcoxon signed-rank; Z=5.66, p<0.001). In the *full arm - incongruent outcome* (median=4.00, IQR=2.50) and the *full arm - incongruent* (median=3.50, IQR=2.37), the outcome agency scores were significantly lower than the respective control statements (Wilcoxon signed-rank; Z=-2.27, p=0.02; Z=-1.88, p=0.05, respectively) [**Figure 5.2C**].

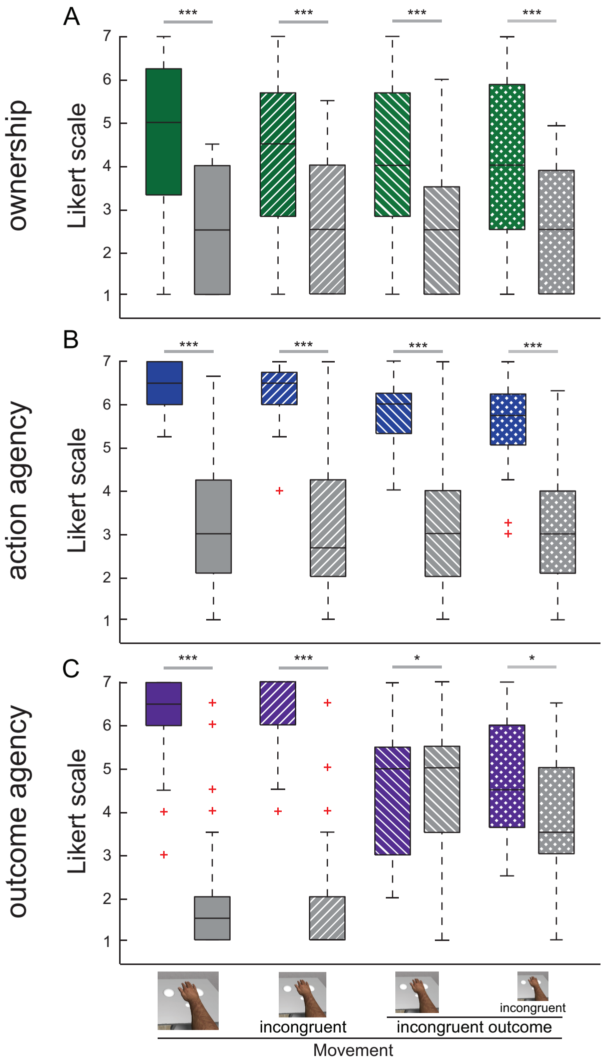


Figure 5.2: **Reported sense of ownership, action agency, and outcome agency over the virtual hand and the respective control statements in Block A**. The ownership (in green), action agency (in blue), and outcome agency (purple) scores for *full arm - movement* (full colors), *full arm - incongruent movement* (ascending thin lines), *full arm - incongruent outcome* (descending thin lines), and *incongruent* (crossed lines) conditions and the respective control statements (gray) (A) The ownership scores scores were significantly higher all conditions (p<0.001). (B) The action agency scores were significantly higher in all conditions (p<0.001). (C) The outcome agency scores were significantly higher in the *full arm - movement* and *full arm - incongruent movement* conditions (p<0.001) and in the *full arm - incongruent outcome* and in the *full arm - incongruent* (p<0.05). The middle quartiles indicate the median value and the whiskers indicate the most extreme values that are not considered an outlier. * p<0.05, *** p<0.001

Block B

	Full arm movement	**Detached hand movement**	**Full arm incongruent outcome**	**Detached hand incongruent outcome**
Ownership	5.25 (2.87)	4.75 (2.50)	4.50 (2.62)	4.00 (2.43)
Ownership*	2.50 (2.00)	2.50 (2.37)	2.50 (2.50)	2.50 (2.37)
Action agency	6.50 (1.00)	6.50 (1.25)	5.75 (1.25)	5.50 (1.50)
Action agency*	3.00 (2.16)	2.67 (2.25)	3.00 (2.00)	3.00 (1.91)
Outcome agency	7.00 (1.50)	7.00 (0.50)	3.50 (3.00)	3.00 (2.50)
Outcome agency*	2.00 (2.50)	1.00 (1.00)	5.00 (2.00)	4.50 (2.37)
Similarity	6.00 (2.00)	6.00 (2.75)	5.00 (2.75)	5.00 (3.00)
Location	6.50 (1.50)	6.50 (1.50)	6.00 (2.00)	6.00 (1.87)

Table 5.2: **Reported median scores and IQR for the sense of ownership, action agency, outcome agency in Block B (Experiment 3)**, and their respective control statements (marked with a *) for *full arm - movement*, *detached hand - movement*, *full arm - incongruent outcome*, and *detached hand - incongruent outcome*.

The participants reported a sense of ownership over the virtual arm in the *full arm - movement* condition (median=5.25, IQR=2.87). The ownership scores in the *full arm - movement* were higher than in the respective control statements (Wilcoxon signed-rank; Z=5.47, p<0.001). The reported sense of ownership in the *detached hand - movement* (median=4.75, IQR=2.50), the *full arm -incongruent outcome* (median=4.50, IQR=2.62), and the *detached hand - incongruent outcome* (median=4.00, IQR=2.43) were also higher than the respective control statements (Wilcoxon signed-rank; Z=5.44, p<0.001; Z=5.10, p<0.001; Z=4.92, p<0.001, respectively) [**Figure 5.3A**].

The participants reported feeling as being the authors over the movements of the virtual arm (i.e. action agency) in the *full arm - movement* condition (median=6.50, IQR=1.00). The reported action agency scores in this condition were higher than the respective control statements (Wilcoxon signed-rank; Z=5.71, p<0.001). The action agency scores in the *detached hand - movement* (median=6.50, IQR=1.25), the *full arm - incongruent outcome* (median=5.75, IQR=1.25), and the *detached hand - incongruent outcome* (median=5.50, IQR=1.50) were also higher than the respective control statements (Wilcoxon signed-rank; Z=5.62, p<0.001; Z=5.46, p<0.001, and Z=5.36, p<0.001, respectively) [**Figure 5.3B**].

In **Block B**, the participants reported outcome agency in the *full arm - movement* condition*full arm - movement* condition (median=7.00, IQR=1.50). The reported outcome agency scores were significantly higher than the respective control statements (Wilcoxon signed-rank; Z=5.18, p<0.001). Reported outcome agency scores in the *detached hand - movement* condition (median=7.00, IQR=0.50) were also higher than the respective control statements (Wilcoxon signed-rank; Z=5.61, p<0.001). However, outcome agency scores in the *full arm - incongruent outcome* (median=3.50, IQR=3.00) and the *detached hand - incongruent outcome* (median=3.00, IQR=2.50) conditions did not yield a significant difference compared to the respective control statements (Wilcoxon signed-rank; Z=1.63, p=0.10; Z=1.39, p=0.16, respectively) [**Figure 5.3C**].

Friedman test

We assessed whether our manipulations affected the individual ownership, action agency, and outcome agency scores. For **Block A**, the outcome agency, action agency, and ownership scores were significantly different across all four conditions (Friedman test; χ^2=103.8 (df=3, n=43), p<0.001; χ^2=38.7 (df=3, n=43), p<0.001; and χ^2=24.1 (df=3, n=43), p<0.001, respectively).

For **Block B**, the outcome agency, action agency, and ownership scores were also significantly different across all four conditions (Friedman test; χ^2=90.0 (df=3, n=43), p<0.001; χ^2=14.73 (df=3, n=43), p=0.002; and χ^2=28.39 (df=3, n=43), p<0.001, respectively).

The subsequent analyses are aimed to assess whether these manipulations changed reported the senses of ownership, action agency, and outcome agency in pairs of conditions.

5.3.2 The outcome agency decreased with the incongruent outcome, but was resistant to incongruent movement and body discontinuity

To understand the effect of the expected outcome on the reported action agency and ownership, we manipulated the consequence of the action of the virtual hand. First, we assessed whether our manipulation affected the reported outcome agency while being resistant to other manipulations.

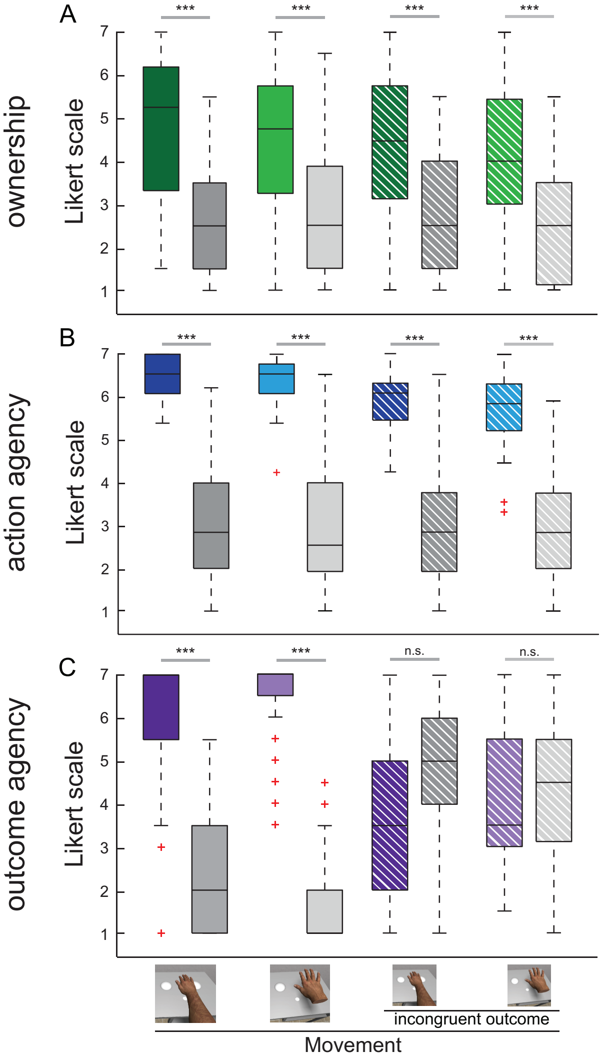


Figure 5.3: **Reported sense of ownership, action agency, and outcome agency in Block B**. The ownership (in green), action agency (in blue), and outcome agency (in purple) scores for the for *full arm - movement* (dark full colors), *detached hand - movement* (light full colors), *full arm - incongruent outcome* (dark descending thin lines), and *detached hand - incongruent outcome* (light descending thin lines) conditions and the respective control statements (gray). (A) The ownership scores scores were significantly higher all conditions (p<0.001). (B) The action agency scores were significantly higher in all conditions (p<0.001). (C) The outcome agency scores were significantly higher in the *full arm - movement* and *detached hand - movement* conditions (p<0.001) and but did not show to be significantly different in the *full arm - incongruent outcome* and in the *detached hand - incongruent outcome* (p=0.10 and p=0.16). n.s. p>0.05, *** p<0.001

For **Block A**, we compared the outcome agency scores in the *full arm - movement* condition to the other conditions. We found that outcome agency scores significantly decreased in the *full arm - incongruent outcome* condition compared to the *full arm - movement* condition (Wilcoxon signed-rank; Z=5.47, p<0.001), but not in the *full arm - incongruent movement* condition compared to the *full arm - movement* condition (Wilcoxon signed-rank; Z=-0.26, p=0.79). The outcome agency scores decreased in the *full arm - incongruent* compared to the *full arm - movement* condition (Wilcoxon signed-rank; Z=5.46, p<0.001) [**Figure 5.4A**].

Additionally, we compared the individual outcome agency scores to the ratio of incorrect to total waves in the *full arm - incongruent outcome* conditions. We found a negative correlation between these two variables (Spearman ρ=-0.46, p=0.001) [**Figure 5.4B**]. Thus, suggesting that the feeling of being the cause of the change in the environment depends on the proportion between incorrect/correct attempts.

For **Block B**, we compared the outcome agency in the *full arm - movement* condition with the other three conditions. Comparison with the *detached hand - movement* condition did not yield a significant difference (Wilcoxon signed-rank; Z=-1.94, p=0.06). However, outcome agency significantly decrease both with incongruent outcome of the task (i.e., *full arm - incongruent outcome* condition) (Wilcoxon signed-rank; Z=4.93, p<0.001) and when they controlled a discontinuous limb with manipulated outcome (i.e., *detached hand - incongruent outcome* condition) (Wilcoxon signed-rank; Z=5.00, p<0.001) [**Figure 5.5A**].

Similarly to the results found **Block A**, we found that the individual outcome agency scores were correlated with the number of incorrect waves in the *incongruent outcome* condition (Spearman ρ=-0.47, p=0.001) [**Figure 5.5B**]. Thus, suggesting that the feeling of being the cause of the change in the environment depends on the proportion between incorrect/correct attempts to turn off the light.

In this section, we report that outcome agency scores are affected by the *incongruent outcome* manipulation, but are resistant to the *incongruent movement* and *detached hand* manipulations. Thus, suggesting that our manipulation worked as intended, independently on the other manipulations performed in the same block.

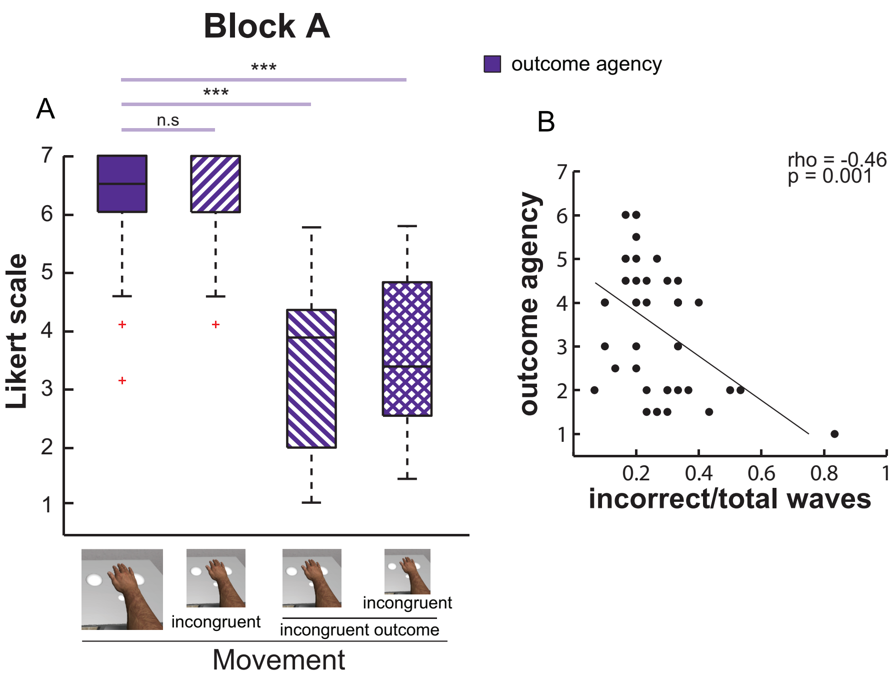


Figure 5.4: **The outcome agency decreased with incongruent outcome, but was maintained incongruent movement**. (A) The outcome agency scores in the *full arm - movement* (full color), *full arm - incongruent movement* (ascending thin lines), *full arm - incongruent outcome* (descending thin lines), and *full arm - incongruent* (crossed lines). The reported outcome agency scores significantly decreased in the *full arm - incongruent outcome* and *full arm - incongruent* conditions compared to the *full arm - movement* condition ($p<0.001$ and $p<0.001$, respectively). Adding noise to the trajectory of the virtual hand (i.e *full arm - incongruent movement* condition) did not decrease the outcome agency scores ($p=0.79$). The middle quartiles indicate the median value and the whiskers indicate the most extreme values that are not considered an outlier. *** $p<0.001$. (B) The individual outcome agency scores and the proportion of incorrect waves to total waves in the *full arm - incongruent outcome* condition were negatively correlated (Spearman ρ=-0.46, $p<0.001$).

In the next sections, we aim to understand the effect of incongruent outcome in the reported action agency and ownership scores.

5.3.3 The reported action agency scores were negatively affected by incongruent outcome

In **Block A**, manipulating the consequence of the action (i.e., *full arm - incongruent outcome* condition) significantly decreased the reported action agency compared to the *full arm - movement* condition (Wilcoxon signed-rank; Z=4.52, $p<0.001$). The combination of both types of manipulation in the *full arm - incongruent* also resulted in a

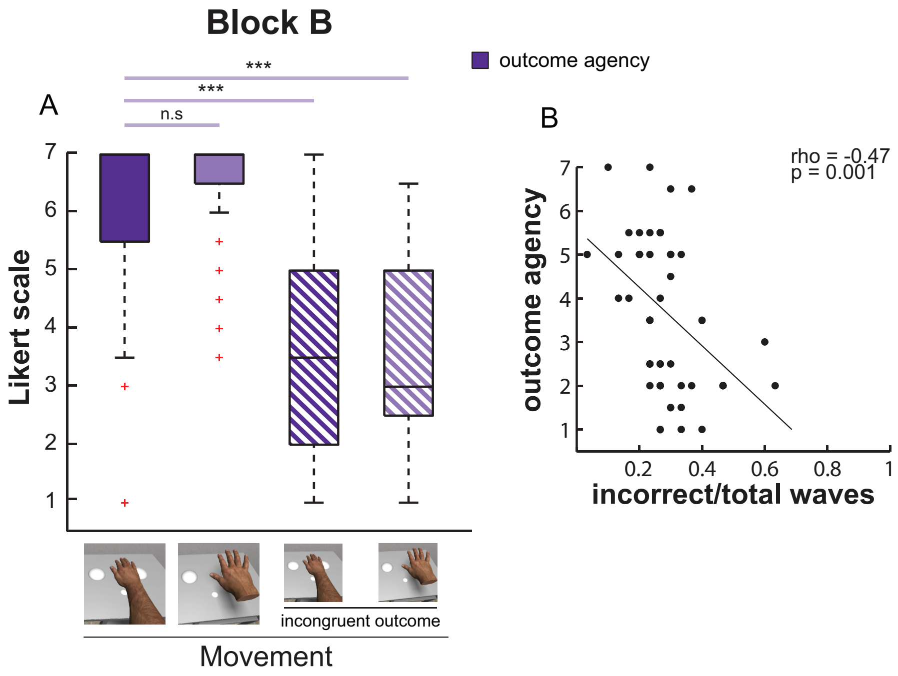


Figure 5.5: **The outcome agency decreases with incongruent outcome, but not with body discontinuity**. (A) The outcome agency scores in the *full arm - movement* (full dark color), *detached hand - movement* (full light color), *full arm - incongruent outcome*(dark descending lines), and *detached hand - incongruent outcome* (light descending lines). The reported outcome agency scores significant decrease in the *full arm - incongruent outcome* and the *detached hand - incongruent outcome* conditions when compared to the *full arm - movement* condition (p<0.001 and p<0.001, respectively). Seeing the hand detached from the body (i.e. *detached hand - movement* condition) did not yield a significant difference in the outcome agency scores (p=0.06). The middle quartiles indicate the median value and the whiskers indicate the most extreme values that are not considered an outlier. *** p<0.001. (B) The individual outcome agency scores (y-axis) and the proportion of incorrect waves to total waves in the *full arm - incongruent outcome* condition were negatively correlated (Wilcoxon signed-rank; Z=-0.47, p<0.001).

significant decrease compared to the *full arm - movement* condition (Wilcoxon signed-rank; Z=4.74, p<0.001). However, the comparison between the *full arm - incongruent outcome* and *full arm - incongruent* did not yield a significant difference (Wilcoxon signed-rank; Z=1.34, p=0.17) [**Figure 5.6A**].

In **Block B**, the action agency scores in conditions with incongruent outcome of the task (i.e., *full arm - incongruent outcome*) were significantly lower than the *full arm - movement* (Wilcoxon signed-rank; Z=3.85, p<0.001). This was also the case for the combination of both manipulations (i.e., *detached hand - incongruent outcome*)

(Wilcoxon signed-rank; Z=4.19, p<0.001). The comparison between the *full arm* - *incongruent outcome* and the *detached hand* - *incongruent outcome* conditions did not yield a significant difference (Wilcoxon signed-rank; Z=1.18, p=0.23) [**Figure 5.6B**].

These results suggest that the reported action agency was negatively affected when the action (i.e., the light turning off) did not match the expected result, even when the appearance of the hand and the trajectory of the movement remain unchanged. Additionally, in these conditions, the action agency seems to be solely affected by the *incongruent outcome* as there was no further decrease in the presence of the other manipulations.

The reported action agency was negatively affected when the outcome of the task did not match the expected result. These results suggest an interaction between action and outcome agency.

5.3.4 The reported ownership scores were negatively affected by the incongruent outcome

We also assessed the effect of *incongruent outcome* in the reported sense of ownership. In **Block A**, incongruent outcome significantly decreased the sense of ownership compared to the *full arm* - *movement* condition (Wilcoxon signed-rank; Z=4.04, p<0.001). The combination of both manipulations in the *full arm* - *incongruent* resulted in a significant decrease when compared to the *full arm* - *movement* (Wilcoxon signed-rank; Z=3.12, p=0.0018). The comparison between the *full arm* - *incongruent outcome* and *full arm* - *incongruent* did not yield a significant difference (Wilcoxon signed-rank; Z=-0.28, p=0.78) [**Figure 5.7A**].

In **Block B**, when comparing the ownership scores in the *full arm* - *incongruent outcome* and the *full arm* - *movement* conditions, we observe a reduction in the reported ownership. However, even though it displayed a trend, it did not reach statistical significance (Wilcoxon signed-rank: Z=2.44, p=0.014, not significant under Bonferroni correction). The combination of both manipulations (i.e. *detached hand* - *incongruent outcome* condition) significantly decreased the sense of ownership (Wilcoxon signed-rank; Z=3.29, p<0.001) compared to the *full arm* - *movement*condition. The comparison

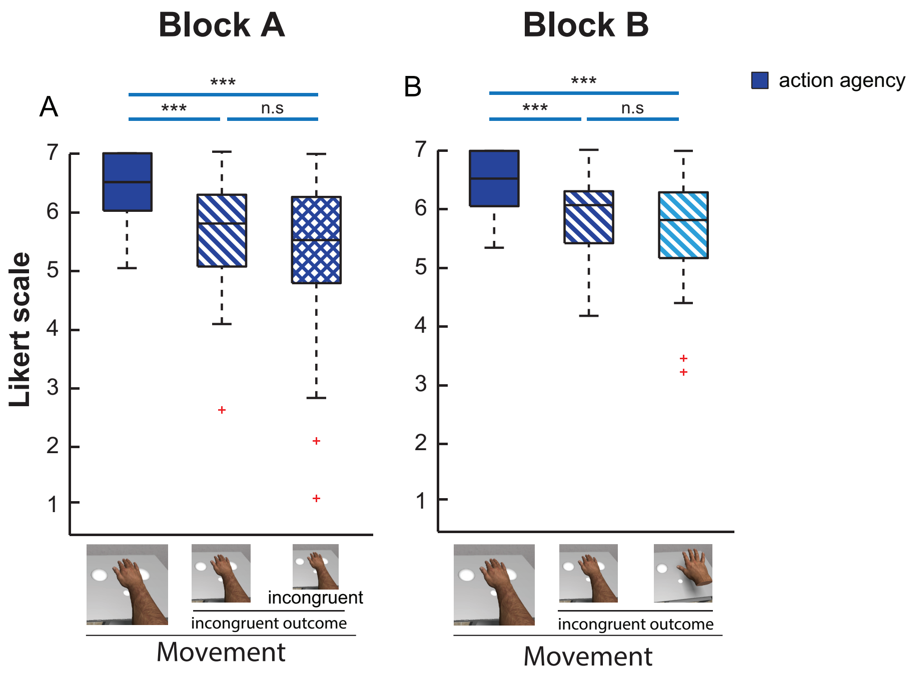


Figure 5.6: **The incongruent outcome decreases the reported action agency**. The action agency (in blue) scores for (A) the *full arm - movement* (full color), *full arm - incongruent outcome* (descending lines), *full arm - incogruent* (crossed lines) in **Block A**. The reported action agency was significantly decreased in the *full arm - incongruent outcome* (p<0.001) and in the *full arm - incongruent* (p<0.001) compared to the *full arm - movement*. The comparison between *full arm - incongruent outcome* and *full arm* - and *incongruent* did not yield a significant difference (p=0.17), (B) and the *full arm - movement* (full dark color), the *full arm - incongruent outcome* (descending dark lines), and the *detached hand - incongruent outcome* (descending light lines) in **Block B**. The reported action agency significantly decreased in the *full arm - incongruent outcome* and the *detached hand - incongruent outcome* conditions compared to the *full arm - movement* condition (p<0.001). The comparison between the *full arm - movement* and the *detached hand - incongruent outcome* conditions did not yield a significant difference (p=0.23). The middle quartile indicates the median value and the whiskers indicate the most extreme values that are not considered outliers. ** p<0.0041 (Bonferroni corrected p-value), *** p<0.001

between the *full arm - incongruent outcome* and the *detached hand - incongruent outcome* conditions did not yield a significant difference (Wilcoxon signed-rank; Z=1.42, p=0.15) [**Figure 5.7B**].

These results suggest that the reported ownership scores were differently affected by the *incongruent outcome* of the action (i.e., the light turning off). However, when both manipulations were present, it negatively affected the reported ownership scores. Thus, suggesting that reported sense of ownership responded differently depending on the available information accompanying the outcome manipulation.

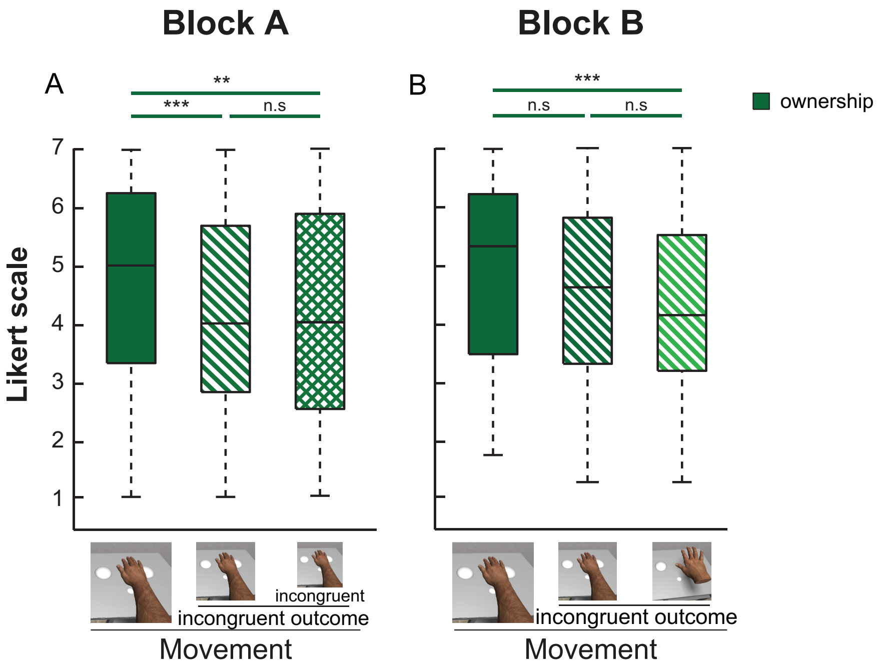


Figure 5.7: **The reported ownership scores were negatively affected by the incongruent outcome in each block**. The ownership (in green) scores for (A) the *full arm* - *movement* (full color), *full arm* - *incongruent outcome* (descending lines), *full arm* - *incogruent* (crossed lines) in **Block A**. The reported sense of ownership was significantly decreased in the *full arm* - *incongruent outcome* (p<0.001) and in the *full arm* - *incongruent* (p=0.0018) compared to the *full arm* - *movement* condition. The comparison between *full arm* - *incongruent outcome* and *full arm* - and *incongruent* did not yield a significant difference (p=0.78), (B) and the *full arm* - *movement* (full dark color), the *full arm* - *incongruent outcome* (descending dark lines), and the *detached hand* - *incongruent outcome* (descending light lines) in **Block B**. The reported sense of ownership did not yield a significantly difference when comparing the *full arm* - *incongruent outcome* and *full arm* - *movement* conditions (p=0.014, not significant under Bonferroni correction). However, when comparing the double manipulation, *detached hand* - *incongruent outcome* there was a significant difference compared to the *full arm* - *movement* condition (p<0.001). The comparison between *full arm* - *incongruent outcome* and *detached hand* - *incongruent outcome* did not yield a significant difference (p=0.15). The middle quartile indicates the median value and the whiskers indicate the most extreme values that are not considered outliers. ** p<0.0041 (Bonferroni corrected p-value), *** p<0.001.

5.3.5 Body discontinuity did not affect the reported sense of ownership and action agency, but the ownership scores were negatively affected by incongruent movement

We assessed the effect of incongruent movement (*full arm* - *incongruent movement* in **Block A**), and body discontinuity, (*detached hand* - *movement* in **Block B**) on the reported sense of ownership and action agency. Additionally, we can compare the results in this chapter to those reported in analogous conditions in **Chapter 4**.

In **Block A**, we found no significant difference when comparing the *full arm* - *incongruent movement* and *full arm* - *movement* conditions for the reported action agency scores (Wilcoxon signed-rank; Z=1.86, p=0.06). In contrast, the ownership scores were negatively affected (although very close to the level of significance) by the noise in the trajectory of the movement (Wilcoxon signed-rank; Z=2.97, p=0.003) [**Figure 5.8A**]. The results from the action agency scores are in contrast with our previous study, in which the participants reported significantly lower action agency values in the *incongruent movement* condition.

In **Block B**, we do not report a significant difference when comparing the *detached hand* - *movement* and the *full arm* - *movement* conditions in the reported action agency scores (Wilcoxon signed-rank; Z=0.65, p=0.51) or in the reported ownership scores (Wilcoxon signed-rank; Z=0.96, p=0.33) [**Figure 5.8B**]. These results are in agreement with those reported in **Chapter 4**.

5.3.6 *Full arm* - *movement* and *full arm* - *incongruent outcome* conditions remained unchanged between blocks

We tested whether there was a difference between the common conditions in both blocks (i.e., *full arm* - *movement* and *full arm* - *incongruent outcome* conditions). The outcome agency scores did not significantly differ in the *full arm* - *movement* (Wilcoxon signed-rank; Z=1.13, p=0.25) nor the *full arm* - *incongruent outcome* conditions (Wilcoxon signed-rank; Z=-0.66, p=0.50) between blocks. The action agency scores did no differ between both blocks for the *full arm* - *movement* (Wilcoxon signed-rank; Z=-0.22,

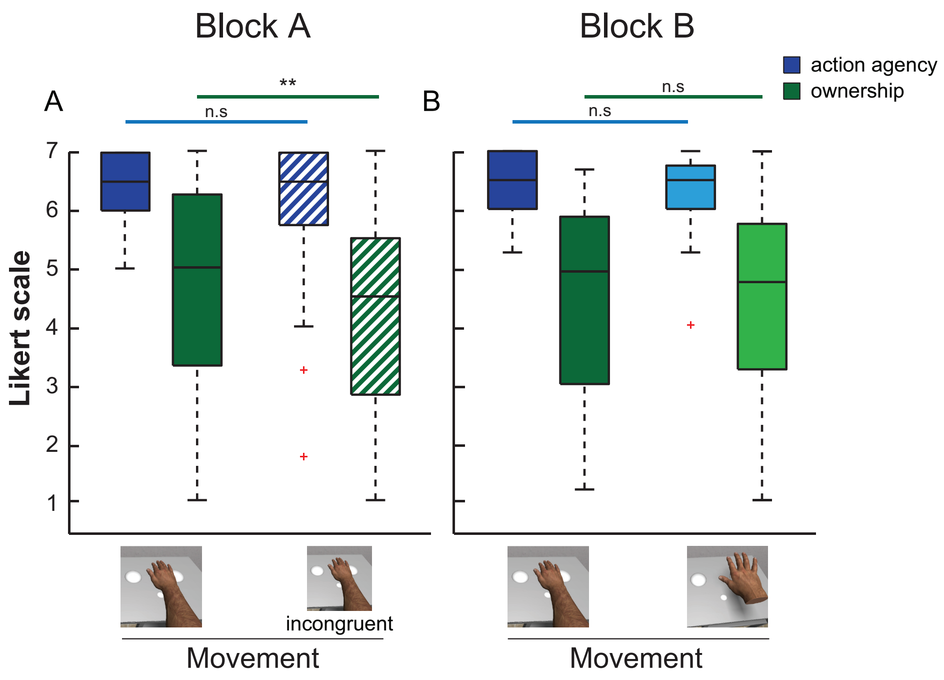


Figure 5.8: **Body discontinuity does not affect the reported sense of ownership and action agency, but the ownership scores are negatively affected by incongruent movement**. (A) The reported action agency (in blue) and ownership (in green) scores in **Block A** for *full arm - movement* (full dark colors) and *full arm - incongruent movement* (ascending thin lines) conditions. The reported action agency did not yield a significant difference in the *full arm - incongruent movement* compared to the *full arm - movement* condition (p>0.06). The reported sense of ownership significantly decreased in the *full arm - incongruent movement* compared to the *full arm - movement* condition (p=0.003). (B) The reported action agency (in blue) and ownership (in green) scores in **Block B** for the *full arm - movement* (full dark colors) and *detached hand - movement* (full light colors) conditions. Neither the reported action agency or sense of ownership yielded a significant difference in the *full arm - incongruent movement* compared to the *detached hand - movement* condition (p>0.33). The middle quartile indicates the median value and the whiskers indicate the most extreme values that are not considered outliers. n.s. p>0.05 ** p<0.0041 (Bonferroni corrected p-value).

p=0.25) nor in the *full arm - incongruent outcome* condition (Wilcoxon signed-rank; Z=-1.50, p=0.13). For the sense of ownership, no significant differences were found for both conditions between the blocks (Wilcoxon signed-rank; Z=0.73, p=0.74; and Z=-1.96, p=0.05, not significant under Bonferroni correction, respectively).

To ensure that these similarities were a result of the that the participants were responding in the same way to both conditions, we measure the correlation between the responses given in the *full arm - movement* condition and the *full arm - incongruent* *outcome* condition between **Block A** and **Block B** [**Figure 5.9**].

For the individual outcome agency scores, we found no correlation between **Block A** and **Block B** in the *full arm* - *movement* (Spearman ρ=0.04, p=0.78) nor the *full arm* - *incongruent outcome* conditions (Spearman ρ=0.23, p=0.13) [**Figure 5.9A**]. The action agency scores in the *full arm* - *movement* condition in each of the blocks were correlated (Spearman ρ=0.52, p<0.001), but not for the *full arm* - *incongruent outcome* condition (Spearman ρ=0.33, p=0.03, not significant Bonferroni correction) [**Figure 5.9B**]. Interestingly, the ownership scores were highly correlated between **Block A** and **Block B** for both *full arm* - *movement* and *full arm* - *incongruent outcome* conditions (Spearman ρ=0.86, p<0.001; and ρ=0.79, p<0.001, respectively) [**Figure 5.9C**].

5.3.7 Manipulations in outcome, movement, and visual appearance affected differently changes in the outcome agency, action agency and ownership

We assessed whether the incongruent outcome caused a similar change in the outcome agency, action agency, and sense of ownership. This analysis provides insight into the relationship between the outcome agency and the ownership and action agency scores, indicating how each component reacts to the incongruent outcome. We measured the correlation of the change between the individual outcome agency scores, the change in the individual agency scores, and the individual ownership scores between the *full arm* - *movement* and the *full arm* - *incongruent outcome* conditions for **Block A** and **Block B**. **Section 5.7** details the handling of the data.

We did not find a significant correlation in the changes in the reported outcome agency scores and the changes in reported ownership scores in **Block A** (Spearman ρ=0.06, p=0.68) [**Figure 5.10A**] or in **Block B** (Spearman ρ=0.14, p=0.37) [**Figure 5.10B**]. Additionally, we did not find a significant correlation between the changes in the reported outcome agency and the changes in the reported outcome action scores in **Block A** (Spearman ρ=-0.18, p=0.25) [**Figure 5.10C**] or in **Block B** (Spearman ρ=0.02, p=0.89) [**Figure 5.10D**].

We also compared the change in action agency scores to the change in the ownership scores between the *full arm* - *movement* and the *full arm* - *incongruent outcome*

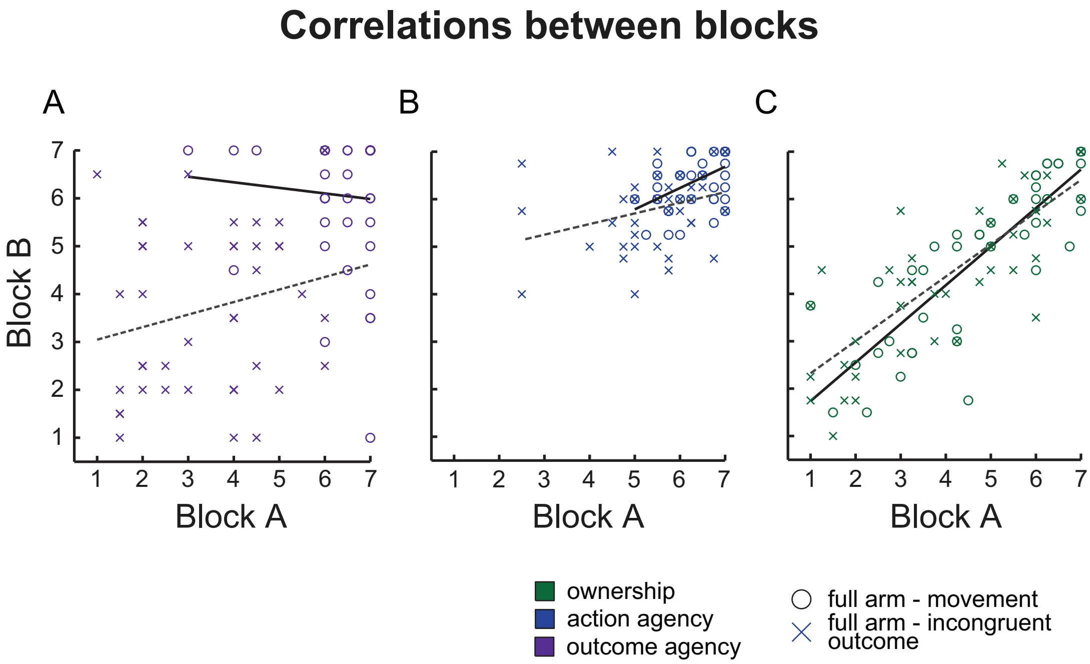


Figure 5.9: **Correlations of *full arm* - *movement* and *full arm* - *incongruent outcome* between Block A and Block B**. The individual outcome agency (purple), action agency (blue), and ownership (green) scores for *full arm* - *movement* (circle markers) and *full arm* - *incongruent outcome* (cross markers). Each axis represents one of the blocks, **Block A** (x-axis) and **Block B** (y-axis). (A) Outcome agency scores were not correlated in the *full arm* - *movement* , nor in the *full arm* - *incongruent outcome* conditions (Spearman ρ=0.04, p=0.78; and Spearman ρ=0.04, p=0.13, respectively) (B) Action agency scores were found to be correlated in the *full arm* - *movement* condition (Spearman ρ=0.52, p<0.001), but not in the *full arm* - *incongruent outcome* condition (Spearman ρ=0.33, p=0.03, not significant Bonferroni correction) (C) Ownership scores were strongly correlated in both conditions (Spearman ρ=0.86, p<0.001 and Spearman ρ=0.79, p<0.001, respectively).

condition. In **Block A**, the changes in the reported ownership and the changes in reported action agency did not show a significant correlation (Spearman ρ=0.30, p=0.05) [**Figure 5.11A**], while they did in **Block B** (Spearman ρ=0.54, p<0.001) [**Figure 5.11B**].

Additionally, we assessed the effect of the *incongruent movement* and *detached hand*. In **Block A**, we report a correlation between the changes in the ownership scores and the changes in action agency between the *full arm* - *movement* and *full arm* - *incongruent movement* (Spearman ρ=0.42, p=0.002) [**Figure 5.11C**]. In **Block**

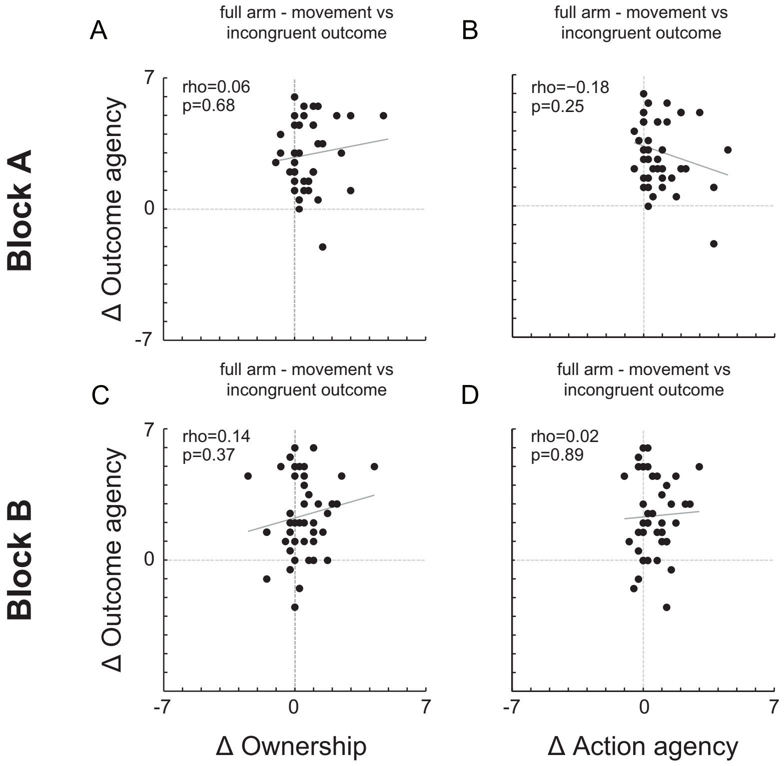


Figure 5.10: **The changes in outcome agency and action agency and ownership were not correlated in neither Block A or Block B in the *full arm - movement* and *full arm - incongruent outcome* conditions**. Difference in the individual scores in the *full arm - movement* and *full arm - incongruent outcome* outcome agency (x-axis), ownership (y-axis, A-B), and action agency (y-axis, C-D). Differences in outcome agency and ownership in Block A did not yield a significant correlation (A) in Block A (Spearman ρ=0.06, p=0.68) or (B) in Block B (Spearman ρ=0.14, p=0.37) or for (C) the difference in reported outcome agency scores and reported action agency scores in Block A (Spearman ρ=-0.18, p=0.25) or (D) for Block B (Spearman ρ=0.02, p=0.89).

B, the changes in the ownership scores and the changes in action agency in the *full arm - movement* and *detached hand - movement* also showed a positive correlation (Spearman ρ=0.53, p<0.001) [**Figure 5.11D**].

In previous sections, the participants reported a decrease in the outcome agency, action agency, and ownership scores in the *full arm - incongruent outcome* condition compared to the *full arm - movement* condition. In this section, we analyze in more detail the relationship between the changes in the outcome agency with the other two. Interestingly, we failed to see a correlation between the changes in the outcome agency

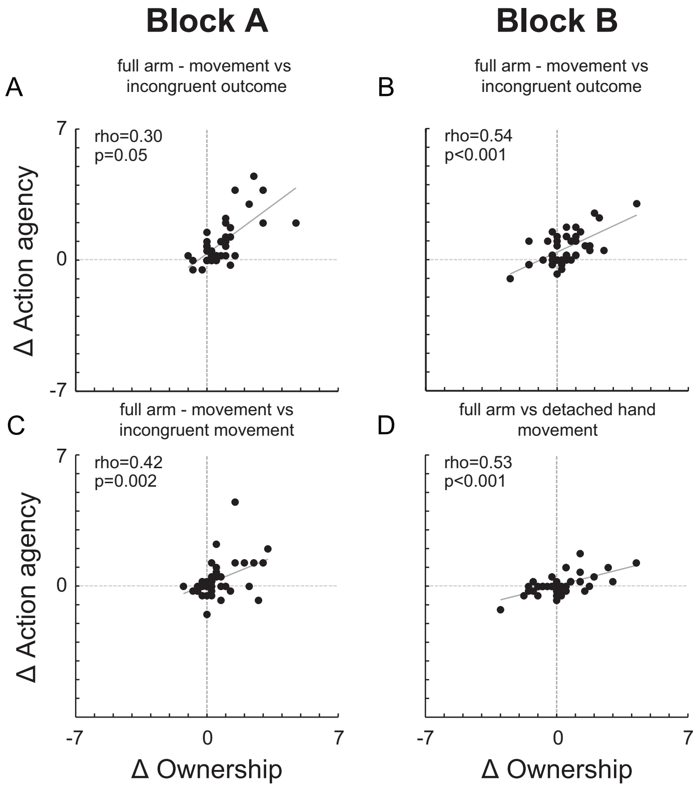


Figure 5.11: **Effects on incongruent outcome, incongruent movement, and detached hand in ownership and action agency scores**. For every pairwise comparison, we compared the changes in the ownership scores and the changes in the action agency scores (A) The changes in ownership and the changes in agency scores did no yield a significant correlation when comparing the *full arm* - *movement* and *full arm* - *incongruent outcome* conditions in **Block A** (Spearman ρ=0.30, p=0.05), (B) but they were in **Block B** (Spearman ρ=0.54, p<0.001). (C) The changes in ownership and the changes in agency scores yielded a significant correlation when comparing the *full arm* - *movement* and the *full arm* - *incongruent movement* in **Block A** (Spearman ρ=0.42, p=0.002). (D) The changes in ownership and the changes in agency scores yielded a significant correlation when comparing the *full arm* - *movement* and the *detached hand* - *movement* in **Block B** (Spearman ρ=0.53, p<0.001)

scores and the changes in the action agency or ownership scores. These results suggest that, even though the three components are affected by the incongruent outcome, they seem to be separately influenced by the perturbation in the expected outcome.

5.3.8 Free form report

At the end of each block, the participants were invited to write down their subjective experience of the task, without any instruction except "Is there anything you want to comment on the experience? Please write it down in the designated area".

In general, the participants noticed the perturbation in the response of the lights, which usually was accompanied of feelings of frustration. Some participants reported feelings of nervousness, anxiety, or aversion towards the virtual hand when the lights did not respond. The participants also reported feeling more in control over the hand when they had control over the lights, suggesting that participants would be more focused on the outcome of the action rather than the movement of the virtual hand itself.

The participants reported noticing changes in the movement in the virtual hand and some referred to feeling a lack of control over the hand when the noise was added. However, this is in contrast with the results in the action agency questionnaires, which show no difference between the *full arm - movement* and the *full arm - incongruent movement* condition. Interestingly, two participants felt as if the movement could be caused by them, doubting whether if it was a problem from their own movement and not restricted to the virtual hand.

Interestingly, one of the participants did not miss the tattoos in their upper limbs, only to realize it later during the day, when no longer in the experimental setting.

5.4 Discussion

The sense of agency has been reported to depend on three aspects: the intention to act, the sensory feedback of body movement, and the external outcome of the action (Khalighinejad and Haggard, 2016; Haggard, 2017). Two components can be differentiated from the sense of agency: body (or proximal) agency and external (or distal) agency (Kalckert and Ehrsson, 2012; Metcalfe, Eich, and Miele, 2013). The former refers to the feeling of being the cause of a body movement, while the latter relies on the mapping between an action and the effect in the environment. In the context of our experimental design, we can dissociate these components. The action consisted of reaching towards a target light that would turn on in the virtual environment, which would turn off the light. We are able to dissociate between the effects of modulating the visuomotor information of the action or the contextual cues of the effect of that action in the environment (i.e., the light turning off). We manipulated each of them independently and assessed the feeling of controlling the action of the virtual arm (hereafter, action agency), the authorship over the changes in the environment as a result of that action (hereafter, outcome agency), and the sense of ownership.

In this chapter, we report two main findings regarding the effect of the sensory consequence of an action on the reported senses of ownership and agency over a virtual limb. First, we found that manipulating the correlation between the action and the expected outcome decreased the reported outcome agency. Furthermore, we replicate our results from the previous experiment: the outcome agency is resistant to the perturbations on the appearance and trajectory of the virtual hand movements. Secondly, we found that manipulating the sensory consequences decreased the feelings of authorship over the virtual hand movements. Interestingly, the perturbation presented two different effects in the reported sense of ownership, depending on whether the experimental block contained an additional perturbation on the action or the hand's appearance.

The manipulation of either the sensory feedback from the movement or the action's sensory consequence has shown to decrease the sense of agency (Villa et al., 2018; Metcalfe, Eich, and Miele, 2013; Metcalfe and Greene, 2007). Introducing temporal delays in the expected external cues (i.e., the outcome) significantly reduces the reported sense of agency (Wen, Yamashita, and Asama, 2015b; Wen, Yamashita, and Asama, 2015a; Wen, Yamashita, and Asama, 2015c) as it depends on the temporal grouping between the action and its effect (Kawabe, Roseboom, and Nishida, 2013). In the studies mentioned above, the participants controlled a square on a screen towards goal elements using key presses. Thus, the experiments did not directly relate to bodily actions. Our results corroborate these findings in the sense of agency over the movements of a body part. In both **Block A** and **Block B**, the reported action agency and outcome agency scores decrease when comparing the *full arm* - *incongruent outcome* and the *full arm* - *movement* conditions. Interestingly, the double perturbation did no further decrease when comparing *full arm* - *incongruent* in **Block A** and *detached hand* - *incongruent outcome* in **Block B** compared to *full arm* - *incongruent outcome*. These results suggest that the correct outcome is crucial for a reported sense of agency over a body part.

Performing a goal-directed action has been shown to enhance the ownership over a virtual limb compared to not having a goal (Wen et al., 2016). Therefore, we expected a decrease in the reported sense of ownership in the *full arm* - *incongruent outcome* conditions. To our surprise, we found that the sense of ownership was differently affected in each block. The ownership scores significantly decreased in the *full arm* - *incongruent outcome* when compared to the *full arm* - *movement* in **Block A**, but that was not the case for **Block B**, even though it was close to significance. At risk of over-interpreting a statistically weak difference across conditions, we propose that in line with the message from the previous chapter, the effect of *incongruent outcome* might depend on the available information. In the conditions of **Block A**, the participants are more exposed to a decreased sense of ownership, since *incongruent movement* alone decreases the ownership scores. In contrast, in **Block B**, the manipulation of the incongruent visual appearance, *detached hand* , does not affect the reported sense of ownership. Even though the participants are told answer based in the immediately previous trial, a larger accumulation of evidence regarding the sense of ownership in **Block B** than in **Block A** might be in the origin of the observed differences. Further studies would require to understand better the transferability of evidence across trials and the effects of evidence accumulation in favor of the sense of ownership.

Nevertheless, we would like to point to the effect of *incongruent outcome* on the sense of ownership. In **Block B**, the presence of both manipulations in the *detached hand* - *incongruent outcome* condition resulted in a significant decrease compared to the *full arm* - *movement* condition. This results suggests that *incongruent outcome* still has a detrimental effect on the reported sense of ownership. Incongruent outcome decreased the reported ownership scores when comparing the *detached hand* - *movement* and *detached hand* - *incongruent outcome* conditions (Wilcoxon signed-rank; Z=3.03, p=0.0024).

The sense of ownership showed a significant decrease in *full arm* - *incongruent movement* compared to the *full arm* - *movement* condition in **Block A**. These results are consistent with our findings reported in the previous chapter. Contrary to our expectations and in contrast with our previous findings (Brugada-Ramentol, Clemens, and Polavieja, 2019), the *full arm* - *incongruent movement* did not yield a significant decrease in the reported action agency scores. Previous research suggests that information relative to movement kinematics may not be adequately monitored as long as the visual feedback is coherent with the goal of the action (outcome) (Fourneret and Jeannerod, 1998). Thus, suggesting the outcome of the action to be more critical than the movement and that participants are less aware of their motor performance once the outcome becomes more evident. This idea was previously demonstrated in studies where a perturbation is introduced while the participants perform a straight line. In these conditions, the participants perform corrective movements, even though they are not aware of the correction (Fourneret and Jeannerod, 1998; Nielsen, 1963). These differences will be further explored in **Chapter 6**.

Both movement- and goal-related errors decrease the sense of agency (Villa et al., 2018). Few studies compare the effect of manipulating the action and the consequence in the environment simultaneously. These studies present contradictory results on whether the contextual information of the action (outcome) the motor-related cues (action) are more important for the sense of agency (David et al., 2016; Caspar et al., 2016b; Villa et al., 2018; Villa et al., 2020). Similarly, we manipulate the action congruence and the goal simultaneously in **Block A**. The participants reported lower action agency scores in the *full arm - incongruent outcome*, but not in the *full arm - incongruent movement* condition. These results suggest stronger influence of outcome-related information than information derived from the virtual hand movements. Further evidence arises from the *full arm - incongruent* condition, which showed no significant difference compared to the *full arm - incongruent outcome*. While our findings are consistent with previous reports (David et al., 2016), our results might stem from the importance given to the outcome of the task (e.g., very explicit feedback and the counter indicating the number of correct and incorrect waves). To control for this, we could it would have interesting to have a condition in which the participants would perform hand movements without specific feedback, such as performing rotational movements (Sanchez-Vives et al., 2010).

Our experimental designs, however, are very different from the ones presented above. In their studies, the participant's movements were restricted to finger movements, while in our experimental design, the participants freely controlled the virtual hand. Additionally, our *incongruent movement* of a different nature. In previous studies, the movement was the opposite of the one performed to the participant's movement (Villa et al., 2018; Villa et al., 2020), our *incongruent movement* maintained the spatiotemporal component of the movement and added noise to the trajectory of the virtual hand. All together, these differences require a cautious comparison between our results and the previous literature.

The reported action agency and ownership did not yield significant differences when comparing *detached hand* - *movement* and *full arm* - *movement* conditions in **Block B**. The results are similar to our findings in **Experiments 1** and **2** and consistent with visuomotor information as adding evidence in favor of the senses of ownership and agency over an arm that appears as discontinuous from the body. In previous studies, body ownership decreased when passively observing a static virtual arm (Tieri et al., 2015a; Tieri et al., 2015b), while passively observing a moving arm (Tieri et al., 2015a), and while controlling the hand (Seinfeld and Müller, 2020). In the latter study, the authors reported a decrease in the sense of ownership in the disconnected, but not in the sense of agency. Similar to our previous findings, our results regarding the *detached hand* conditions contrast with the literature regarding body discontinuity.

The results presented in this chapter suggest a crucial role of the correlation of expected and observed outcome of a continuous-goal directed task in the senses of ownership and agency. In line with our observations of the previous chapter, our results are also consistent with the effect of the perturbation to be contingent on the available information.

5.5 Conclusions

- In this chapter, we report that the outcome agency, the feeling of being the cause of the changes in the environment, decreased when the outcome of the task became unpredictable. The decrease correlated with the number of outcome errors. Additionally, outcome agency was maintained when perturbations to the trajectory of the movement or changes in the morphology of the limb were presented.
- Perturbing the expected outcome of the task (i.e., lights not turning off when the hand reached the virtual light) decreased the reported action agency. While the reported sense of ownership was affected in one of the blocks, suggesting that there might be an effect of condition presentation order.
- The action agency and ownership were resistant to body discontinuity, replicating our previous results. Active control over the virtual hand maintains and adds evidence for the sense of ownership and agency.
- Adding noise to the virtual hand movement decreased the reported sense of ownership; however, it did not affect the reported action agency scores.

5.6 Conclusões

- Neste capítulo, reportamos que a agência sobre os resultados - a sensação de ser a causa das mudanças no ambiente - diminuiu quando o resultado da tarefa se torna imprevisível. Esta diminuição está correlacionada com o número de erros nos resultados da ação. Além disso, a agência sobre os resultados mantém-se quando perturbações na trajetória do movimento ou mudanças na morfologia do braço foram adicionadas.
- Perturbar o resultado esperado da tarefa (ou seja, as luzes não desligam quando a mão alcança a luz virtual) diminuiu a agência de ação reportada. Enquanto o sentido de propriedade foi afetado em apenas um dos blocos, sugerindo um possível efeito da ordem das condições.
- A agência sobre ação e o sentido de propriedade são resistentes à descontinuidade corporal, replicando os nossos resultados no capítulo anterior. O controlo ativo sobre os movimentos da mão virtual mantém e adiciona evidência favorável aos sentidos de propriedade e agência.
- Adicionar ruído ao movimento da mão virtual diminui o sentido de propriedade reportado; no entanto, não afetou a agência sobre ação reportada.

5.7 Data Handling

All data were analyzed using Matlab 2014b.

Data preprocessing

The questionnaires included more than one statement for the sense of ownership, action agency, outcome agency, and their respective control statements [see **Table 3.6**]. To avoid artifacts related to pseudoreplication, for each participant, we calculated the individual mean score for each category (e.g., sense of ownership) in each condition (e.g., *full arm - movement*). Thus, for each category and condition, we obtained a total of 43 individual scores.

Normality

Using the Shapiro-Wilk test, we found that the individual ownership, action agency, and outcome agency scores followed a normal distribution in the *full arm - movement*, *full arm - incongruent movement*, and *full arm - incongruent outcome* conditions in **Block A**. In **Block B**, the individual ownership, action agency, and outcome agency scores also followed a normal distribution in the *full arm - movement*, *detached hand - movement*, and *full arm - incongruent outcome*. The individual ownership, action agency, and outcome agency scores in the *full arm - incongruent* condition (**Block A**) and the *detached hand - incongruent outcome* condition (**Block B**) did not follow a normal distribution. Therefore, we decided to use non-parametric tests for the remaining analysis. We used the Friedman ANOVA to compare across all the conditions and the Wilcoxon signed-rank test for pairwise comparisons.

Pairwise comparisons

First, needed to assess whether the incongruent outcome manipulation was affecting the outcome agency statements and that these were exclusively affected by incongruent outcome. Therefore, we compared the outcome agency scores in the *full arm - movement* condition against the other three conditions. In **Block A**, we performed three comparisons: *full arm - movement* against *full arm - incongruent movement*, *full* *arm* - *movement* against *full arm* - *incongruent outcome*, and *full arm* against *incongruent*. Conversely, for **Block B**, we also compared to the following conditions: *full arm* - *movement* against *detached hand* - *movement*, *full arm* - *movement* against *full arm* - *incongruent outcome*, and *full arm* - *movement* against *detached hand* - *incongruent outcome*. Thus, for a total of six pairwise comparisons, each with a Bonferroni corrected p-value of 0.0083.

For **Block A**, we performed the following comparison in the sense of ownership and action agency: *full arm* against *full arm* - *incongruent outcome*, *full arm* against *full arm* - *incongruent*, and *full arm* - *incongruent outcome* against *full arm* - *incongruent*. For **Block B**, we performed the following comparisons: *full arm* against *full arm* - *incongruent outcome*, *full arm* - *incongruent outcome* against *detached hand* - *incongruent outcome*, and *full arm* - *incongruent outcome* against *full arm* - *detached hand* - *incongruent outcome*.

Our design contained two conditions that were previously used in **Experiment 2**, *full arm* - *incongruent movement* (**Block A**) and *detached hand* - *movement* (**Block B**). We assessed the reported sense of ownership and action agency in these conditions compared to the *full arm* - *movement* condition in their respective block. We performed the following comparisons: *full arm* - *movement* against *full arm* - *incongruent movement* for **Block A** and *full arm* - *movement* against *detached hand* - *movement* for **Block B** for the ownership scores and the agency scores.

Thus, for each the sense of ownership and action agency in both blocks, we performed 12 pairwise comparisons, each with a Bonferroni corrected p-value of 0.0041.

Finally, our blocks of conditions contained two conditions that were consistent in both of them, *full arm* - *movement* and *full arm* - *incongruent outcome*. We compared the ownership, agency, and outcome agency scores in each of these conditions between the two blocks. This analysis would determine whether the participants were reporting consistent values in both blocks. Thus, we performed the following comparisons: the individual ownership, action agency, and outcome agency scores in *full arm* - *movement* in **Block A** against the values in *full arm* - *movement* in **Block B**. We also compared the individual ownership, action agency, and outcome agency scores in *full arm* - *incongruent outcome* in **Block A** against the values in *full arm* - *incongruent* *outcome* in **Block B**.

Correlations

For ownership, agency, and outcome agency, we assessed the correlation, using the Spearman ρ correlation coefficient, between both blocks in the *full arm* - *movement*, and the same for *full arm* - *incongruent outcome*. Thus, we performed a total of six tests, each with a Bonferroni corrected p-value of 0.0083.

Similar to the analysis performed in **Chapter 4**, we assessed the correlation between the changes in the outcome agency, the changes in the sense of agency, and the changes in the sense of ownership in two conditions. First, for each pair of compared conditions, we calculated the individual changes in the sense of ownership and the sense of agency, which we labeled ownership difference and agency difference ($\Delta Ownership$, $\Delta Agency$, and $\Delta OutcomeAgency$, respectively)

$$\begin{aligned} \Delta Ownership_i &= Ownership_{i_A} - Ownership_{i_B} \\ \Delta Agency_i &= Agency_{i_A} - Agency_{i_B} \\ \Delta OutcomeAgency_i &= OutcomeAgency_{i_A} - OutcomeAgency_{i_B} \end{aligned} \tag{5.1}$$

where $\Delta Ownership$, $\Delta Agency$, and $\Delta OutcomeAgency$ are the differences between condition A and condition B for a given individual, i. Thus, we obtained 43 Δ values.

We calculated the correlation between the values obtained using the Spearman ρ correlation coefficient. Since our goal was to assess the effect of the incongruent outcome in the senses of ownership and agency, we compared *full arm* - *movement* against *full arm* - *incongruent outcome* between the sense of ownership and outcome agency and between the action agency and outcome agency in both blocks. Subsequently, we compared these same conditions between the sense of ownership and action agency. Later, as a result of the results seen in these comparisons, we wanted to assess if the previous chapter's effect was maintained due to incongruent movement. Thus, we compared *full arm* - *movement* against *full arm* - *incongruent movement* in **Block A** and *full arm* - *movement* against *detached hand* - *movement* in **Block B**.

This resulted in a total of eight conditions, each with a Bonferroni corrected p-value of 0.00625.

6 | General Discussion

> *“Saberemos cada vez menos o que é um ser humano.”*
> *“We will know less and less what a human being is.”*
>
> José Saramago,
> As intermitências da morte

6.1 Overview

In this thesis, we have investigated whether actively controlling the movements of a virtual hand in a goal-directed task affected the senses of ownership and agency. To address the question, we took advantage of Immersive Virtual Reality (IVR) environments. Specifically, we built an IVR variation of the moving Virtual Hand Illusion (mVHI) paradigm. This approach involved designing a custom-made environment using hierarchical state machines. This design allowed us to maintain constant underlying characteristics of the environment across experiments.

We have presented three different experiments. In these experiments, we manipulated: the congruence of visual and proprioceptive information, the visual appearance of the virtual limb (precisely, body continuity), the absence or presence of active control over the movements of the virtual hand, whether the observed movements were congruent or incongruent to the movements performed by the participant, and whether the actual sensory consequence met the expected outcome of the action. The participants reported their subjective experience of the senses of ownership and agency by responding to questionnaires.

In brief, our results suggest that the reported senses of ownership and agency are susceptible to different manipulations. However, the extent of this effect depended on the available sensory information in each scenario. For instance, perturbing the virtual limb's visual appearance showed a detrimental effect only in the absence of movement. This result was not replicated when the participants controlled the virtual hand. Additionally, adding noise to the trajectory of the virtual hand's movement negatively affected the sense of ownership and agency, only when the expected outcome of the action and the actual outcome were highly correlated.

In this chapter, we discuss the findings made across the thesis. We also place them into a Bayesian framework for the generation of the sense of ownership. Finally, we explore the limitations and future directions from the current work.

6.2 Virtual Reality as a medium to study embodiment

The experience of the bodily self is a complex phenomenon and it is difficult to dissociate from the physical body itself. Using fake limbs, such as rubber hands, is an effective method to induce illusions of ownership over fake body parts and (Botvinick and Cohen, 1998). However, the classical RHI presents some limitations regarding the perturbations that the fake body can withstand, such as changes in size, visual appearance, or motor information regarding the limb movement. The latter being of particular interest in the studies presented here.

VR environments present a highly realistic and ecological valid scenario to the participants (Bohil, Alicea, and Biocca, 2011). Simultaneously, the use of VR opens up the possibility to manipulate experimental variables that would otherwise be nearly impossible. For example, VR environments allow for the embodiment of virtual bodies that are of different sizes (Banakou, Groten, and Slater, 2013), a dissociation from the perspective of the physical and virtual body (Slater et al., 2010), extend certain body parts (Kilteni et al., 2012), and manipulating the visuomotor feedback of an action (Sanchez-Vives et al., 2010).

To test for our hypothesis, we required to manipulate the limb's morphological appearance, allow the users to actively and finely control the virtual limb, and perturb both the seen movement and outcome of the action. Our custom-made VR environment allowed us to flexibly manipulate these variables in a controlled manner, either in isolation or simultaneously. Given the aforementioned limitations in classical RHI studies, the use of VR scenarios seemed to be an appropriate choice. A good example lies in our *detached hand - movement* condition, which required precise control of the movements of a hand that was disconnected from the body. These conditions are more challenging to reproduce in a physical setup, but not impossible. For example, there is a variation of the mRHI where the movement of the physical finger controlled a finger of rubber or robotic hands (Kalckert and Ehrsson, 2012; Kalckert and Ehrsson, 2014; Romano et al., 2014) that was cut at the wrist. Controlling the arm movements using the LEAP Motion controller allowed for a broader range of movements, and the participants could move freely. Analogous reasoning can be done for the *incongruent movement* condition. While studies have perturbed the relationship between the performed and seen movement in physical setups by providing asynchronous feedback (Kalckert and Ehrsson, 2012; Kalckert and Ehrsson, 2014), we could manipulate the spatial component of the movement instead of the temporal component (Padrao et al., 2016). Finally, the perturbation of the outcome (*incongruent outcome* conditions) was controlled and could be easily randomized.

Thus, using a virtual environment where the participants controlled a virtual hand in a non-movement restricted manner allowed us to test the role of visuomotor information in the sense of ownership over a virtual hand.

6.3 The contribution of morphological appearance in the senses of ownership and agency

The visual appearance of the virtual hand is an essential component for the sense of ownership (Tsakiris et al., 2010). As far as we know, there is a single study that has reported that the RHI can be induced over non-body shaped objects (Armel and Ramachandran, 2003). In our study, we have manipulated body continuity to modify the visual appearance of the virtual body. Previous research has reported a decrease in the sense ownership and agency after passive observation of a static virtual arm (Tieri et al., 2015a; Tieri et al., 2015b; Tieri et al., 2017) and after synchronous visuotactile stimulation (Perez-Marcos, Slater, and Sanchez-Vives, 2009). We replicate the same results in our *no movement* conditions. In **Experiment 2**, we found that the participants reported lower ownership and agency scores when comparing *detached hand* to *full arm* conditions.

Our initial hypothesis was that the presence of visuomotor information arising from voluntary movement should circumvent these top-down modulations (i.e., the need to fit a pre-existing model of the hand). Our results from **Experiment 1** were consistent with this hypothesis. Under active control, seeing the hand as discontinuous from the body did not decrease the reported sense of agency or ownership. This result suggests that bottom-up modulations (i.e., congruent movement) could override the need to fit a pre-existing model of the hand. Our findings appear to be robust, as these results were replicated in **Experiments 2** and **3** (and additional studies that are not presented here). These results are also consistent with previous studies that have reported that the senses of ownership and agency were maintained when controlling a discontinuous arm while performing a reaching-like task (Tran et al., 2017).

However, our results are in contrast with previous literature. Body discontinuity has been shown to decrease the sense of ownership over a virtual hand when passively observing a moving arm (Tieri et al., 2015a). In contrast, our studies included active control of the virtual hand. This difference in the experimental design could explain the opposing results. Our results are also in contrast with those from Seinfeld, et al. (Seinfeld and Müller, 2020). The authors found that under active control over the hands in a freely moving bimanual task, body discontinuity significantly decreased the reported sense of ownership. While the type of task that the participants had to perform could be at the origin of the observed differences, it is not sufficient to explain precisely the differences in the results.

Thus, our results suggest a crucial role of visuomotor information in maintaining a sense of ownership and agency over a discontinuous virtual body. We further explored the role of active control in enhancing the sense of ownership over a virtual limb in a goal-directed task.

6.4 The contribution of visuomotor information to the sense of ownership

The contribution of visuomotor information to the sense of ownership is still a matter of debate. Some studies have reported that active control enhanced the sense of ownership over a hand (Kalckert and Ehrsson, 2012; Ma and Hommel, 2013; Sanchez-Vives et al., 2010; Slater et al., 2010; Tsakiris, Prabhu, and Haggard, 2006; Dummer et al., 2009) and full-body avatars (Llobera, Sanchez-Vives, and Slater, 2013; Banakou, Groten, and Slater, 2013; Banakou and Slater, 2014; Slater et al., 2010). However, other studies have failed to find this effect (Kalckert and Ehrsson, 2014; Longo and Haggard, 2009; Riemer et al., 2013; Walsh et al., 2011). We considered that this discrepancy could result from differences in the experimental design and the visual appearance of the artificial limb used for the illusion.

Our results presented in **Experiment 2** allow us to understand the effect of active control on the sense of ownership over a virtual hand by comparing *no movement* and *movement* conditions. Contrary to our expectations, the sense of ownership was enhanced by active control solely when the evidence for the sense of ownership was lowered by seeing the arm in a discontinuous form. These results suggest that the effect of active control depends on the available evidence for ownership that arises from proprioceptive information and the virtual hand appearance.

Even though it is contingent on the visual appearance, our results suggest that active control over the movements of the virtual hand is relevant for the sense of ownership. Previous studies compared the sense of ownership under actively self-generated movements and externally generated movements over the fake hand. These studies report that passive movement does not elicit a sense of ownership compared to actively generated actions (Dummer et al., 2009; Kalckert and Ehrsson, 2012). Active movement has also been proposed to facilitate the onset of the illusion compared to passive movement (Kalckert and Ehrsson, 2017). Thus, suggesting that voluntary movement through active control is crucial for the illusion of ownership to occur.

A common trait of the studies that find a positive effect of active movement is that it requires to be temporally congruent, as asynchronous movement abolishes the illusion of ownership over a fake body. In a setup where the experimenters can manipulate the synchrony of the displayed movement, a stronger ownership illusion was found when the movement was synchronous to the participants' movement rather than asynchronous (Tsakiris, Prabhu, and Haggard, 2006). This result has been replicated in virtual environments over a virtual limb (Sanchez-Vives et al., 2010) and a full-body (Slater et al., 2010). Thus, temporal synchrony of the seen movement of a hand and the participant's physical movement is crucial for the sense of ownership (Kalckert and Ehrsson, 2012; Newport, Pearce, and Preston, 2010; Sanchez-Vives et al., 2010; Tsakiris, Prabhu, and Haggard, 2006). Spatial incongruences also result in a decrease of sense of ownership when the virtual limb moves in an opposite direction to the movement of the participants (Padrao et al., 2016). Our *incongruent movement* condition is in line with these results, as we found that the manipulation of the trajectory of the virtual hand resulted in a decrease of the reported sense of ownership. Thus, spatio-temporal deviations can negatively affect self-recognition (Farrer et al., 2008). Altogether, our results are consistent with a need for spatial and temporal congruence of the active movement of the fake and physical hand to elicit a sense of ownership.

Goal-achievement is an important component of the sense of agency (Gallagher, 2000; Haggard and Chambon, 2012). Perturbations in action-outcome correlation have been shown to decrease the sense of agency when controlling an element on a screen (Wen, Yamashita, and Asama, 2015a) and over the movements of a virtual finger (Villa et al., 2018; Caspar et al., 2016b). Thus, we expected that perturbations in the outcome of the actions would decrease the reported sense of agency and, subsequently, ownership. Once present, the information on the task's outcome has been suggested to play a key role in updating the body representation (Wen et al., 2016; Bos and Jeannerod, 2002). In **Experiment 3**, we manipulated the action-consequence correlation. We found a significant reduction of the sense of agency over the movements of the virtual hand (i.e., action agency). Furthermore, the reported sense of ownership was also negatively affected by the incongruent outcome. However, the effect of the incongruent outcome depended on the available information within each block of conditions.

Altogether, the results presented here show that active control plays a crucial role in eliciting a sense of ownership over the virtual hand. Moreover, we found that the effect of visuomotor information depends on the available sensory information (such as visual appearance). Thus, these could reconcile the differences reported on the role of visuomotor information on the sense of ownership.

6.5 The interplay between agency and ownership in bodily illusions

In our daily life activities, the senses of ownership and agency are felt as a unitary experience. However, it is suggested that the senses of ownership and agency act through independent mechanisms (Kalckert and Ehrsson, 2012; Tsakiris, Longo, and Haggard, 2010). While the sense of agency is mainly dependent on efferent information, body ownership is mainly afferent driven (Tsakiris and Haggard, 2005a).

The sense of ownership depends on both bottom-up and top-down modulations. For instance, the matching of the sensory information (e.g., visual, tactile, and proprioceptive) is required for a sense of ownership to arise over a fake limb (Botvinick and Cohen, 1998; Armel and Ramachandran, 2003). However, such bottom-up perceptual mechanisms are not sufficient to explain all the body ownership illusions (Kammers et al., 2009b), as the limb needs to adhere to anatomical constraints of the body (Ehrsson, Spence, and Passingham, 2004; Tsakiris and Haggard, 2005b; Kalckert and Ehrsson, 2012). Among these, matching visual appearance is a key factor for body ownership (Maselli and Slater, 2013; Argelaguet et al., 2016; Pyasik, Tieri, and Pia, 2020). When the limb is seen from a first-person perspective, congruent visual appearance induces a sense of ownership without the need for additional sensory information (Maselli and Slater, 2013). Overall, these results suggest that a visual representation of the hand that is congruent with a known representation of a hand is necessary for the illusion of ownership to occur. The results from our *no movement* conditions are in agreement with the previous literature, as the participants reported a sense of ownership over a realistic-looking limb presented in a congruent anatomical position.

It has been suggested that the sense of agency can be modulated by the body ownership (Kalckert and Ehrsson, 2012) and that the feeling of owning a body leads to the sense of agency (Burin et al., 2019). In agreement with this idea, in the absence of visuomotor information (i.e., *no movement* conditions), we found the sense of agency is affected by changes in the morphological appearance of the hand. In contrast, our results from the *movement* conditions suggest that feeling as the author of the movements of the virtual hand affects the sense of ownership. We found that the senses of ownership and agency become resistant to body discontinuity. These results suggest that bottom-up processes can override top-down modulations (i.e., fitting a pre-existing model of the hand). Thus, under the voluntary movement of the virtual hand, the presence of action-related information acts as evidence for the senses of ownership and agency.

Interestingly, it has been reported that a sense of agency can be felt over elements that are external to the body (Kalckert and Ehrsson, 2012). Therefore, it is consistent that, under active control over the movements of the virtual hand, the sense of agency would not be negatively affected by seeing the limb in a discontinuous form. These results were replicated across the three experiments presented in this thesis. Overall, suggesting that the sense of agency elicits a sense of ownership when visuomotor information is present (Argelaguet et al., 2016). Further evidence for this relationship arises from the *incongruent movement* and *incongruent outcome* conditions. Our results show that the reported senses of agency and ownership are negatively affected by the action and outcome incongruences, even when maintaining a congruent body morphology.

The results presented here suggest an interplay between visual appearance and visuomotor information of the action to induce the mVHI. The importance of each of the components that interact to elicit the sense of ownership and agency depends on the available information, which is supported by previous literature (Beers, Wolpert, and Haggard, 2002). Moreover, we suggest that the senses of ownership and agency are not entirely independent processes.

6.6 A qualitative Bayesian framework for the sense of ownership over a virtual limb

The results reported here are consistent with a Bayesian framework previously proposed to explain the mechanisms underlying the feelings of ownership in the RHI paradigm (Kilteni et al., 2015; Samad, Chung, and Shams, 2015; Armel and Ramachandran, 2003). In the classical RHI, the sensory information is integrated to estimate whether the sensory information originates from a single common source (i.e., virtual hand, which leads to the illusion of ownership) or two (i.e., virtual and real hands) that arises from the morphological appearance of the limb, the proprioceptive information from the position of the fake and physical hands, and the visuotactile information (Kilteni et al., 2015; Samad, Chung, and Shams, 2015). It has been suggested that the high probability of the seen and felt touch co-occurring facilitates the perception from the different modalities becoming more tightly bound and arising from the same source (Armel and Ramachandran, 2003).

We propose a similar model to explain the here reported results qualitatively. In our scenario, the probability that there is a single hand is estimated given the following information: visual appearance of the virtual hand (i.e., a realistic hand model with or without body continuity), the level of congruence of the proprioceptive information from the physical hand and the position of the virtual hand, the level of congruence of the information from motor feedback of the physical hand and visual input of the virtual hand during movement, and the correlation between the intended consequence of the action in the environment (i.e., lights turning off when the virtual hand reached them) and the actually observed consequence.

Our results suggest that when passively observing a static realistic-looking virtual arm in a congruent position, the evidence in favor of all the sensory information arising from a single arm is high enough for many to declare high ownership scores. In this scenario of relatively high ownership, the added evidence from the control of movements does not change the final estimation. On the other hand, in the absence of movement, seeing the hand as detached from the body increases the evidence in favor of two hands and, thus, reduces the illusion of ownership. In this condition, where the evidence for one hand is decreased, adding active control provides evidence in favor of a single hand. Thus, explaining the resistance to morphological incongruence under active control. Adding noise to the movement of the hand and breaking the correlation between expected and observed outcomes are other manipulations that decrease evidence in favor of a single hand. In these conditions, the reported ownership scores decrease, despite the semantic information and the action information corresponding to the expected.

Further information and the mathematical formulation can be found in **Appendix B**.

6.7 Comparison of the *incongruent movement* conditions in Experiments 2 and 3

It is worth noting that the *incongruent movement* manipulation did not present a detrimental effect in the sense of agency in all experiments. In **Experiment 2**, *incongruent movement* resulted in a correlated decrease in both the sense of ownership and agency. Suggesting that, in the provided context, the sense of ownership and agency were dependent on each other. This is not the case in **Experiment 3**, in which most participants seemed unaffected in the sense of agency. The reason for this might be that sense of agency can rely on different kinds of signals that are weighted according to the context and sensory availability (Moore and Fletcher, 2012; Synofzik, Vosgerau, and Newen, 2008a). The *full arm - movement*, *detached hand - movement*, and *incongruent movement* conditions were the same across the three experiments presented in the main text. Then, it is possible to compare across the three experiments

Our results from **Experiment 3** contrast with our results from **Experiment 2** and two preliminary unpublished data sets, which found that adding noise to the trajectory of the virtual hand significantly decreased the senses of ownership and action agency. In an attempt to understand the reason for these differences, we compared the *full arm - movement* and *full arm - incongruent movement* conditions between **Experiment 2** and **Experiment 3, Block A**. The *full arm - movement* did not yield a difference between both experiments (Mann Whitney U test; Z=-1.29, p=0.19). Thus, suggesting that the average for the sense of agency was similar in both experiments. The *full arm - incongruent movement* showed significant higher values in the reported action agency scores in **Experiment 3** compared to **Experiment 2** (Mann Whitney U test; Z=-3.44, p<0.001) [**Figure 6.1A**]. Thus, suggesting that the participants were responding differently to the same condition.

Experiment 2 and **Experiment 3** presented two main differences in their experimental design [see **Section 3**]: how feedback was provided to the participant and the order in which the *full arm - incongruent movement* condition was presented. In **Experiment 2**, the feedback was presented from the lights that would change to green when the participant correctly reached the light; or change to red when the participant failed to reach the light or made an error. In contrast, in the **Experiment 3**, the feedback was delivered from a separate screen larger presented in front of the participant in the virtual environment. Additionally, in **Experiment 3**, the participants were presented with a counter with the correct and incorrect waves for each condition. At the beginning of the **Experiment 3**, the participants were instructed that the task's goal was to turn off the lights within the time limit. Altogether, these changes emphasize the value of the outcome of the task in **Experiment 3** compared to **Experiment 2**. This modification might have shifted the attention towards the outcome in detriment of action congruence. As a result, the participants might not be aware of the virtual hand's movements' incongruence when the outcome correlates with the expected result.

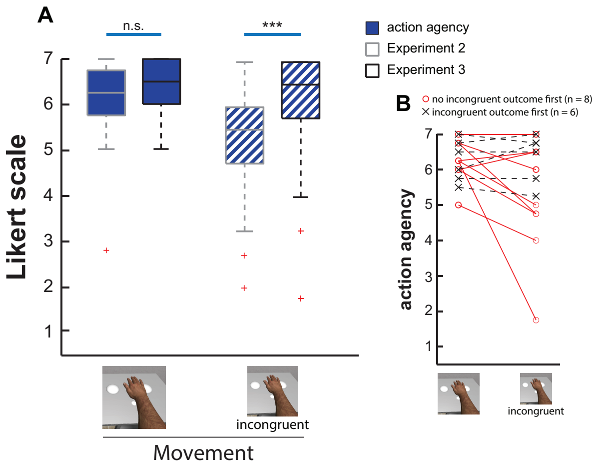


Figure 6.1: **Comparison of the incongruent movement conditions in Experiments 2 and 3**. (A) The reported action agency (in blue) in the *full arm* - *movement* and *full arm* - *incongruent movement* conditions in **Experiments 2** (outlined in gray) and **3** (outlined in black). The reported action agency scores did not differ between both experiments in the *full arm* - *movement* condition (p=0.19). On the other hand, reported ownership scores in the *full arm* - *incongruent movement* condition were greater in **Experiment 3** compared to **Experiment 2** (p<0.001). (B) The action agency scores in the *full arm* - *movement* and *full arm* - *incongruent movement* in **Block A** of **Experiment 3**. The participants that experienced the two congruent outcome conditions (i.e., *full arm* - *movement* and *full arm* - *incongruent movement*) qualitatively showed a decrease in the reported outcome agency, while the participants that experienced the two incongruent movement conditions first (i.e., *full arm* - *incongruent outcome* and *full arm* - *incongruent*) did not.

An additional difference was the order in which the conditions were presented. In **Experiment 2**, the *full arm* - *incongruent movement* was always presented at the end of the experiment, while the conditions were fully counterbalanced in **Experiment 3**. To test for a potential effect of order, we checked with individuals in which *full arm* - *movement* and *full arm* - *incongruent movement* preceded *full arm* - *incongruent outcome* and *full arm* - *incongruent*) and vice versa. We found that the participants that did not experience the incongruent outcome in the two first conditions showed a decrease in the *full arm* - *incongruent movement* condition compared to the *full arm* - *movement* conditions (p=0.04), whereas the groups in which the participants experienced first the two conditions with incongruent outcome (i.e. *full arm* - *incongruent outcome* and *full arm* - *incongruent*) did not yield a difference between the *full arm* - *incongruent movement* and the *full arm* - *movement* [**Figure 6.1B**]. However, due to the randomization of the order of the conditions, we have little data that met the criteria for a more robust analysis. Further information needs to be collected on the effect of order presentation of the conditions in the reported sense of ownership and agency.

6.8 Limitations of this thesis

In this section of the General Discussion, we enumerate the limitations of the current work.

First of all, a small limitation is that we did not present the participants with a *detached hand* - *incongruent movement* condition. This condition would have allowed us to understand further the interplay between visual appearance and movement congruence on the senses of ownership and agency. We would expect that the participants would report lower levels of ownership and agency compared to conditions with congruent control over the movements of the virtual hand, regardless of the visual appearance of the limb. Testing this condition could provide further evidence on our hypothesis that congruent movement is crucial for the sense of agency and ownership in a goal-directed task.

We designed our *incongruent outcome* condition so that the participants could not map the action and the outcome, as we randomized the probability of the light responding to the hand after a fixed 500ms delay. We only asked for the experience of the sense of agency at the end of the condition. Therefore, we could not capture the effects of specific temporal delays on the action agency. A more detailed analysis of the different time delays would provide more in-depth insight into the effects of action-outcome correlation in the action agency Farrer, Valentin, and Hupé, 2013 and ownership.

Finally, a limitation is the lack of implicit measure for the senses of ownership and agency. Several approaches can be used to assess body ownership and agency illusions, including both explicit or implicit measures. In this dissertation, we present our findings regarding the qualitative experience of the illusion in the form of subjective questionnaires, which is a well-established measure. However, it has been suggested that subjective measures should be complemented with quantifiable implicit measures (Slater, 2004).

The proprioceptive drift refers to the change in the perceived position of the participants' physical hand towards the fake embodied rubber hand by either pointing towards the rubber hand (Botvinick and Cohen, 1998) or reporting the perceived position compared to a numeric measurement in the environment (Tsakiris and Haggard, 2005b). However, some studies fail to see the relation between the illusory experience of ownership and proprioceptive drift measures and suggest that they are modulated by different factors (Kammers et al., 2009a; Rohde, Di Luca, and Ernst, 2011). Another alternative lies in the recording of physiological reactions to a change in the environment. These measures usually consist of a threatening event to the fake body. For instance, stabbing the fake limb with a knife elicits an increased Galvanic Skin Response (GSR) (Armel and Ramachandran, 2003), which is also reported in virtual reality (Tieri et al., 2015b). These changes occur when the illusion takes place (e.g., synchronous sensory stimuli). Analogously, GSR changes have been reported in full-body illusions, when stabbing the fake body (Ehrsson, 2007; Petkova, Khoshnevis, and Ehrsson, 2011). Studies have reported a direct relationship with the strength of the body ownership illusion and the anxiety evoked by threatening the fake body (Ehrsson et al., 2007).

Here, we also attempted to collect implicit measures for ownership: we used a variation of the proprioceptive drift and measured physiological reactions to a threat to the virtual hand. However, they resulted in inconclusive results. We present and discuss these results in **Appendix C**.

6.9 Future directions

We finish this thesis by proposing three different follow-up directions from work developed here.

First, during the course of the present thesis, we have mainly studied how our manipulations decreased the reported senses of ownership and agency (i.e., *detached hand*, *incongruent movement* and *incongruent outcome*). Only one of our comparisons aimed to understand whether visuomotor information enhanced the reported sense of ownership (i.e., comparing *full arm* and *detached hand* conditions in **Experiment 2**). Thus, the next experiments should aim to understand whether facilitating the outcome of the task enhanced the reported senses of ownership and agency, as it has been reported that participants tend to do so (Tsakiris et al., 2005). We could achieve this effect through various mechanisms: (1) facilitating the outcome by increasing the collision area of the virtual lights, (2) intensifying the feedback provided to the participants by providing auditory cues, (3) attributing positive values to the action-outcome relation, by increasing the reward or attributing emotional valence to the actions (Wilke, Synofzik, and Lindner, 2012), or (4) positively priming the participants regarding the outcome of the action (Aarts, Custers, and Wegner, 2005) (contrary to what has been shown in negatively primed actions (Caspar et al., 2016a)).

Second, humans are social animals and, as such, our actions usually occur in a social context and the presence of other individuals. Thus, the correct attribution of actions is crucial for self-other distinction (Bos and Jeannerod, 2002). Previous studies have shown that visuotactile stimulation can induce a self-other overlap, as is the example of the *enfacement illusion* (Tajadura-Jiménez, Lorusso, and Tsakiris, 2013). Embodying an outgroup (e.g., embodying a dark-skinned avatar) has shown to change social attitudes over an outgroup (Maister et al., 2015), such as reducing implicit racial biases (Peck et al., 2013; Fini et al., 2013) and improving the ability to recognize fear towards aggressive attitudes (Seinfeld et al., 2018). Finally, embodying others can result in increased self-compassion in a self-counseling paradigm (Slater et al., 2019; Falconer et al., 2014). Following analogous reasoning, future directions of this work could aim to understand how the integrating different body- and action-related information induces a self-other overlap in a joint-goal interaction. An adapted version of the paradigm presented here would include a joint-goal by having two participants simultaneously perform a goal-directed task. Thus, adding an extra layer of sensory information for the sense of agency and ownership (i.e., body ownership, action agency, outcome agency, joint-outcome agency). In this scenario, the already presented manipulations (i.e., *detached hand*, *incongruent movement* and *incongruent outcome*) and a manipulation affecting the joint task would test the role of a joint-goal achievement in the sense of ownership and whether it promotes self-other overlap. Illusory ownership has shown to be crucial in different social scenarios.

Finally, embodiment has shown to be affected by neurodevelopmental disorders (e.g., autism spectrum disorder, Palmer et al., 2015; Conson et al., 2015) and neurological conditions (e.g., hemiplegia, Garbarini et al., 2015). Thus, another interesting aspect would be to understand whether the sensory information is integrated differently in clinical populations. In an experimental setup similar to the one presented in this thesis, the different aspects of the senses of ownership and agency could be manipulated simultaneously. The would results be compared to a healthy cohort to understand whether the manipulations had a different effect in clinical populations.

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A | Class Documentation

A.1 ICStateMachine

The State Machines (SMs) used in this project are instantiated from the generic ICStateMachine class. This generic SM has three main properties that define when and how a specific SM started:

StartOnInstantiation This property controls when the machine is started. If set to *true*, the SM starts when the scene is opened. Otherwise, if set to *false*, the SM starts when the **StartMachine()** method is called (e.g. from a parent SM).

InitialState This property defines the first active state when the state machine is started.It can be accessed and changed from the Unity Inspector.

StartOnStopMachine This property controls whether the SM restarts or not after it has been stopped. If set to *true*, the SM starts in the **InitialState** after it has been stopped by calling the **StopMachine()** method is called.

The ICStateMachine also contains a set functions that are called when the machine is started or stopped:

StartMachine() sets the **started** property of the SM to *true*, calls the textbfOnStart() method and sets the **currentState** to the **initialState**.

StopMachine() stops a started machine, calls the **OnStop()** method, and sets the **started** property to *false*.

OnStart() This method is called when the machine is started and defines the actions that need to be triggered when the machine is started.

OnStop() This method is called when the machine is stopped and defines the actions that need to be triggered when the machine is stopped.

When a new SM from the ICStateMachine class, the SM states and events need to be defined, which are called as a public[1] enum outside the class. For example, in the TrialController we defined four states and two events [**Figure A.2**].

A.1.1 GetState()

The **GetState()** function is called when a transition between two states is triggered. This function returns the **state** property, which is the current state of the machine [**Figure A.3**].

A.1.2 HandleEvent(event)

The **HandleEvent(**event**)** method controls the transitions that are triggered by an **event**. The event is passed as an argument to this function. The **GetState()** function is called and returns the current state of the machine. A set of different actions occur only for a specific event that occurs within a state.

To illustrate with an example, the TrialController class [**Figure A.4**]) has two events: SpTrialFinished and the QuestionsFinished. For instance, when the SpTrialFinished is triggered, the **GetState()** function checks the current state. If the machine is in the SpecificTrial state, the event triggers a change to the Questionnaire state by calling the **ChangeState()** method. Similarly, when the machine is in the Questionnaire, QuestionsFinished event triggers a transition to the End state. Additionally, the **StopMachine()** method is called from the QuestionnaireController.

A.1.3 GetTimeInState()

The **GetTimeInState()** method controls the transitions that are triggered when a **timeout** expires. This requires the **Update()** function, which is called every frame. The **GetTimeInState()** measures the elapsed time since the last state change [**Figure A.5**]. When this number matches the threshold, a transitions between states is triggered by calling the **ChangeState()** method.

In our case example, when the TrialController is started in the Idle state. After two seconds, it transitions to the SpecificTrial state.

---

[1] A public variable is accessible from outside of the class and can be edited from the Unity Inspector.

```
public abstract class ICStateMachine<States, Events> :  MonoBehavior {
    private States state;
    private float timeAtStateChange;
    private bool started;

    ...

    public States initalState; % first active state when the machine is started

    public bool StartOnInstantiation = false;

    public bool StartOnStopMachine = false;

    protected void WriteLog(string message) {
       if (logToConsole)
          Debug.Log(message);
       if (logger != null)
          logger.Write(this.GetType().ToString() + "\t" + message);

    public void StartMachine() {
       if (!started) {
          started = true;
          OnStart();
          state = initialState;
          timeAtStateChange = Time.time;

          WriteLog("Started");

          OnEnter(state);
       }
    }

    public void StopMachine() {
       if (started) {
          OnExit();
          timeAtStateChange = Time.time;
          started = flase;

          WriteLog("Stopped");

          ...
       }
       if (StartOnStopMachine)
          StartMachine();
    }

    ...  % these functions are referred to in subsequent sections

    public bool IsStarted() {
       return started;
    }

    public void Start() {
       if (StartOnInstantiation)
          StartMachine();
    }

    virtual protected void OnStart() { }

    virtual protected void OnStop() { }

    abstract protected void OnExit(States newState);

    abstract protected void OnEnter(States oldState);
}
```

Figure A.1: **ICStateMachine class script**

```
public enum TrialStates {
    Idle,
    SpecificTrial,
    Questionnaire,
    End,
}

public enum TrialEvents {
    SpTrialFinished,
    QuestionsFinished,
}

public class TrialController :  ICStateMachine <TrialStates, TrialEvents> {
    ...
}
```

Figure A.2: **Instantiating a State Machine**.

```
public  States GetState() {
    ...
    return state;
}
```

Figure A.3: GetState() function script

```
public void HandleEvent(TrialEvents ev) {
    ...
    switch (GetState()) {
    case TrialStates.Idle:
       break;

    case TrialStates.SpecificTrial:
       if (ev == TrialEvents.SpTrialFinished);
          ChangeState(TrialStates.Questionnaire);
       break;

    case TrialStates.Questionnaire:
       if (ev == TrialEvents.QuestionsFinished) {
          questionnaireController.StopMachine();
          ChangeState(TrialStates.End);
       }
       break;

    case TrialStates.End:
       break;
    }
}
```

Figure A.4: **Example for the HandleEvent() function**. In the TrialController example, there are four states in which the HandleEvent() can be called, and each of them triggers a different behaviour and call the ChangeState() function causing the transition to a different state.

```
public void Update() {
    ...
    switch (GetState()) {
    case TrialStates.Idle:
        if (GetTimeInState() > 2.0f)
            ChangeState(TrialStates.SpecificTrial);
        break;

        ...  % Here all the behaviors for each of the states, if applicable

    }
}
```

```
public void GetTimeInState() {
    float time = Time.time;
    return time - timeAtStateChange;
}
```

Figure A.5: **Example of the Update() and GetTimeInState() functions in TrialController SM**. A transition between two states can be triggered when a timeout expires. Two functions are needed, the Update() function that is called once every frame and the GetTimeInState() function. When the time elapsed in a determined state equals the timeout a transition is triggered.

A.1.4 ChangeState(newState)

The transition between the different states is controlled by the **ChangeState(**newState**)** function, which has the **newState** as an argument. The **ChangeState()** function changes the current **state** to an **oldState** variable and the **newState** is set as the state of the machine (i.e. the current state). Additionally, this method calls the **WriteLog()** function to log this transition into the .log file with the corresponding timestamp **A.3**.

The **ChangeState()** method calls two additional methods, **OnEnter()** and **OnExit()**, in which we define that actions that take place when a state is entered an exited. In the **ChangeState()** method the **OnExit()** is called before the current state is changed. This means that it takes the actions of the current state at the moment of the change, that become the **oldState** in the next lines of code. After the current state has been updated, the **OnEnter()** method is called. The **GetState()** is invoked to obtain the current state.

In our example, TrialController, when the Questionnaire state is entered, the system sets the hands to *false* (i.e. they won't show up in the environment), and it starts the QuestionnaireController SM.

```
public void ChangeState(States newState) {
    ...
    OnExit(newState);

    States oldState = state;
    state = newState;
    timeAtStateChange = Time.time;

    WriteLog("Entering state " + state.ToString()

    OnEnter(oldState);
}
```

```
protected override void OnEnter(TrialStates oldState); {
    switch (GetState()) {
    case TrialStates.Idle:
       handSwitcher.showRightHand = true;
          testLights.SetActive(true);
       break;

    case TrialStates.SpecificTrial:
       switch (experimentType) {
          case ExperimentType.VisuomotorInformation:
             visuomotorTrialController.StartMachine();
             WriteLog("Visuomotor Information Trial started");
             break;

          ...  % Here all the specific trial state machines implemented

          }
       break;

    case TrialStates.Questionnaire:
       handSwitcher.showRightHand = false;
       questionnaireController.StartMachine();
       break;

    case TrialStates.End:
       this.StopMachine();
       break;
}

protected override void OnExit(TrialStates newState); {
    switch (GetState()) {

          ...  % Same for this function

}
```

Figure A.6: **ChangeState() function from the ICStateMachine, and examples for the OnExit and OnEnter() handlers**. The ChangeState() function is called to transition between the current state the SM is in and the state defined by the argument passed when it is called. This function in turn invokes the OnExit() and OnEnter() handlers.

A.2 ICTrialList

```
public class ICTrialList {
    public ICTrialList(string filename) {
       StreamReader reader = new StreamReader(filename)
       string[] header = reader.ReadLine().Split(’, ’);

       trials = new Queue<Dictionary<string,string»();

       while(!reader.EndOfStream) {
          string line = reader.ReadLine();
          string[] columns = line.Split(’, ’);

          Dictionary<string,string> trial = newDictionary<string,string>

          for(int i = 0; i < columns.Length, i++) {
             trial[header[i]].Trim()] = columns[i].Trim();
          }

          trials.Enqueue(trial);
       }
    }

    public bool HasMore() {
       return trials.Count !=0;
    }

    public int Count() {
       return trials.Count;
    }

    Dictionary<string,string> Pop() {
       return trials.Dequeue();
    }
}
```

Figure A.7: **Code for the ICTrialList class**

The ICTrialList class reads the **ProtocolFile** and obtains the parameters that define the characteristics of a single trial of a experiment. It has three main functions:

HasMore() returns a boolean that is set to *true* when the current trial count equal to 0 (i.e. there are no more trials on the list to be run), or *false* when it is not. When the number equals 0 (!hasMore), the experiment finishes.

Count() counts the amount of trials in the list when called.

Pop() . This method is called by the ExperimentController when a trial is finished, and it removes it from the list.

A.3 ICLogger

```
public class ICLogger :  MonoBehaviour {

    ...

    public void OpenLog(string filename) {
        writer = new StreamWriter(filename, true);
        Write("Logger\tStarted logging");
    }

    public void CloseLog() {
        Write("Logger\tStopped logging");
        writer.Close();
    }

    public void Write(string message) {
        if(writer != null) {
            writer.WriteLine(DateTime.UtcNow.ToString("o") + "\t" + message);
            writer.Flush();
        }

        ...
    }

}
```

Figure A.8: **Code for the ICLogger class**

The ICLogger class is used to log all the events and actions that take place during a single experiment onto a single text file. It logs the actions in order, using the timestamps when the action occurred, the state machine which called the action, and the message (i.e. the action). It has several important functions:

OpenLog() opens the text file where all the actions are logged.

CloseLog() closes the text file, once the experiment is finished

Write() introduces a new line in the text file with the required information.

A.4 SimpleCollision

```
public class SimpleCollision :  MonoBehaviour {

    public class WaveController waveController;

    public WaveEvents triggerEvent;
    public GameObjects[] objects;
    public float probability;

    public bool CompareByName = false

    void OnTriggerStay(Collider col) {
        probability = Random.Range(0.00f, 1.00f);
        if (col.name == "HandContainer") {
            if (objects.Length == 0) {
                waveController.HandleEvent(triggerEvent);
            } else {
                for (int i = 0; i < objects.Length; i++) {
                    if(CompareByName) {
                        if(col.gameObject.name == objects[i].name)
                            waveController.HandleEvent(triggerEvent);
                    } else {
                        if(col.gameObject == objects[i])
                    }
                }
            }
            waveController.randomProbability = probability;
        }
    }
}
```

Figure A.9: **Code for the SimpleCollision script**

The SimpleCollision class it is used in the conditions that include the goal-directed task and is attached to a collider object that is placed on the lights. It recognizes when another object interacts with it. In this case, the **HandContainer**, which is a rectangular shaped invisible element that includes the whole palm of the virtual hand. The encounter triggers the **SimpleCollision**.

In the *incongruent outcome* conditions, we need to manipulate the probability of reaction of the collider. This represents the threshold at which the collider responds to the presence of the virtual hand. In the *movement* conditions the probability is set to 1. In the *incongruent outcome* conditions, when the **SimpleCollision** is triggered the probability is compared to the threshold each frame the **HandContainer** interacts with the collider.

A.5 RiggedHandEx

```
namespace Leap.Unity {

    public enum NoiseType {
        NoNoise,
        NormalAroundPalm,
        NormalRandomWalk
    }

    public class RiggedHandEx :  HandModel {
        public Transform arm;
        public bool partOfAvatar;

        public bool firstUpdate = true;
        public bool ignoreUpdates = false;

        public NoiseType noiseType;
        public float noiseLevel;
        public float lambda;

        private Vector3 prevVitualPostion;
        private Vector3 prevActualPostion;

        ...

    }
}
```

Figure A.10: **RiggedHandEx script**. This is a modified version of the original RiggedHand class (Leap Motion, Inc) to allow for changes in the virtual hand characteristics, such as the addition of noise to the movement of the virtual hand or blocking the updates of the hand position.

The RiggedHandEx is a modified version of the RiggedHand class that is provided by the Leap Motion SDK. We made small modifications in the class so that we could add features that are desired for our experimental designs. For instance, stopped the hand from moving in the trials where control is not required (i.e. *movement* trials) and the addition of noise in the *incongruent movement* conditions.

The **ignoreUpdate** bool is used for the *no movement* trials, in which the virtual hand needs to remain still. This parameter is controlled by the **ProtocolFile**, and when it is set to *true*, the position of the virtual hand is not. By default, **ignoreUpdate** is set to *false*.

For the *incongruent movement* condition, we created two additional Vector3 variable, which store the position in the previous frame of both the virtual and the physical hand. These variables are used to add the noise to the trajectory of the virtual hand. There are two types of noise: NormalAroundPalm and NormalRandomWalk.

B | A qualitative Bayesian framework in which control adds evidence for the sense of ownership

In a Bayesian framework for a virtual environment, the participants are modeled as estimating whether their perception is compatible with a scenario with two hands (i.e. real and virtual hands) or a single hand (Samad, Chung, and Shams, 2015; Kilteni et al., 2015). The evidence arises from semantic information of the limb, proprioceptive information, and the tactile information applied.

Conversely, the evidence in our virtual scenario has semantic information (shape of the arm, body continuity, texture, color), proprioceptive information of the position of the participant's arm, a comparison of the intended trajectory and the observed trajectory, and a correlation between the intended outcome and the observed outcome of the action.

We extend the current model of Samad, Chung, and Shams, 2015 and Kilteni et al., 2015 to consider action control of a virtual limb as further evidence in favor that perception is compatible with a scenario with one hand (i.e. virtual hand) and not of two hands (i.e. real and virtual hand) as being the source of all sensory information. The evidence in our virtual scenario has the following elements: semantic information, m_v (shape of the arm, attachment to body, texture, color); proprioceptive information, x_p; action control as measured by a function comparing the intended trajectory, x_i, and the observed trajectory, x_o, with the form $\epsilon(x_i, x_o)$; and the outcome control as measured by the correlation between the intended consequence of the action, c_i, and the observed consequence of the action, c_o, with the form $\rho(c_i, c_o)$; and any priors. In the experiments presented in this thesis, we manipulated the semantic information (i.e. attachment to the body or not), the observed trajectory, and the observed consequences of the actions (i.e. lights responding to the hand or not). Thus, we are only considering m_v, $\epsilon(x_i, x_o)$, and $\rho(o_i, o_o)$ in the following. The estimated probability that the scenario corresponds to a single hand, $h = 1$, can be written using Bayes theorem as

$$\begin{aligned}&P\left(h=1|m_v,\epsilon\left(x_i,x_o\right),\rho\left(c_i,c_o\right)\right)=\\&\frac{P\left(m_v,\epsilon\left(x_i,x_o\right),\rho\left(c_i,c_o\right)|h=1\right)P\left(h=1\right)}{P\left(m_v,\epsilon\left(x_i,x_o\right),\rho\left(c_i,c_o\right)|h=1\right)P\left(h=1\right)+P\left(m_v,\epsilon\left(x_i,x_o\right),\rho\left(c_i,c_o\right)|h=2\right)P\left(h=2\right)}\end{aligned} \tag{B.1}$$

Assuming for simplicity that semantic information, action control, and the information on the outcome of the actions are independent and comparing the probabilities for the one hand and the two scenarios, we get

$$\begin{aligned}&\frac{P\left(h=1|m_v,\epsilon\left(x_i,x_o\right),\rho\left(c_i,c_o\right)\right)}{P\left(h=2|m_v,\epsilon\left(x_i,x_o\right),\rho\left(c_i,c_o\right)\right)}=\\&\qquad\frac{P\left(m_v|h=1\right)P\left(\epsilon\left(x_i,x_o\right)|h=1\right)P\left(\rho\left(c_i,c_o\right)|h=1\right)P\left(h=1\right)}{P\left(m_v|h=2\right)P\left(\epsilon\left(x_i,x_o\right)|h=2\right)P\left(\rho\left(c_i,c_o\right)|h=2\right)\left(1-P\left(h=1\right)\right)}\end{aligned} \tag{B.2}$$

We further model that an illusion occurs when this ratio is above a certain threshold or when the logarithm of the ratio is above a threshold

$$log\frac{P\left(h=1|m_v,\epsilon\left(x_i,x_o\right),\rho\left(c_i,c_o\right)\right)}{P\left(h=2|m_v,\epsilon\left(x_i,x_o\right),\rho\left(c_i,c_o\right)\right)}>\Theta \tag{B.3}$$

giving

$$\begin{aligned}&\left[log\left(P\left(m_v|h=1\right)\right)-log\left(P\left(m_v|h=2\right)\right)\right]+\\&\qquad\left[log\left(P\left(\epsilon\left(x_i,x_o\right)|h=1\right)\right)-log\left(P\left(\epsilon\left(x_i,x_o\right)|h=2\right)\right)\right]+\\&\qquad\qquad\left[log\left(P\left(\rho\left(c_i,c_o\right)|h=1\right)\right)-log\left(P\left(\rho\left(c_i,c_o\right)|h=2\right)\right)\right]>\Theta_2\end{aligned} \tag{B.4}$$

where we have absorbed the priors into a new threshold constant, Θ_2

For a comparison between *full arm* - *no movement* and *full arm* - *movement*, note that the first term in square brackets (i.e. morphological appearance) is the same in both cases, as the morphological appearance is congruent with a pre-existing model of the body. For the second term in square brackets (i.e. proprioceptive information of the action), note that the *full arm* - *no movement* is compatible with a single hand but even more so the *movement* one, and should give a higher value for the *movement* case. The *movement* case might then have a higher total value sum of the two terms but both *no movement* and *movement* can be above the threshold and therefore give similar ownership illusions. It is interesting to speculate that experimental differences among different groups might then arise because the priors are set-up differently and, therefore, in how easy subjects might go above the threshold.

The situation is different in the case of the *detached hand*. When the hand appears as detached from the body, the term related to the morphological appearance of the hand is smaller than in the *full arm* conditions, if not negative, both for *no movement* and *movement* scenarios, going against the illusion. However, in the *movement* case, the second square bracket has a much higher value than in the *no movement* condition because the intended and observed trajectories coincide. Thus, making it less likely compatible with a scenario with two hands. The sum of the two terms is then much more likely to be above a threshold in the *movement* conditions. Additional information arises from the correlation between the expected and observed consequence of the action, which is the third term in the equation. In the *movement* conditions, which add information in favor of a one hand scenario. In the *incongruent outcome* conditions, where the correlation action-outcome is disrupted, the third term becomes much smaller, increasing the compatibility with a scenario with two hands (which is against the illusion).

Other results might also be explained using similar logic. For example, in the *incongruent movement* condition from **Experiment 2**, the first term in square brackets is the same as in a *movement* scenario. However, the second term has a lower value as the situation is now more compatible with two hands, as it gives a smaller total sum of the three terms, most likely below the threshold.

The results presented throughout this thesis suggest that when subjects observed a realistic-looking virtual arm, even if still, the evidence in favor of a single arm is high enough for many to declare a high ownership score given then morphological appearance and congruent proprioceptive information. Adding the evidence of control of movements does not change the final estimation as already the evidence from the appearance was high for the experimental set-up. Only increasing the evidence in favor of two hands by presenting the virtual hand as detached from the body, there is room for the evidence of active control to impact the estimation of a single hand. Adding noise to the movement of the hand is another manipulation that reduces the illusion of ownership as the evidence for all the information arising from one hand decreases. Finally, perturbing the expected outcome of the action (i.e. the lights turning off when the virtual hand reaching them) also decreases evidence in favor of one hand, as the reported ownership scores decrease, despite the semantic information and the action information correspond to the expected.

In the results from the *full arm* - *no movement* presented in this thesis, in the absence of visuomotor information, the probability of there being a single hand is estimated based on the morphological appearance and proprioceptive information. With a realistic appearance of the hand and consistent proprioceptive information, we expect a high probability of estimating that the sensory information arises from a single hand. The results reported in the *full arm* - *no movement* condition are consistent with this prediction. By introducing a break in body continuity, we expect that the probability that there is a single hand to decrease, which is consistent with a reduction of reported ownership in the *detached hand* - *no movement* condition.

These predictions change when the subject actively controls the movements of the virtual hand in the *movement* conditions. The additional evidence, provided by the visuomotor information and the congruent outcome information increases the probability of integrating all the information as arising from the virtual hand compared to the *no movement* condition. This is consistent with our *movement* conditions, as the comparison between *full arm* - *movement* and *detached hand* - *movement* did not yield a significant difference. According to the model, the highest probability of sensory input corresponding with a single hand should take place without a break in continuity and under the active control of the arm (*full arm* - *movement* condition). However, our results failed to find an increase compared to the *full arm* - *no movement* condition. One possible explanation is that there is a saturation effect in which ownership scores cannot be manipulated to be higher given the experimental conditions.

Further support for this model comes from the *incongruent movement* and *incongruent outcome* conditions. We would expect that the noise added to the trajectory of the virtual hand would decrease evidence in favor of a single hand, consistent with a reduction of ownership scores in the *incongruent movement* condition. Unexpectedly, the reduction of the reported sense of ownership as a result of *incongruent movement* was found in **Experiment 2** and **3**. Additionally, we would expect that an unexpected lack of correlation between the predicted and observed outcome of the action would decrease evidence in favor of a single hand, which is consistent with the reduction of ownership observed in the *full arm* - *incongruent outcome* condition **Block A** of **Experiment 3**. Even though it was not the case in the same condition in **Block B**, we find that it decreases the evidence in favor of one hand in the *detached hand* - *incongruent outcome* condition. Both these results suggest that information is weighted differently according to the perturbations performed in a single experiment.

While at this point the model does allow for a more quantitative test, there is a qualitative agreement that suggests further tests might be fruitful.

C | Implicit measures for sense of ownership

C.1 Introduction

During the main results of the present dissertation, we have discussed the effects of visuomotor information in the context of subjective reports of sense of ownership and agency. However, it has been widely discussed which is the best approach to measure body ownership illusions (Vignemont, 2011; Moseley et al., 2008; Tsakiris, 2010). For instance, Galvanic Skin Response (GSR) has been used as a non-subjective proxy of sense of ownership (Armel and Ramachandran, 2003; Vignemont, 2011). A threat directed towards the static fake limb results in an increase of the GSR (Armel and Ramachandran, 2003; Tieri et al., 2015a). Another widely used objective measure of the illusion as been the so-called proprioceptive drift (PD), understood as mislocalization of the own hand position in favour of the position of the rubber hand (Botvinick and Cohen, 1998; Tsakiris, 2010; Tsakiris and Haggard, 2005a; Kammers et al., 2009a) (i.e., the spatial difference between the felt position of their own hand before and after experimental manipulation). Other measures have been proposed, these include changes in the local temperature of the hand (Moseley et al., 2008) or changes in reaction times in a cross-modal congruency task (Pavani, Spence, and Driver, 2000; Zopf, Savage, and Williams, 2010).

Other options include behavioral measures such as changes in the size perception of external objects (Tajadura-Jiménez et al., 2017; Banakou, Groten, and Slater, 2013), or the perceived length of the own arm using a bisection task (Sposito et al., 2012). Additionaly, the illusory feeling of ownership over a rubber hand has several physiological effects measurable on the corresponding real hand, including cooling (Moseley et al., 2008), reduced sensitivity to temperature (Llobera, Sanchez-Vives, and Slater, 2013), and corrections of the action performed by the alien hand (Nielsen, 1963).

While a broad variety of implicit measures are available for the sense of ownership, few implicit measures are reliable objective measures of sense of agency. Among them, a well-established measure, known as the intentional binding, measures the sense of agency by the time compression between the voluntary action (e.g., a key press) and a subsequent sensory consequence (such as a tone). Voluntary, in contrast to involuntary, actions are perceived as closer in time to the sensory consequence (Haggard, Clark, and Kalogeras, 2002).

C.2 Results

C.2.1 Physiological reaction to a threat to the virtual hand

In preliminary experiments, we recorded the GSR in participants during the *movement* conditions, where a threat was directed to the virtual hand at the end of each condition. In this setup, our participants underwent similar *movement* conditions to the ones presented in **Experiment 2** and **3** (*full arm* - *movement*, *detached hand* - *movement*, *detached hand* - *movement*, and *full arm* - *incongruent movement*). We obtained similar results in terms of self-reported senses of ownership and agency. In this study, the virtual hand of the participant was shifted ten centimeters to the right of the real hand. After the task was completed a virtual knife fell onto the center of the virtual hand and was visible during three seconds. We analyzed the data obtained by a peak-to-base measure (Armel and Ramachandran, 2003; Tieri et al., 2015b), and obtained the amplitude of the GSR for each condition by comparing the maxima in the 5 seconds post-threat with the mean of the 0.3 seconds pre-threat. We expected that the incongruent movement condition would show a significant difference with respect to the full arm dynamic condition as participants reported a decrease in the reported ownership.

The participants reacted in all three conditions. We found no significant difference between the *full arm* - *movement* conditions and the *detached hand movement* and the *full arm* - *incongruent movement* conditions [**Figure C.1**].

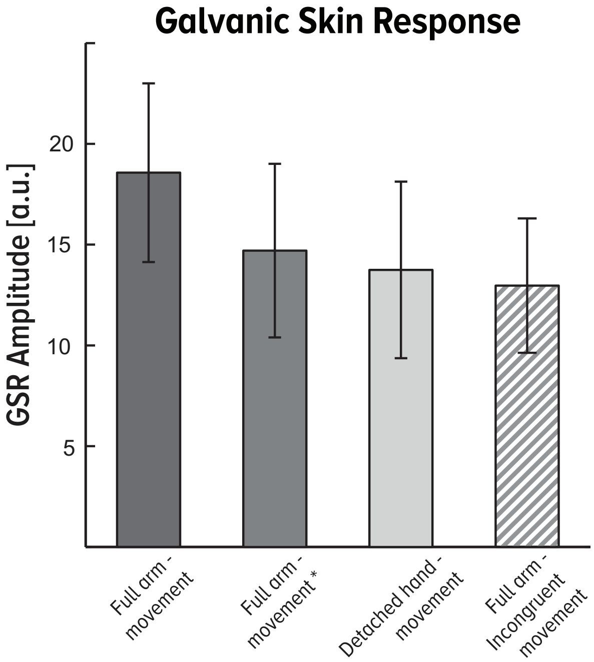

Figure C.1: **Galvanic Skin Response amplitude did not change in *movement* conditions**. GSR amplitude measured as the difference between the maxima in the five seconds post-threat and the mean of the 0.3 seconds pre-threat for the *full arm* - *movement*, *full arm* - *movement** (threat displaced ten centimeters), *detached hand* - *movement*, and *full arm* - *incongruent movement* conditions.

C.2.2 Proprioceptive Drift

In **Experiment 1** (**Chapter 4**), we included an adaptation of the proprioceptive drift measure. Proprioceptive drift is defined as the proprioceptive mislocation in favour of the rubber hand position as a result of visuotactile stimulation. In some cases it has shown to correlated with the reported sense of ownership (Botvinick and Cohen, 1998; Longo et al., 2008). Proprioceptive drift could be used as behavioral proxy of the sense ownership. A drift towards the external object can be interpreted as experienced ownership over the fake object, while away from it is failure to incorporate.

Furthermore, we had to forgo of this measure, in **Experiments 2** and **3** the hands were collocated to avoid errors related to the hand tracking. Additionally, our results might be incorrect as a result of the constant adaptation of the proprioceptive information in a moving hand. The relationship between the proprioceptive drift and the subjective report of the illusion is still unclear (Abdulkarim and Ehrsson, 2016; Rohde,

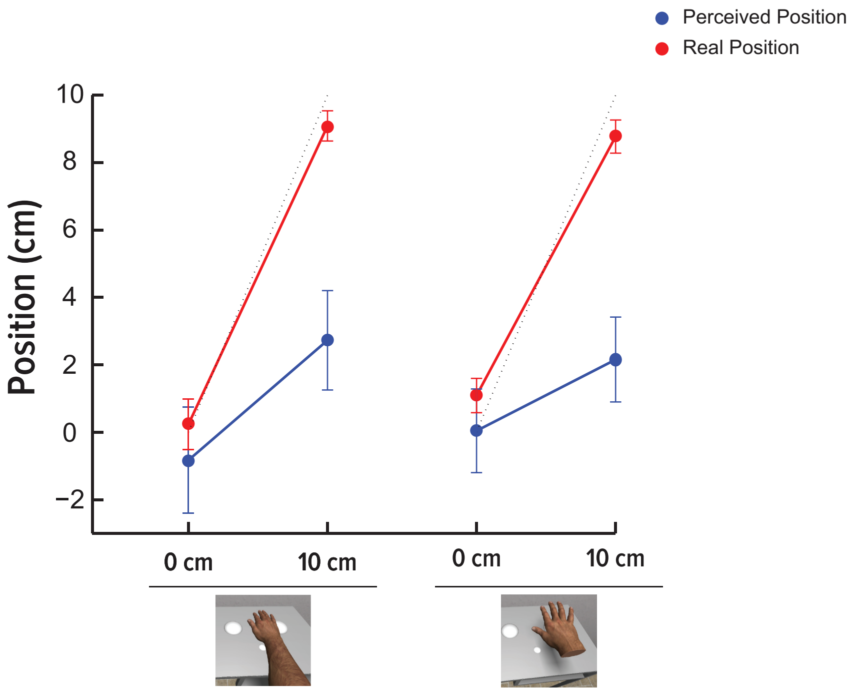

Figure C.2: **Proprioceptive Drift**.

Di Luca, and Ernst, 2011). There is a difference between the proprioceptive drift (the difference between pre and post exposure) and the proprioceptive shit (the difference between the position of the hand across different conditions). By either not inducing the drift even tough there is illusion (Rohde, Di Luca, and Ernst, 2011) or by not making changes whether the hand moves away towards the real hand (Abdulkarim and Ehrsson, 2016). Rather, they suggest that proprioceptive drift is an independent process that, under certain conditions, is correlated with or caused by the subjective illusion (Abdulkarim and Ehrsson, 2016). This concern stems in part from the fact that changes in hand proprioception can occur without changes in limb ownership (Makin, Holmes, and Ehrsson, 2008).

C.3 Analysis of kinematic parameters

Kinematic analysis, such as velocity, have shown to predict subjective and behavioral measures of the moving hand (Perepelkina and Arina, 2018). In **Experiment 3**, we logged the hand position data using the Leap Motion controller during the whole experiment and used this hand position to assess differences in kinematic parameters, such as velocity, displacement, and tortuosity as a result of the perturbation (i.e. incongruent movement or outcome and body discontinuity).

As a brief reminder, **Experiment 3** consisted of two blocks of four different experimental conditions. In each condition, the participants had to perform 30 movements towards the light that turned on in the virtual environment, which we labelled as *waves*, which would correspond to the trajectory from the **initialLight** to the corresponding **targetLight**. To this end, the hand positions (in x, y, and z) for every individual wave were extracted from the **HandPosition** file in each trial and cropped using the timestamps corresponding to the initiation and finishing of a waving event from the **Experiment 3** .log file. Subsequently, the thirty waves of each trial were averaged to obtained an average wave divided by left and right directions for **Block A** [**Figure C.3A**] and **Block B** [**Figure C.3C**]

C.3.1 Wave duration

Wave duration is the time, measured in milliseconds, that the participant took from turning off the the **intialLight** until the end of the waving event, that is either the light turning off or after the 3 second timeout.

For each participant, we calculated the average duration across all waves in every condition. In **Block A** the median and IQR (in parenthesis) of the wave duration, measured in milliseconds, was 306.7 (96.5), 312.1 (62.0), 969.2 (162.2), and 1009.5 (136.3), for the *full arm - movement*, *full arm - incongruent movement*, *full arm - incongruent outcome*, and *full arm - incongruent*, respectively. A comparison between the four groups showed a significant difference across conditions (Friedman test; χ^2=100.08 (df=3, n=43), p<0.001) [**Figure C.4**].

In **Block B** the median and IQR (in parenthesis) of the wave duration, measured in milliseconds, was 303.0 (77.0), 302.0 (50.7), 984.5 (184.9), and 991.7 (202.1), for the *full arm - movement*, *detached hand - movement*, *full arm - incongruent outcome*, and *detached hand - incongruent outcome*, respectively. A comparison between the four groups showed a significant difference across conditions (Friedman test; χ^2=103.21

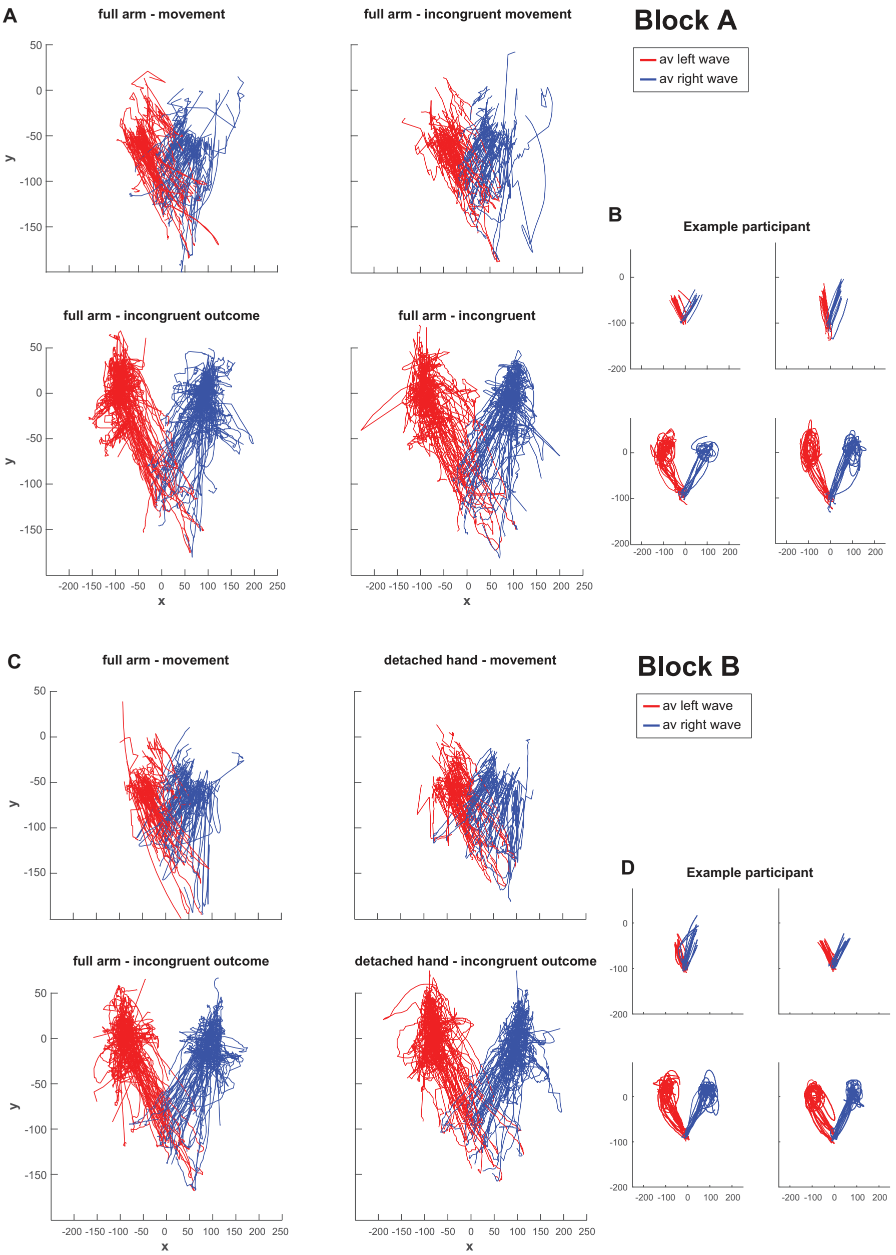

Figure C.3: **Average and example of participants wave trajectories for Experiment 3 for Block A (A and B) and Block B (C and D).** (A) Left (in red) and right (in blue) average wave trajectory for every participants in the *full arm - movement*, *full arm - incongruent movement*, *full arm - incongruent outcome*, and *full arm - incongruent* in **Block A**, (B) Individual left (in red) and right (in blue) wave trajectories for one subject for the the *full arm - movement*, *full arm - incongruent movement*, *full arm - incongruent outcome*, and *full arm - incongruent* in **Block A**, (C) left (in red) and right (in blue) average wave trajectory for every participants in the *full arm - movement*, *detached hand - movement*, *full arm - incongruent outcome*, and *detached hand - incongruent outcome* in **Block B**, (D) Individual left (in red) and right (in blue) wave trajectories for one subject for the the *full arm - movement*, *detached hand - movement*, *full arm - incongruent outcome*, and *detached hand - incongruent outcome* in **Block B**.

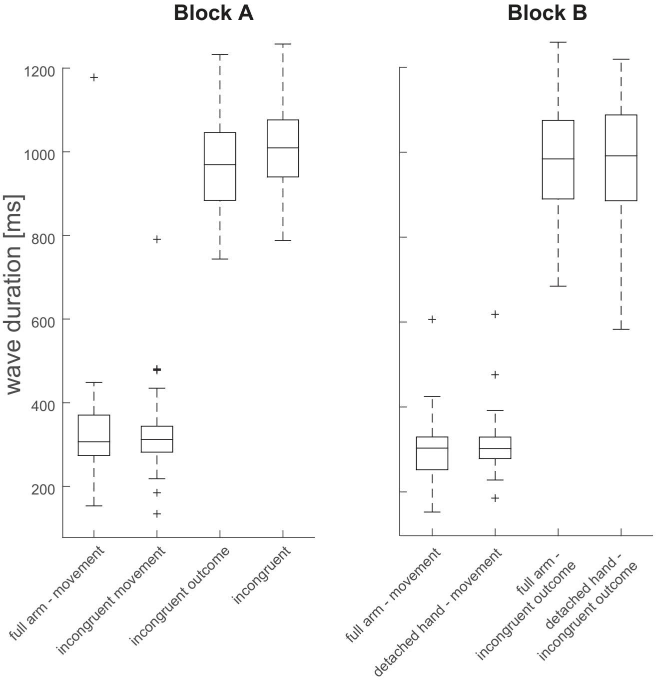

Figure C.4: **Average wave duration in Blocks A and B from Experiment 3**. (A) Average wave duration for the *full arm - movement*, *full arm - incongruent movement*, *full arm - incongruent outcome*, and *full arm - incongruent* in **Block A** for all participants, (B) Average wave duration for the *full arm - movement*, *detached hand - movement*, *full arm - incongruent outcome*, and *detached hand - incongruent outcome* in **Block B** for all participants. The middle quartile indicates the median value of all participants and the whiskers indicate the most extreme values that are not considered outliers.

(df=3, n=43), p<0.001). This result was expected, since the conditions in which the outcome of the task was manipulated the participants took longer to turn off the light [**Figure C.4**].

C.3.2 Maximum displacement

Maximum displacement, measured in millimeters, is the furthest distance from the starting point for every individual wave.

For each participant, we calculated the average maximum displacement across all waves in every condition. In **Block A** the median and IQR (in parenthesis) of the maximum displacement, measured in millimeters, was 96.19 (46.03), 90.44 (36.73), 146.28 (34.99), and 147.08 (37.70), for the *full arm - movement*, *full arm - incongruent movement*, *full arm - incongruent outcome*, and *full arm - incongruent*, respectively.

A comparison between the four groups showed a significant difference across conditions (Friedman test; χ^2=91.38 (df=3, n=43), p<0.001). A post-hoc analysis yielded a significant increase when comparing *full arm - movement* and the *full arm - incongruent outcome* condition (Wilcoxon signed-rank; Z=-5.67, p<0.001), while no significant differences were found between the *full arm - movement* and *full arm - incongruent movement* conditions (Wilcoxon signed-rank; Z=1.64, p=0.10) [**Figure C.5**].

In **Block B** the median and IQR (in parenthesis) of the maximum displacement, measured in millimeters, was 90.59 (37.01), 89.66 (39.94), 148.64 (28.81), and 147.59 (35.19), for the *full arm - movement*, *detached hand - movement*, *full arm - incongruent outcome*, and *detached hand - incongruent outcome*, respectively. A comparison between the four groups showed a significant difference across conditions (Friedman test; χ^2=93.95 (df=3, n=43), p<0.001). A post-hoc analysis yielded a significant increase when comparing *full arm - movement* and the *full arm - incongruent outcome* condition (Wilcoxon signed-rank; Z=-5.67, p<0.001), while no significant differences were found between the *full arm - movement* and *detached hand - movement* conditions (Wilcoxon signed-rank; Z=0.58, p=0.56) [**Figure C.5**].

C.3.3 Instantaneous velocity

The instantaneous velocity, measured in millimeters per second, was calculated for each wave. Then, we averaged all the waves for every participant in a given condition. The resulting traces depicted in **Figure C.6** show no qualitative differences across experimental conditions for the first 600 ms. Consistent with **Figure C.4**, we observe that *incongruent outcome* conditions have a longer tail as result of longer duration. It worth noting that velocity is not zero for these conditions, which suggest that the participants kept moving their hand.

C.3.4 Turtuosity

The turtuosity is the ratio between the distance and the displacement for any point during a wave. We averaged all the waves for every participant in a given condition. The resulting traces depicted in **Figure C.7** show no qualitative differences across experimental conditions for the first 600 ms. Consistent with **Figure C.4**, we observe that

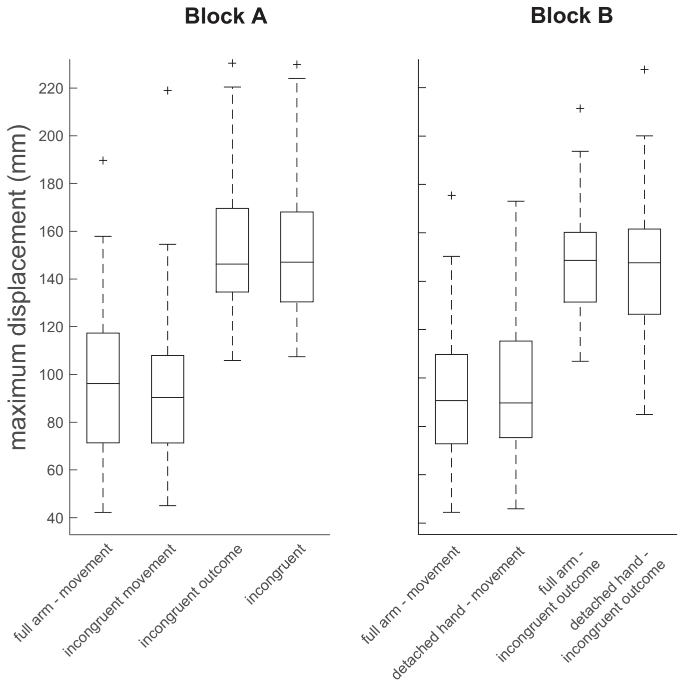

Figure C.5: **Average maximum displacement for Blocks A and B from Experiment 3**. (A) Average maximum displacement for *full arm* - *movement*, *full arm* - *incongruent movement*, *full arm* - *incongruent outcome*, and *full arm* - *incongruent* conditions in **Block A** for all participants, (B) Average maximum displacement for the *full arm* - *movement*, *detached hand* - *movement*, *full arm* - *incongruent outcome*, and *detached hand* - *incongruent outcome* in **Block B** for all participants. The middle quartile indicates the median value of all participants and the whiskers indicate the most extreme values that are not considered outliers.

incongruent outcome conditions have a longer tail as result of longer duration. Interestingly for the *incongruent outcome* conditions, the turtuosity appears to keep increasing with some oscillation, suggesting that the movement is more localized and possibly is of an oscillatory character.

C.4 Conclusions

In this appendix, we present our results from our attempts to find implicit measures of embodiment, such as behavioral or physiological changes to different conditions in the virtual reality environment.

We did not find any significant differences in the physiological responses to a threat directed to the virtual hand. We found that the reported sense of ownership significantly decreased in the *full arm* - *incongruent movement* condition in **Experiment 2**, which we

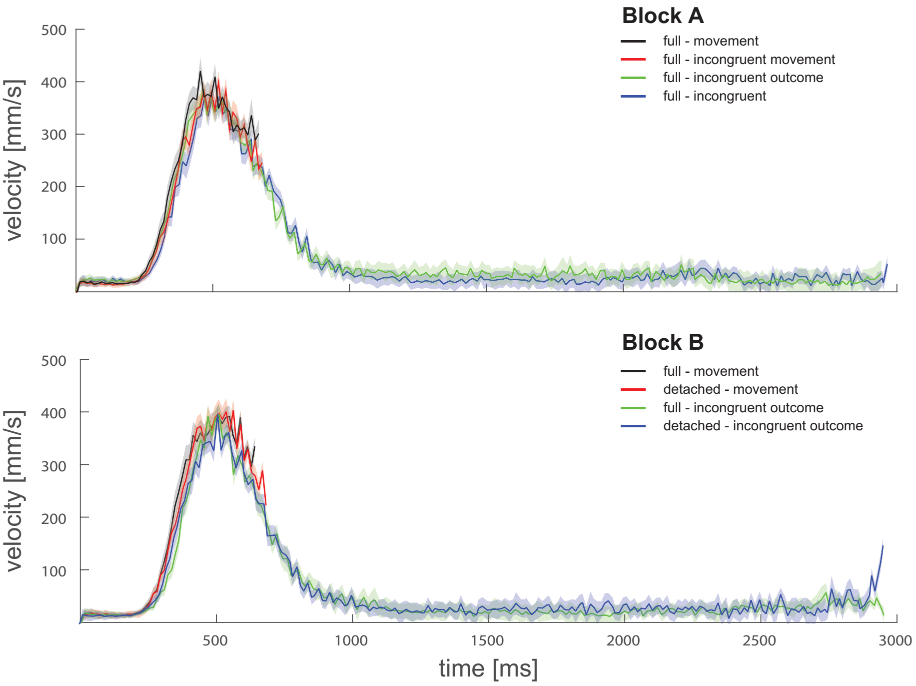

Figure C.6: **Average instantaneous velocity for Blocks A and B from Experiment 3**. (A) Average instantaneous velocity for *full arm - movement* (black), *full arm - incongruent movement* (red), *full arm - incongruent outcome* (green), and *full arm - incongruent* (blue) conditions in **Block A** for all participants, (B) Average instantaneous velocity for the *full arm - movement* (black), *detached hand - movement* (red), *full arm - incongruent outcome* (green), and *detached hand - incongruent outcome* (blue) in **Block B** for all participants. Shaded area represents the standard deviation of the mean.

would expect to be accompanied with a decreased reaction to the threat. This could be due to several factors. Firstly, our *full arm - incongruent movement* condition, even though it cause a significant decrease in reported sense of ownership, could not be causing a strong enough decrease in feeling of ownership. In studies were discontinuity caused a decrease in the GSR, they found a decrease of one point in the reported median ownership scores, that was accompanied by a decrease in the amplitude in GSR (Tieri et al., 2015a).

Another possible explanation for the lack of difference is that hands were too close together and there was the need for a larger distance between them. Our setup had the limitation that we could not make the separation larger than ten centimeter without compromising the tracking. This might have caused that when the knife felt on the participants hand, it was still within the peripersonal space of their hand, which caused

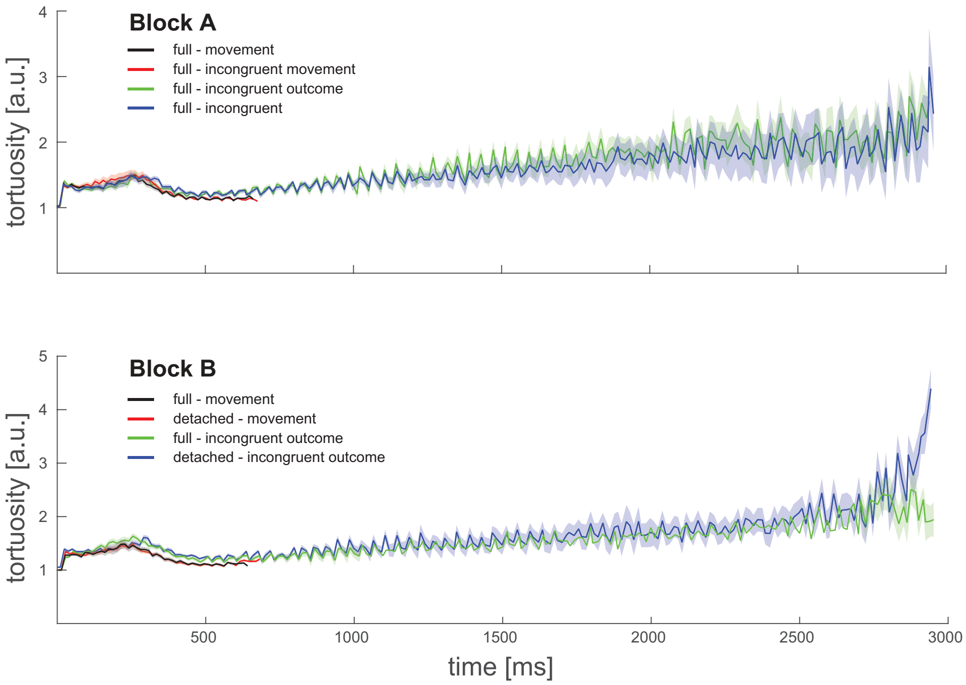

Figure C.7: **Average turtuosity for Blocks A and B from Experiment 3**. (A) Average turtuosity for *full arm - movement* (black), *full arm - incongruent movement* (red), *full arm - incongruent outcome* (green), and *full arm - incongruent* (blue) conditions in **Block A** for all participants, (B) Average turtuosity for the *full arm - movement* (black), *detached hand - movement* (red), *full arm - incongruent outcome* (green), and *detached hand - incongruent outcome* (blue) in **Block B** for all participants. Shaded area represents the standard deviation of the mean.

them to react in the same way. In favour of this hypothesis, we also had a condition in which the knife felt into the position of the real hand (which was ten centimeters to the right of the virtual hand) (i.e., *threat displaced* condition). The comparison with the knife falling in the virtual hand yield no significant difference in the amplitude of the response [**Figure C.1**].

Within the behavioral measures, we looked at the proprioceptive drift in conditions where the virtual and physical hand were either in the same position or separated by ten centimeters. Following previous studies, we would have expected a proprioceptive displacement in the *full arm - displacement* and *detached hand - displacement* towards the virtual hand. However, we did not find any significant effect on the perceived position of the real hand. In part, this might be due to the fact that the participants are actively controlling the virtual hand, and therefore, they are moving their own hand. Thus, constantly updating their own proprioceptive information.

We also looked at some kinematic parameters that could act as proxy for the senses of ownership and agency. We observed that average wave duration is larger in the *incongruent outcome* conditions, which was to be expected given the experimental design. Interestingly, the maximum displacement was larger in the *incongruent outcome* conditions, suggesting that the participants reached further in the environment to achieve the goal. For the first 600 ms the profiles of velocity and turtuosity did not qualitatively differ among any of the conditions, suggesting that the ballistic movement that the participants perform is not influenced the perceived ownership or agency. For the *incongruent outcome*, we see an increase in turtuosity and oscillations in the trajectories by the later part of the wave. Together with what can be observed in the example traces suggest that the participants perform a series of short and fast movement that could relate to frustation to the lights not responding.

D | Sociodemographic Data

D.1 Overview

In the present section, we present the data regarding the sociodemographics aspects of the participants in **Experiment 2** and **3**. In the Experiment 1, no information on the sociodemographics of the participants was collected.

As we reported at the end of **Chapter 4**, we observed a wide range of responses in the reported sense of ownership, and that these responses affected the subsequent response to different perturbations (e.g. body discontinuity or incongruent movement to the participant's movements). Thus, we explored whether the ownership in the *full arm - movement* condition was affected by any of the collected sociodemographic measures. We asked the participants for their gender, as we were adapting the hand model to the reported gender. It is possible that different levels of similarity between the female and male hand models could be affecting the reported sense of ownership. Secondly, we assessed whether the gaming habits and the experience with VR environments could be affecting the experience of the virtual hand. We hypothesized that those who often played video-games or were already familiar with VR environments could be more receptive to the experience. Finally, we also checked whether the reported sense of ownership was related to age.

At the end of this chapter, an example sheet can be found both in English and Portuguese.

D.2 Summary of the sociodemographic data

D.2.1 Experiment 2

Table D.1 shows all the data for the 37 participants that were analyzed for **Experiment 3**. We analyzed the data regarding the gender (Column A), age (Column B), gaming habits (Column D), and prior VR experience (Column E) of the participants. Regarding gender, 23 identified as females (62.16%) and 14 as males (37.84%). The mean age of the participants was 27.59 (standard deviation = 6.99) with a range between 18 and 45 years. Regarding VR use, most of the participants had not had any contact with VR prior to taking part in the study. Specifically, for 26 participants (70.27%) it was their fist contact with VR, 8 (21.62%) had already used it before, while 3 (8.11%) used VR on a regular basis. As for gaming habits, most of the participants were not regular video-games players, 20 participants (54.04%) reported not playing video-games, while 2 participants (5.41%) reported playing seldomly. From the remaining 15 participants, 5 participants (13.51%) reported playing monthly, 6 participants (16.22%) reported playing weekly, and 4 participants (10.81%) reported playing on a daily basis.

	A	B	C	D	E	F
01	M	22	4	4	2	50
02	M	22	3	5	1	20
03	F	35	6	1	1	71
04	F	18	2	3	2	90
05	F	33	5	1	1	80
06	M	27	5	1	1	100
07	F	22	4	1	1	46
08	F	38	6	1	2	90
09	M	38	4	1	1	84
10	M	32	4	4	1	88
11	M	25	4	2	1	100
12	F	25	4	5	2	100
13	F	21	4	3	1	100
14	F	25	4	1	1	40

15	F	29	6	1	1	90
16	M	19	4	5	1	86
17	F	35	6	1	1	83
18	M	30	5	4	1	100
19	F	20	2	3	1	60
20	F	19	2	1	1	75
21	F	20	4	1	1	60
22	F	29	4	2	1	50
23	F	23	4	1	1	100
24	F	22	1	1	2	100
25	M	26	4	4	1	20
26	F	43	4	1	1	100
27	M	20	4	3	1	67
28	M	32	5	1	2	100
29	F	31	4	3	3	42
30	F	25	5	1	1	87
31	M	27	5	4	2	50
32	M	22	4	4	1	33
33	F	31	4	1	2	100
34	F	37	6	1	1	67
35	M	22	5	5	3	100
36	F	31	5	1	1	100
37	F	45	5	1	3	78

Table D.1: **Summary of the sociodemographic data for Experiment 2**, (A) **Gender**, (B) **Age** in years, (C) **Education Level completed**, where 1=no schooling, 2=high school, 3=college credit, no degree, 4=bachelor's degree, 5=master's degree, 6=doctorate degree (D) **Gaming Experience**, where 1=do not play video-games, 2=seldom play video-games, 3=once per month, 4=once per week, 5=daily (E) **Experience with VR**, where 1=first time user, 2=already used, 3=regular user, (F) **Edinburgh Handedness Inventory results**.

D.2.2 Experiment 3

Table D.2 shows all the data for the 43 participants that were analyzed for **Experiment 3**. We analyzed the data regarding the gender (Column A), age (Column B), gaming habits (Column D), and prior VR experience (Column E) of the participants. Regarding gender, 24 identified as females (55.81%) and 19 as males (44.19%). The mean age of the participants was 28.83 (standard deviation = 5.35) with a range between 21 and 42 years. Regarding VR experience prior to the participation, we found that 19 participants (44.19%) had not had previous contact with VR before taking part in the experiment, 24 participants (55.81%) had already used VR, while none used VR on a daily basis. As for gaming habits, we found that 15 (34.88%) participants said they did not play, 11 (25.58%) play seldomly video-games, 8 (18.61%) reported to play monthly, another 8 (18.61%) reported playing once per week, while 1 (2.32%) reported playing daily.

	A	B	C	D	E	F
01	M	23	3	4	1	70
02	F	24	4	3	2	87
03	F	23	3	3	2	90
04	F	40	4	1	1	44
05	M	29	4	4	1	100
06	M	29	3	4	2	100
07	F	25	4	3	2	100
08	M	23	4	2	2	60
09	F	22	3	2	2	35
10	M	24	4	1	1	82
11	F	27	4	2	2	70
12	F	34	5	2	2	20
13	F	34	3	2	1	100
14	M	33	4	3	2	100
15	F	28	4	1	2	70
16	M	27	2	4	1	100
17	M	25	3	3	1	25
18	M	28	4	3	2	100
19	F	27	4	1	1	100
20	M	24	3	1	1	100
21	F	26	3	1	1	100

22	M	33	2	1	2	100
23	M	36	3	1	2	6
24	F	26	4	1	2	100
25	M	31	3	4	2	25
26	F	33	5	1	2	65
27	M	28	3	5	2	100
28	M	21	2	2	2	50
29	F	37	3	2	1	100
30	F	24	2	4	1	80
31	F	37	3	2	1	90
32	F	29	4	1	2	48
33	M	40	5	1	2	88
34	M	31	4	2	2	42
35	F	24	3	2	2	50
36	F	33	5	3	1	88
37	F	24	4	1	1	50
38	F	42	3	4	1	60
39	F	27	4	2	1	48
40	M	30	4	3	1	60
41	M	22	2	4	2	70
42	F	27	4	1	1	50
43	F	30	4	1	2	85

Table D.2: **Summary of the sociographic data for Experiment 3**, (A) **Gender**, (B) **Age** in years, (C) **Education Level completed**, where 1=no schooling, 2=high school, 3=bachelor's degree, 4=master's degree, 5=doctorate degree (D) **Gaming Experience**, where 1=do not play video-games, 2=seldom play video-games, 3=once per month, 4=once per week, 5=daily (E) **Experience with VR**, where 1=first time user, 2=already used, 3=regular user, (F) **Edinburgh Handedness Inventory results**.

D.3 The reported sense of ownership was unaffected by the sociodemographics characteristics of the individuals in both studies

D.3.1 Experiment 2

We compared whether there was a difference in the *full arm* - *no movement* depending on the gender, gaming habits, and VR experience, and whether the reported sense of ownership correlated with age.

We found no significant difference in the ownership scores in the *full arm* - *no movement* between female (median=4.50, IQR=2.25) and male (median=4.37, IQR=2.25) (Wilcoxon rank-sum test; Z=-0.12, p=0.90) [**Figure D.1A**]. We found a weak correlation between age and the reported ownership scores in the *full arm* - *no movement* (Spearman ρ=0.33, p=0.04) [**Figure D.1B**].

We divided the participants according to their gaming habits: those that were not regular video-game players (i.e. the participants that replied 1 or 2 in column D, n=22) (median=4.87, IQR=2.25) and those that were regular video-game players (i.e. replied 3, 4 or 5 in column D, n=15) (median=4.25, IQR=2.00). We found no significant difference between both groups in the *full arm* - *no movement* condition (Wilcoxon rank-sum test; Z=0.09, p=0.90) [**Figure D.1C**].

Additionally, we divided the participants into two groups depending on whether the had any previous contact with VR prior to the experiment (i.e. the participants that replied 1 in column E, n=26) and those that already had had previous contact with any form of VR systems (i.e. replied 2 or 3 in column E, n=11). We found a marginally significant higher reported ownership scores in the *full arm* - *no movement* between the first-time VR users (median=3.88, IQR=1.06) and the VR users group (median=4.84, IQR=1.28) (Wilcoxon rank-sum test; Z=-1.93, p=0.05) [**Figure D.1D**].

Interestingly, no difference were found in the *full arm* - *movement* condition for gender (Wilcoxon rank-sum test; Z=0.42, p=0.67), gaming habits (Wilcoxon rank-sum test; Z=0.74, p=0.45), or prior VR experience (Wilcoxon rank-sum test; Z=-1.61, p=0.10) [**data not shown**].

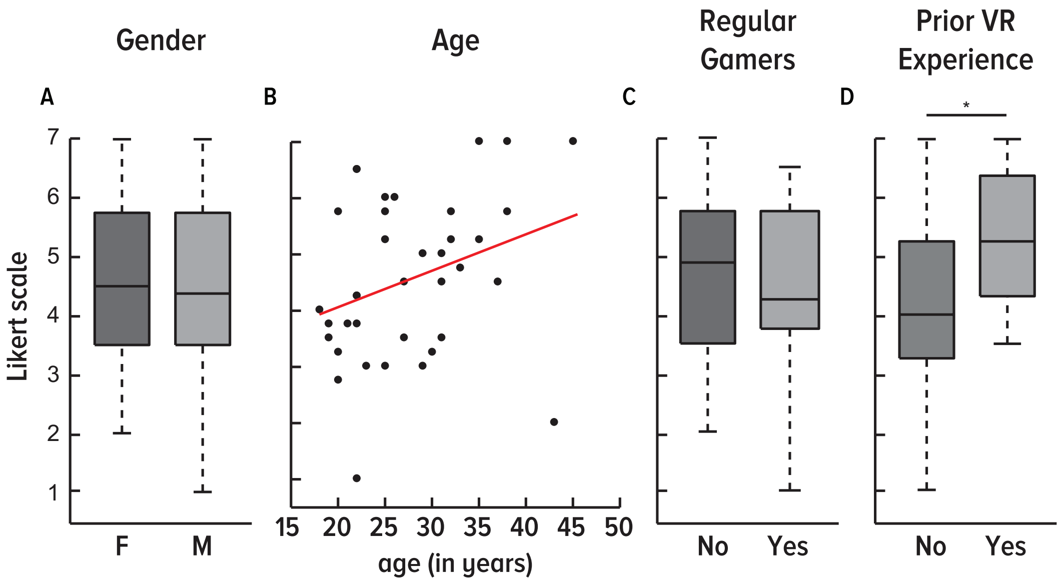

Figure D.1: **The reported sense of ownership did not depend on the gender or gaming habits, but was marginally related to age and prior VR experience in Experiment 2**. (A) There was no significant difference between the ownership scores reported in the males (darker shade of grey) and the females (lighter shade of gray) in the *full arm* - *no movement* (p=0.90), (B) A weak correlation was found between the age in years and the reported ownership scores in the *full arm* - *no movement* condition (ρ=0.33, p=0.04), (C) The reported sense of ownership was unaffected by the gaming habits in the *full arm* - *no movement* condition (p=0.90), (D) The participants that had previous contact with VR prior to the experiment marginally reported higher levels of ownership compared to those that had not used VR before (p=0.05).

Finally, we compared whether having active control over the virtual hand had a different effect ton the participants depending on the aforementioned categories. When comparing *full arm* - *no movement* and *full arm* - *movement* conditions, neither the females (Wilcoxon signed-rank; Z=0.22, p=0.82) or the males (Wilcoxon signed-rank; Z=0.00, p=0.52). Also, no differences were found in those who declared not to be regular gamers (Wilcoxon signed-rank; Z=0.15, p=0.87) or in those who are usual videogame players (Wilcoxon signed-rank; Z=0.00, p=0.37). Finally, no difference was found between the *full arm* - *no movement* and the *full arm* - *movement* conditions in the first time VR users (Wilcoxon signed-rank; Z=0.31, p=0.75) or those who had prior contact with VR (Wilcoxon signed-rank; Z=0.00, p=0.53) [**data not shown**].

D.3.2 Experiment 3

We took the mean between the blocks of the *full arm* - *movement* conditions in **Experiment 3** as we found no significant difference between them and they were strongly correlated [**Figure 5.9C**].

First, we checked whether there was a difference in the ownership scores in the *full arm* - *movement* condition when we split the participants data by gender. We found no significant difference between the females (median=5.87, IQR=3.00) and the males (median=4.37, IQR=2.56) in the reported ownership scores (Wilcoxon rank-sum test; Z=-1.60, p=0.10) [**Figure D.2A**]. We found no significant correlation between the age of the participants and the reported ownership scores in in *full arm* - *movement* (Spearman ρ=0.18, p=0.25) [**Figure D.2B**].

We divided the participants according to their gaming habits: those that declared not to be regular video-game players (i.e. those that replied 1 or 2 in column D, n=26) (median=6.06, IQR=1.53) and those that were regular video-game players (i.e. those that replied 3, 4, or 5 in column D, n=17) (median=3.87, IQR=2.50). We found a significant difference between both groups in the *full arm* - *movement* condition (Wilcoxon rank-sum test; Z=2.82, p=0.004) [**Figure D.1C**].

We divided the participants into two groups, those that had not had any previous contact with VR prior to the experiment (i.e. replied 1 in column E, n=19) and those that already had had contact (i.e. replied 2 or 3 in column E, n=24). We found no significant difference in the reported ownership scores in the *full arm* - *movement* between the first-time VR users (median=5.25, IQR=2.65) and the VR users group (median=5.00, IQR=3.06) (Wilcoxon rank-sum test; Z=-0.31, p=0.75) [**Figure D.1D**].

D.4 Conclusions

In both studies shown in this section, we found that the reported sense of ownership varied in some factors. However, these factors were inconsistent across the two studies: in **Experiment 2** both age and experience with VR seemed to be related to the reported ownership scores, while in **Experiment 3** a difference in the reported ownership scores was found depending on the gaming habits.

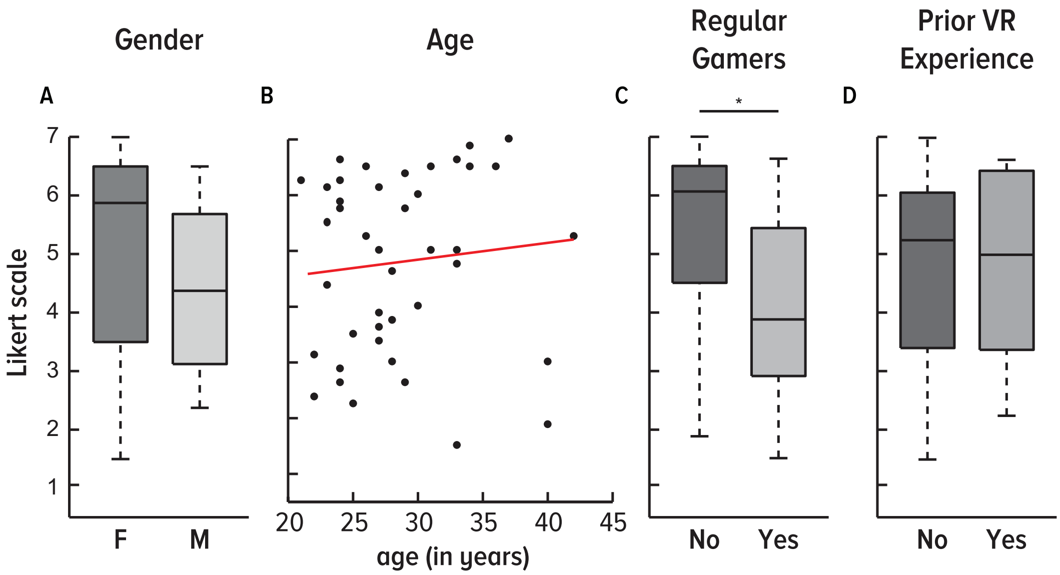

Figure D.2: **The reported sense of ownership did not depend on the gender, age or prior VR experience, but depended on the gaming habits in Experiment 3**. (A) There was no significant difference between the ownership scores reported in the males (darker shade of grey) and the females (lighter shade of gray) in the *full arm - movement* (p=0.10), (B) We found no correlation between the age in years and the reported ownership scores in the *full arm - movement* condition (ρ=0.18, p=0.25), (C) The reported sense of ownership depended on the gaming habits of the participants *full arm - movement* condition (p=0.004), (D) The was no significant difference in the reported sense of ownership in the *full arm - movement* condition between the first-time VR users and those that had used VR prior to the experiment (p=0.75).

We found no difference between the genders in the reported sense of ownership in the *full arm - movement* condition. This results was particularly interesting to us. In the free-form reports at the end of the experiments, the hand was perceived more similar to their real hand than females. Usually, females report that the nails and the shape of the fingers did not resemble their own.

We expected to find a stronger correlation between age and the reported ownership. The results from a preliminary study (not reported in this dissertation) suggested that age was playing a role in the mVHI. In that study, we divided the participants according to age and found that older participants reported lower feelings of ownership over the virtual hand, compared to their younger peers. Those results were consistent with another study that reported that older individuals were more resistant to the experience of a full-body illusion (Serino et al., 2018). However, this is not the case in the results presented in this appendix, where we either report a weak positive correlation or none at all.

We did not find a consistent effect of the gaming habits and the previous with VR environments. In **Experiment 2**, those who had previous experience with VR seemed to report higher values of feelings of ownership, while no differences were found in gaming habits. In **Experiment 3**, regular gamers reported lower ownership scores, while no differences were found in prior VR experience. These results suggest that, while does features might have an impact on feelings of ownership over a virtual hand, they might be as an indirect effect of other interpersonal differences.

Overall, we found no consistent relationship between any of the collected sociodemographic data and the reported feelings of ownership in the *full arm - movement*. However, it is interesting to explore which personal factors might be affecting the experience of the mVHI. Future studies might include collecting a wider range of personal information to explore these relationship or to constrict the inclusion criteria in the experimental groups.

SOCIO-DEMOGRAPHIC

Gender: ☐ F ☐ M

Date of birth: ______________

Education level:
- ☐ No schooling completed
- ☐ High school completed
- ☐ College credit, no degree
- ☐ Bachelor’s degree
- ☐ Master’s degree
- ☐ Doctorate degree

Gaming experience
- ☐ I usually don’t play any video-games
- ☐ I seldom play video-games
- ☐ I usually play video-games once per month
- ☐ I usually play video-games once per week
- ☐ I usually play video-games everyday

Experience with Virtual Reality:
- ☐ First time using virtual reality
- ☐ I have used virtual reality before
- ☐ I usually use/work with virtual reality

DADOS SOCIODEMOGRAFICOS

Sexo: ☐ F ☐ M

Data de nascimento: _______________

Nacionalidade: __________________

Nível educacional:
☐ Sem escolaridade concluída
☐ Ensino médio concluído
☐ Licenciatura/Graduado
☐ Mestrado
☐ Doutoramento

Experiência de jogo:
☐ Eu normalmente não jogo vídeo-jogos
☐ Eu raramente jogo vídeo-jogos
☐ Eu costumo jogar vídeo-jogos, uma vez por mês
☐ Eu costumo jogar vídeo-jogos uma vez por semana
☐ Eu costumo jogar vídeo-jogos todos os dias

Lateralidade:
☐ Destro
☐ Canhoto
☐ Ambidestro

Experiência com realidade virtual:
☐ Este seria o meu primeiro contacto
☐ Eu já tive contacto prévio com realidade virtual
☐ Eu actualmente trabalho com realidade virtual

E | Peer-reviewed Publications

frontiers
in Human Neuroscience

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Toward a Molecular Profile of Self-Representation

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Feeling embodiment over our body or body part has a major role in the understanding of the self and control of self-actions. Even though it is crucial in our daily life, embodiment is not an homogenous phenotype across population, as quantified by implicit and explicit measures (i.e., neuroimaging or self-reports). Studies have shown differences in neuropathological conditions compared to healthy controls, but also across healthy individuals. We discuss examples of self-perception differences, and the molecular origin of embodiment, focusing on clinical cases, during the first and second section. We then discuss two important questions in this molecular-to-embodiment relationship: (i) which are the molecular levels (and their associated techniques) that can be relevant to embodiment, and (ii) which are the most adequate experiments to correlate molecular profiles and embodiment quantification across individuals. Potential answers for both questions will be outlined during the third and fourth sections, respectively, in order to design a framework to study the molecular profile of body embodiment.

Keywords: self-representation, OMICS techniques, sense of agency, sense of ownership, proteomics

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EMBODIMENT AND VARIABILITY

Sense of embodiment refers to the feeling of owning and controlling a body (Kilteni et al., 2012), leading to the believe that it is the own body. This contributes to generate the representation of the bodily-self in the brain. Self-representation has two distinct subcomponents, sense of ownership (i.e., attributing a body or body part to the self) and sense of agency (i.e., having sense of control over the action). The former arises from the combination of multiple information sources, such as visual or tactile (Gallagher, 2000), the latter arises when the efferent copy of an intention of an action and its actual sensory outcome match (Wolpert and Miall, 1996; Gallagher, 2000).

Since Botvinick and Cohen developed the Rubber Hand Illusion paradigm (Botvinick and Cohen, 1998), the study of self-representation has grown interest in the field of cognitive sciences. The way the bodily-self is represented becomes crucial for the interaction of the individual with the environment and with other individuals. Moreover, this relationship is not unidirectional, as this self-representation is updated with the information obtained from the interaction with external sources. By means of the sensory organs, the brain receives multisensory information that is used to update and change self- and other-representation constantly. Due to this plasticity the process is malleable experimentally, thus generating embodiment over fake body parts or full bodies (Botvinick and Cohen, 1998; Lenggenhager et al., 2007; Slater et al., 2008). The effect of these changes has not only been reported behaviorally, but also through neuroimaging studies using fMRI. It has been shown that changes in the representation of the self caused experimentally (i.e., rubber hand illusion, or full body swap illusion) cause changes in activity in multisensory brain areas, when compared to conditions in which there is no reported illusion by the subjects (Ehrsson et al., 2005; Petkova et al., 2011). The implication of these areas (i.e., premotor cortex, intraparietal cortex, and putamen) suggests the importance of the multisensory integration on the feeling of ownership.

More importantly, embodiment has been shown to be affected by neurodevelopmental disorders (e.g., autism spectrum disorders) and in several psychiatric and neurological conditions (see a summary in **Table 1**). Autism spectrum disorder patients have been shown to be less susceptible to feel ownership of a rubber hand (Palmer et al., 2015). Also, other experimental paradigms reported an altered sense of embodiment over the own body in the case of autistic patients (Conson et al., 2015), as their findings suggest that these patients rely less on one's own information to infer states over another person or external object. On the other hand, schizophrenic patients perceive other-generated actions as their own in a bimanual interference task, thus presenting an increased sense of agency (Garbarini et al., 2016). This could be due to an alteration in the comparison between estimation and actual sensory feedback of the action. Another case is the one of hemiplegic patients that can feel ownership over another person performing an action, even when the arm is in the position of the limb over which they have no control (Garbarini et al., 2015). Moreover, some dementias (e.g., frontotemporal dementia) can also affect patient's sense of ownership (measured by the rubber hand illusion) and sense of agency (using a test for the attribution of an action) (Downey et al., 2014). Interestingly, Alzheimer's patients seem to have a similar self-perception than their healthy counterparts, but with defects in the attribution of self- vs. non-self memories (Bond et al., 2016). Finally, anorexia nervosa causes profound alterations in body image perception (Keizer et al., 2011, 2012) and patients with Medically Unexplained Symptoms (MUS) also show defects in body representation (Miles et al., 2011).

Nonetheless, variability in phenotypes related to embodiment can also be seen in healthy subjects, which, for example, have different levels of reported sense of ownership and agency when embodying a virtual limb. Moreover, the response to modulations to the embodied virtual limb is also different depending on the participant (Brugada-Ramentol et al., in preparation). In addition, tactile discrimination is variable in non-psychotic subjects, an effect related to schizotypic differences among subjects (Lenzenweger, 2000). The existence of these basal differences in addition to the embodiment alterations observed in pathological conditions suggest the presence of genetic and molecular risk factors associated to embodiment defects. In addition, the heterogeneity of phenotypes observed in the different disorders points to specific components of embodiment that can be impaired, and to different molecular and neural pathways that can affect to these components.

POSSIBLE EMBODIMENT-RELATED MOLECULAR MECHANISMS

The variability across population observed in embodiment can be due to two specific sources: the genetic differences among individuals and the unique environmental or external factors that modulate the physiology of each subject. We have not found any reports on possible genetic factors altering the sense of embodiment in healthy individuals, but there are specific mutations in patients affected by frontotemporal dementia that correspond to self-perception alterations. For example, the presence of C9ORF72 or MAPT mutations correlate to different embodiment defects (Downey et al., 2014). In addition, we have previously mentioned that schizophrenic patients have an increased sense of agency (Garbarini et al., 2016) and several genetic factors have been associated to this condition using genome-wide association studies (GWAS) (Schizophrenia Working Group of the Psychiatric Genomics Consortium, 2014; Sekar et al., 2016). Interestingly, autism spectrum disorders, which also affect embodiment, share some of these genetic mutations in the following genes: APH1A, CNOTC, CSMDC, CUL3, CYPC7AC, CYP26BC, EPHX2, LRPC, MAPK3, MEF2C, MPP6, MYOC5A, NISCH, PBRMC, PRKDC, RIMS1, TSNAREC, WDR55, and ZNF80HA (Schizophrenia Working Group of the Psychiatric Genomics Consortium, 2014). Other mutations from neuropathological conditions (see **Table 1** for a summary) can also be obtained, and, therefore, future studies could assess the overlapping mutations among these conditions that can be linked to specific alterations in embodiment, and

TABLE 1 | Summary of the neuropathological conditions affecting self-perception and embodiment.

Condition	Phenotype	Genes altered	References
Schizophrenia	Increased sense of agency in a bimanual interference task	More than 100, not specifically associated to embodiment	Schizophrenia Working Group of the Psychiatric Genomics Consortium, 2014; Sekar et al., 2016
Autism Spectrum Disorders	Decreased sense of ownership in rubber hand illusion	More than 100, not specifically associated to embodiment	Schizophrenia Working Group of the Psychiatric Genomics Consortium, 2014
Hemiplegia	Increased sense of ownership over an external arm	ATP1A3	Heinzen et al., 2012
Frontotemporal dementia	Increased sense of ownership in rubber hand illusion and tactile discrimination	C9ORF72, MAPT	Downey et al., 2014
Alzheimer	Deficit for recognizing self voice	APP, PSEN1	Bond et al., 2016
Anorexia Nervosa	Altered tactile estimation	ESRRA, HDAC4	Cui et al., 2013
Medically Unexplained Symptom (MUS)	Reduced sense of ownership in rubber hand illusion	NA	

their relationship to self-perception differences in healthy subjects.

From a physiological point of view, the diverse origins of embodiment variability could converge into similar outputs. For example, a genetic change or a pharmacological treatment might target to different molecules, but at a downstream level they might merge into a common pathway. As embodiment is a complex phenotype requiring several cognitive components, it is evident that multiple pathways might be involved. The use of neuronal imaging techniques like fMRI will be needed to assess how molecular differences can correlate with brain activation patterns, as some of these pathways will converge at the neural level, as shown for the oxytocin receptor epigenetic changes (Puglia et al., 2015). Nevertheless, in this article we only focus on the molecular pathways for two reasons: (i) the efficiency of state-of-the-art molecular techniques to obtain a complete picture of the physiological state of the subject at different biological levels, and (ii) the simplicity of these methods for scientists in fields other than molecular biology. In summary, our key point is that we can study the differences in embodiment looking for intermediate, molecular outputs instead of genetic and environmental differences, much more complex and uncontrollable. This studies could be complementary to the analyses of neural circuitry.

TECHNIQUES FOR MOLECULAR PROFILING OF EMBODIMENT

Embodiment is a complex phenotype in which several molecular pathways and neural circuits probably contribute to a proper self-representation. We thus expect the implication of several molecules and circuits at the same time in self-representation variability. This argues for the use of *-omic* techniques to obtain system-level results using a single sample from an individual. The combination of several of these *-omic* techniques will also increase the reliability of the markers obtained, reducing the amount of false positives (Ge et al., 2003).

We will describe three different classes of *-omic* techniques, depending on their functional level within the body. First, genomic techniques try to assemble the complete set of DNA of an organism. As every cell in the body has the same genome, individual samples can be obtained from simple procedures like either saliva or blood extraction. Massive DNA sequencing would be usually performed in an external facility, with a minimal sample preparation, and with a cost decreasing due to technical advances. Its main problem is the distance between DNA sequence and its actual cellular function, like neuronal activation. Therefore, the effect observed in cognitive phenotypes is usually very low, and thousands of subjects need to be studied in order to find significant associations with genetic factors (Sekar et al., 2016).

As a second level of *-omic* techniques, we include epigenomics and transcriptomics. These normally use sequencing as in genomics, so the complete set of chromatin (epigenetic) and expression (transcriptional) states of a sample, respectively, can be obtained. We can describe both results as regulatory profiles of an individual, because epigenomic and transcriptomic changes correspond to variations in the physiology of the subject. This is their main difference respect to genomics, resulting in a more functional level that can reflect significant correlations even in cognitive phenotypes. Their cost and simplicity is similar to genomics, but they also have a clear disadvantage: epigenetic and transcriptional changes are tissue-specific, so you need to either access brain samples or analyze the indirect changes produced in other tissues like blood or saliva. Nevertheless, efforts are made in order to assess neuroepigenetic changes using brain imaging (Yeh et al., 2013; Wey et al., 2016).

Finally, the third level of *-omic* techniques are proteomics and metabolomics. The set of proteins and metabolites, respectively, of a sample cannot be obtained by sequencing as in the former cases. The cost is usually higher, the protocols needed to prepare the samples are not as simple, and it is sometimes difficult to find an external facility that can analyze the samples. Nevertheless, proteomics and metabolomics have three strong advantages. They are regulated like in the case of epigenomics and transcriptomics, they are often secreted into fluids like blood or saliva, so we can use a simple extraction, and, in addition, proteins and metabolites are usually final outputs of the organism, so they are very close to the real function that we want to measure. In this case, some metabolomic approaches have deciphered brain neurophysiology and connectomics (Piomelli et al., 2007; Ivanisevic et al., 2014).

MOLECULAR-TO-EMBODIMENT WORKFLOW

When studying the behavioral component of embodiment, there is an increasing need to rely more on physiological and implicit measures, and less on the use of explicit measures (e.g., self-report statements). In this case, molecular assessment could be used complementary to implicit behavioral measures of body ownership and sense of agency (i.e., proprioceptive drift, threat to virtual body or body-part, and intentional binding) and their changes related to embodying over a fake body part. They can also become complementary to the already existing imaging studies.

Previous studies has shown that people feel ownership over a virtual arm or body in experimental conditions that allow first-person perspective (Slater et al., 2010), shape and texture of the fake hand (Haans et al., 2008), congruent position of the hand (Tsakiris and Haggard, 2005), among others. Moreover, recently there has been an increasing use of virtual reality. For a potential experiment to study embodiment using molecular techniques, we would suggest taking advantage of virtual reality. This technique allows to create environments with ecological characteristics that resemble the real environment, while still being able to control for experimental variables (Tarr and Warren, 2002; Parsons, 2015). We propose that tissue samples (saliva or blood) could be extracted before exposure to the experiment of embodying a virtual arm; this will allow to study possible correlations with basal proteomic levels of each participant and the explicit self-report answers, implicit measures, and neuronal imaging patterns. Moreover, samples should also be extracted after exposure, allowing to compare changes in proteomic content before and after exposure to the experiment. For this end, we would suggest two experimental groups. The control group would be exposed to a virtual reality environment, measuring their basal capability to embody an external object as part of their own representation, without any modulation to decrease this embodiment. Moreover, a second group would be necessary, in which the embodiment over the virtual arm would be diminished using self-perception modulations. Finally, we would look for (i) molecular markers for the basal differences in the embodiment of the virtual arm in all participants; and (ii) molecular markers for the embodiment differences between groups with and without manipulation of self-perception, as a result of the manipulations that were applied to the virtual arm with the intention to reduce the embodiment over it. Furthermore, these embodiment differences could be assessed by explicit measures like self-reports or implicit techniques like brain activation pattern changes (Ehrsson et al., 2005; Petkova et al., 2011). Indubitably, we are aware that this kind of experiment would require a large number of subjects to have a significant quantity of data for each of the groups. Furthermore, we suggest that these studies could try to manipulate the sensory input and feedback in neuropathological conditions known to alter embodiment and to compare them to healthy controls.

Moreover, self-perception in healthy subjects could be altered in a way that resembles a specific neurological disorder. In this context, the use of *-omic* techniques to study the molecular profile of embodiment would benefit in understanding the effect of manipulations on the bodily self-representation. Additionally, it has been shown that the hormone oxytocin can modulate judgment over self-owned vs. other-owned objects (Wu et al., 2013). Therefore, we suggest to use the already proposed experiment combined with its treatment to improve sense of ownership and agency over the virtual arm. In this context, considering the virtual arm could be felt as an external object that is included into the self-representation. Therefore, the treatment with hormones like oxytocin should improve embodiment over these external objects. In addition, oxytocin treatments have been shown to alter the activity of specific brain areas using fMRI (Bethlehem et al., 2013). Finally, *-omic* techniques should help to assess the specific molecular changes in ownership and agency that are related to the neural changes after the administration of the hormone.

CONCLUSION

In conclusion, the study of self-representation is a growing field in both healthy and clinical populations, due to the alterations that can be observed during pathological or experimental conditions. To this day, the use of imaging approaches is providing a greater insight to the study of embodiment, adding relevant brain activity information to behavioral assays. In addition to these, we propose that molecular profiling of healthy and clinical subjects could offer a new entry point to study embodiment. The combination of state-of-the-art techniques from different scientific fields, such as virtual reality, neuroimaging and *-omic* methods, is a promising approach to understand self-representation from a systems perspective.

AUTHOR CONTRIBUTIONS

GGdP, ÁCR, and VBR wrote the manuscript. ÁCR and VBR developed the idea of the manuscript.

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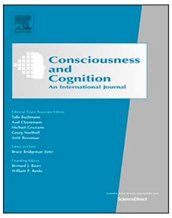

Active control as evidence in favor of sense of ownership in the moving Virtual Hand Illusion

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ABSTRACT

The sense of ownership, the feeling that our body belongs to ourselves, relies on multiple sources of sensory information. Among these sources, the contribution of visuomotor information is still debated. We tested the effect of active control in the sense of ownership in the moving Virtual Hand Illusion. Participants reported sense of ownership and sense of agency over a virtual arm in which we manipulated the morphological congruence of the hand and the visuomotor information. We found that congruent active control enhanced and maintained the reported sense of ownership over a hand that appeared detached from the body, but not in a morphological congruent limb. Also, incongruent active control, achieved by adding noise to the trajectory of the movement, decreased both reported sense of agency and ownership. Overall, our results are consistent with a framework in which active control acts as evidence for eliciting a sense of ownership.

1. Introduction

> "What is more important for us, at an elemental level, that the control, the owning and operation, of our own physical selves? And yet it is so automatic, so familiar, we never give it a thought." (Sacks, 1985)

The integration of multiple sources of sensory information creates and constantly updates the representation of the body in the brain (Gallagher, 2005; Metzinger, 2003). Multisensory integration, of both exteroceptive and interoceptive information, is crucial for the sense of ownership (Gallagher, 2005; Longo, Schüür, Kammers, Tsakiris, & Haggard, 2008; Makin, Holmes, & Ehrsson, 2008), the feeling that a body or body part belongs to the self (Gallagher, 2000; Longo et al., 2008).

Manipulating the sensory signals received by the body can elicit a sense of ownership over a fake body part. Such is the case of the Rubber Hand Illusion (RHI) paradigm (Botvinick & Cohen, 1998). Participants are presented with a rubber hand in an anatomically plausible position, while their real hand is hidden from their sight. Visuotactile stimulation on both the real and the rubber hand generates a sensory conflict between the felt tactile stimulation on the hidden real hand and the seen stimulation on the rubber hand. Differential integration of the visual, tactile, and proprioceptive sensory information resolves this conflict. When the stimulation is synchronous, visual information dominates, resulting in an illusion of ownership over the fake limb (Botvinick & Cohen, 1998; Makin et al., 2008; Tsakiris, 2010). However, this illusion is abolished by both temporal (Botvinick & Cohen, 1998; Perez-Marcos, Sanchez-

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Vives, & Slater, 2012) and spatial asynchrony (Kammers, Longo, Tsakiris, Dijkerman, & Haggard, 2009).

A Bayesian causal inference model has been proposed to explain this phenomenon (Kilteni, Maselli, Kording, & Slater, 2015; Samad, Chung, & Shams, 2015). In this model, the multisensory conflict is reconciled in one of two ways: either the sensory information is inferred from one common source (i.e. rubber hand), resulting in the illusion of ownership; or from two different sources (i.e. rubber and real hand), which abolishes the illusion. The likelihood of the origin of this sensory data depends on the semantic information of the hand (i.e. morphological appearance), the anatomical constraints, the proprioceptive information, the visual and tactile information of the stimulation applied, and prior expectations (Kilteni et al., 2015). In this model, the RHI occurs with congruent visual and tactile information increasing the likelihood of integrating all the information as originating from the rubber hand. This model considers the integration of tactile, visual and proprioceptive information, but does not account for the role of visuomotor information as a trigger for the sense of ownership.

In the present study, we were primarily concerned with how congruent motor information from a voluntary action and visual information of the moving limb elicit and maintain a sense of ownership. Currently, there is no consensus on the effect of active control on the sense of ownership over a fake limb. Using a moving version of the RHI (mRHI), some studies have reported that active control enhanced the sense of ownership (Kalckert & Ehrsson, 2012; Ma & Hommel, 2013; Sanchez-Vives, Spanlang, Frisoli, Bergamasco, & Slater, 2010; Slater, Spanlang, Sanchez-Vives, & Blanke, 2010; Tsakiris, Prabhu, & Haggard, 2006), while others have failed to find this effect (Dummer, Picot-Annand, Neal, & Moore, 2009; Kalckert & Ehrsson, 2014; Longo & Haggard, 2009; Riemer, Kleinböhl, Hölzl, & Trojan, 2013; Walsh, Moseley, Taylor, & Gandevia, 2011). Controlling the movement of the index finger of a rubber hand elicited a sense of ownership when the movement was synchronous, but not if it was asynchronous to the movement of the participant (Kalckert & Ehrsson, 2012; Tsakiris et al., 2006). Active synchronous control also resulted in a stronger reported sense of ownership compared to passive observation of movement and asynchronous active control (Dummer et al., 2009). This effect has also been reported in a virtual reality environment (Sanchez-Vives et al., 2010; Slater et al., 2010), and is not restricted to upper body limbs (Kokkinara & Slater, 2014). On the other hand, some studies have failed to find that sense of ownership is enhanced by the active movement of the fake limb. In a setup where participants controlled the index finger of a fake hand, active control did not increase in ownership scores with respect to externally generated passive movement (Kalckert & Ehrsson, 2014; Longo & Haggard, 2009; Walsh et al., 2011), or compared to the reported feeling of ownership after visuotactile stimulation (Dummer et al., 2009; Kalckert & Ehrsson, 2014; Longo & Haggard, 2009). Furthermore, active control failed to elicit a sense of ownership when controlling hands that have an unusual appearance such as hands with supernumerary fingers (Hoyet, Argelaguet, Nicole, & Lécuyer, 2016) or on non-hand objects (Yuan & Steed, 2010).

This lack of agreement on the effect of active control might be due to differences in the experimental setups. For instance, some studies used a rubber hand (Kalckert & Ehrsson, 2012), while others used virtual reality environments (Sanchez-Vives et al., 2010). Also, the tasks were different, ranging from single finger movements (Kalckert & Ehrsson, 2014) to full arm movements in a cognitive task (Padrao, Gonzalez-Franco, Sanchez-Vives, Slater, & Rodriguez-Fornells, 2016). Here, we propose that differences in the visual appearance of the hand could, in part, explain the differences in the effect of voluntary movement. It has been shown that the appearance of the hand needs to be congruent to the pre-existing model of the hand (Tsakiris, 2010). For instance, the illusion is abolished by non-hand shaped objects (Haans, Ijsselsteijn, & de Kort, 2008; Tsakiris & Haggard, 2005), with increasing degrees of transparency of the hand (Martini, Kilteni, Maselli, & Sanchez-Vives, 2015), when the limb has been stretched beyond a certain extent (Kilteni, Normand, Sanchez-Vives, & Slater, 2012), or with a break in body continuity (Perez-Marcos et al., 2012; Tieri, Gioia, Scandola, Pavone, & Aglioti, 2017; Tieri, Tidoni, Pavone, & Aglioti, 2015a). Specifically, seeing the hand detached from the virtual body decreased sense of ownership over static limb (Tieri et al., 2017, 2015a; Tieri, Tidoni, Pavone, & Aglioti, 2015b) and passive observation of movement (Tieri et al., 2015b). However, whether active control of the movement helps maintain the sense of ownership of a hand that appears detached from the body remains to be tested. We reasoned that, if active control was relevant for the sense of ownership, the decrease in sense of ownership due to morphological incongruence should not occur.

The sense of agency refers to the subjective experience of being the source of the action (Haggard, 2017) and its consequences in the environment (Caspar, Cleeremans, & Haggard, 2015; Moore & Fletcher, 2012) and is closely related to action awareness and action planning (de Vignemont, 2011). In a voluntary action, motor commands sent to the muscles generate an efference copy that will be used to predict the future bodily states (Wolpert, 1997). Sensory information predicted from the motor command is compared to the actual sensory feedback from the body and the environment (Farrer & Frith, 2002); when these two match, sense of agency arises (Blakemore, Wolpert, & Frith, 1998). Conversely, a visual or temporal mismatch abolishes sense of agency (Blakemore, Wolpert, & Frith, 2002). This comparator model highlights the importance of visuomotor effects of the movement for the sense of agency (see Haggard, 2017 for review). However, a sense of agency can also be present without any actual movement (Tieri et al., 2015b; Wegner, Sparrow, & Winerman, 2004). In the absence of motor commands, passively observing a limb moving generates vicarious agency over the movements of the limb (Pezzetta, Nicolardi, Tidoni, & Aglioti, 2018; Tieri et al., 2015b; Wegner et al., 2004).

In the present study, we assessed the role of active control as evidence in favor of a sense of ownership over the virtual hand. We used a variation of the mVHI paradigm in which participants controlled the virtual hand during a goal-directed task. We hypothesized that visual appearance plays a role in the effect of active control. If that is case, active control would enhance the sense of ownership over the virtual limb when the evidence was lower. We used a manipulation in which the hand appears detached from the body (Perez-Marcos et al., 2012; Tieri et al., 2017; 2015a, 2015b). Additionally, we tested the importance of movement congruence to the movement of the participants in sense of ownership. Overall, we aim to understand the role of congruent active control in sense of ownership.

2. Materials and methods

2.1. Participants

A total of 44 volunteers (29 females; age range = 18–45; mean age = 28.2 ± SD = 7.5 years) took part in the study. Participants signed up through a public online form. Those that declared having no neurological conditions and to be right-handed were contacted to participate. All subjects were naïve to the purposes of the study. Seven participants were excluded from the analysis: four participants were excluded due to technical issues (e.g. the tracking of the virtual hand failed during a dynamic trial) and another three were excluded as they failed to follow the instructions (e.g. moved their hand before or during the static trials). In all the cases, participants performed the experiment until completion, but the data were excluded from the analyses. Thus, all analyses were performed on a sample of 37 participants (23 females, age range = 18–45; mean age = 27.6 ± SD = 6.7 years). Participants were tested for handedness using the Edinburgh Handedness Inventory (Olfield, 1971) (mean = 75.86 ± SD = 24.83). 73% never had any previous contact with virtual reality and 55% declared not to be regular video game players.

The experimental protocol was approved by the Institutional Review Board at the Champalimaud Foundation and was carried out in accordance with the ethical standards of the Declaration of Helsinki. All participants provided written informed consent prior to participation. At the end of the experiment, participants were paid €15 in a voucher and were debriefed. The whole experiment lasted approximately 30 min.

2.2. Virtual environment and apparatus

Participants were immersed in the virtual environment using an Oculus Rift DK2 (Oculus VR, LLC) head-mounted display and saw the virtual environment from a first-person perspective. The virtual environment consisted of a large room with the same size and appearance as the experimental room. All components of the virtual environment were designed using 3DS Max 2015 (Autodesk, Inc) and implemented in Unity 3D Engine (Unity Technologies SF). The room contained a table, which was a 1:1 replica of the real one, with the same shape, size (100 cm × 36 cm × 77 cm), and position. Both the real and the virtual table had three circles on top that acted as lights in the virtual environment. The virtual and the real scenes were carefully aligned by measuring the location of the positional tracking camera of the Oculus Rift (near-infrared CMOS sensor) in the real room with the same point in the virtual scene.

Participants controlled a gender-matched right arm in an anatomical congruent position that was collocated with their real, hidden right arm (Fig. 1A, B). The virtual arm was controlled using a LEAP motion controller (Leap Motion, Inc). This device captures the kinematics of the real hand of the participants and transforms it online into the virtual hand movement. The virtual and real hands were carefully aligned by measuring the LEAP Motion controller in the experimental room and using the same location in the virtual world as the origin for the hand models. We used two different hand models: one that appeared attached to the body and one detached without a forearm (Fig. 1B). These hand models were provided by the LEAP motion SDK. Throughout the whole experiment, the trajectories of the participants' hand were logged using the LEAP motion. Due to technical limitations, we did not show a virtual body in the environment. However, participants were always requested to look at the hand, which minimized the effect of this constraint.

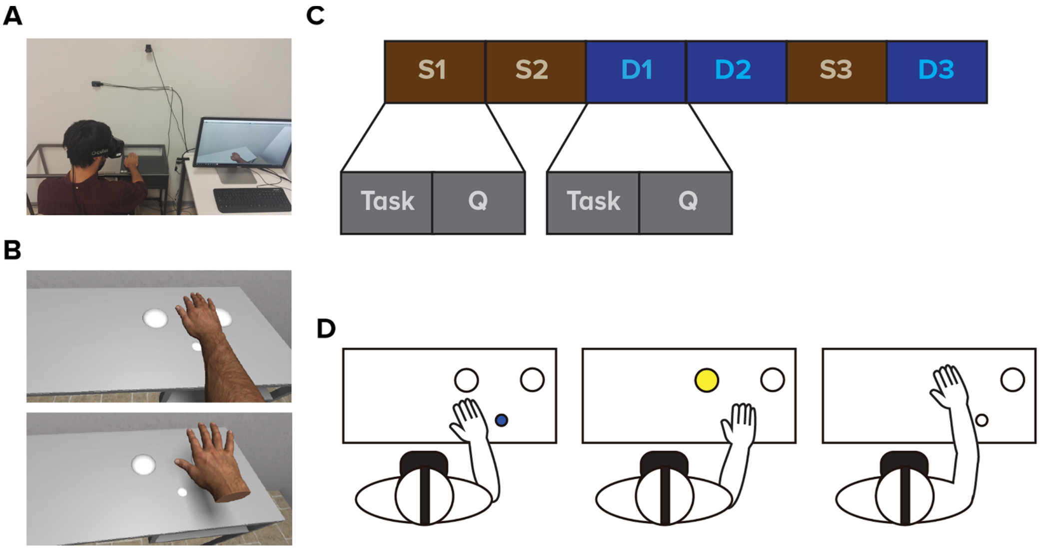

Fig. 1. Virtual reality environment and experimental design. (A) Virtual and real set up. (B) Male virtual hand model for full arm and detached hand. Hand models were gender-matched. (C) Experimental design. Participants underwent four blocks consisting in a total of six conditions, three static (S1, S2, S3) and three dynamic (D1, D2, D3). Each condition consisted of a task followed by the subjective report of the illusion. (D) In the dynamic conditions, participants performed a reaching task consisting of 25 reaching movements.

2.3. Procedures

Upon arrival, participants were asked to read and sign a consent form. The experimenter verbally explained the instructions of the experiment to them. Participants were seated in front of the table and requested to place their right hand on top of it. We instructed the participants to refrain from moving the hand from this point until told otherwise. The experimenter fitted the head mounted display and the experiment started.

Each participant experienced a total of six conditions. Each condition consisted of a task, followed by the subjective report of the sense of ownership and sense of agency (Fig. 1C). The task differed depending on the type of condition. Participants either observed a static right hand without attempting to move it (static conditions) or controlled the hand in a goal-directed task that required performing reaching movements (dynamic conditions). When the task was completed the right hand disappeared, and participants verbally reported their subjective sense of ownership and sense of agency by responding to the questionnaires (see Section 2.6). After this, the next condition began. Participants did not remove the headset at any point during the experiment. At the end of all the conditions, participants were asked for their overall qualitative experience of the experiment, were paid, and dismissed.

2.4. Experimental design

We divided the conditions into four blocks (Fig. 1C). The first block consisted of two static conditions (S1 and S2): one in which the arm appeared attached to the body (*full arm static*) and one in which the forearm was missing (*detached hand static*). These two conditions were counterbalanced within this block across participants. The second block consisted of two dynamic conditions (D1 and D2): one in which the arm appeared to be attached (*full arm dynamic*) and one in which the forearm was missing (*detached hand dynamic*). These two conditions were counterbalanced within this block across participants. To avoid artifacts coming from participants having controlled the virtual arm, S1 and S2 were always used before D1 and D2. The third block consisted of a single static condition, which we labeled *full arm static - post* (S3). This condition was used as a control for the effects of active control on a subsequent static condition, after participants were allowed to control the virtual hand. Finally, the last block consisted of a single dynamic condition (D3) in which participants controlled a full arm where the movement was incongruent to the actual movement of the participant (*incongruent movement* condition).

2.5. Details of the conditions

2.5.1. Static conditions

During the static tasks, participants were asked to keep their hand still and stare at it during 60 s. To ensure that no hand movement could be seen or performed during these trials, the position of the hand model was not updated and the participant was carefully monitored by the experimenter during the whole task.

2.5.2. Dynamic conditions

The dynamic tasks consisted of performing a set of reaching movements towards a target light. A schematic of the task is depicted in Fig. 1D. Before the task started, participants were requested to lift their hand from the table and abstain from placing it back until told otherwise, as to avoid tactile information from the real arm. First, the small central light turned on blue. Participants were required to place their hand on top without touching it. This caused one of the two large target lights to turn on yellow, determined randomly. The subject had to reach towards the newly illuminated light and to turn it off within the specified time of five seconds. If performed correctly, the target light would change to green; otherwise, it changed to red. After 0.5 s, the blue central light turned on again and the process was repeated for a total of 25 times. Each dynamic task lasted approximately three minutes.

2.5.3. Detached arm condition

Previous studies reported that a break in body continuity negatively affects sense of ownership and vicarious agency over a virtual arm at rest or during passive observation of the moving arm (Perez-Marcos et al., 2012; Tieri et al., 2017; 2015a). To manipulate sense of ownership over the virtual hand, we used a virtual hand model that appeared detached from the body with a clean cut at the wrist (Fig. 1B).

2.5.4. Incongruent movement condition

In the *incongruent movement* condition the visual information from the movement of the virtual hand was incongruent to the action performed by the participant. To do this, we added noise to the trajectory of the rubber hand.

The virtual arm position, $\widehat{p}_i$, is defined by a combination of the current hand location with the virtual hand location in the previous frame, and some noise defined by the equation:

$$\widehat{p}_i = \lambda p_i + (1 - \lambda)(\widehat{p}_{i-1} + (p_i - p_{i-1}) + r)$$

where $\widehat{p}_{i-1}$ is the previous virtual hand location; p_i and p_{i-1} are the present and previous real hand locations; and r is Gaussian random noise of mean 0 and standard deviation σ; and the parameter λ determines the weight of the present location in favor of the noisy virtual location. In our experiment $\sigma = 0.015$ m and $\lambda = 0.9$. This means that 90% of the virtual hand movement was based on the current sample (i.e. with added latency), and the other 10% was composed of the actual delta (previous vs present virtual hand location) and random noise to the previous virtual hand location.

Table 1

Statements of the questionnaires for both static and dynamic conditions. We presented two questionnaires depending on the type of condition (static or dynamic). Statements regarding sense of ownership were the same in both static and dynamic conditions, while sense of agency differed.

	Category	Condition Type	Statement
1	**Sense of ownership**	Static and Dynamic	I felt as if I were looking at my hand, rather than a virtual hand
2	**Sense of ownership**	Static and Dynamic	I felt as if the virtual hand was my hand
3	**Sense of ownership**	Static and Dynamic	It seemed like the virtual hand belonged to me
4	**Sense of ownership**	Static and Dynamic	It seemed that the virtual hand was part of my body
5	**Sense of ownership - control**	Static and Dynamic	I felt as if I had more than one right hand
6	**Sense of ownership -control**	Static and Dynamic	I felt like my real hand was turning virtual
7	**Similar**	Static and Dynamic	I felt as if the virtual hand physically resembled my real hand in terms of shape, freckles and other features
8	**Sense of agency**	Static	I felt that I could control the virtual hand if I wanted to
9	**Sense of agency**	Static	I felt that I started to move my hand, the virtual hand would obey my will
10	**Sense of agency – control**	Static	I had the feeling of forgetting my own hand, focusing only on the virtual hand
11	**Sense of agency**	Dynamic	I felt that I could control the virtual hand
12	**Sense of agency**	Dynamic	I felt that the movements of the virtual hand were cause by me
13	**Sense of agency**	Dynamic	I felt as if the virtual hand was obeying my will
14	**Sense of agency**	Dynamic	I felt that I controlled the virtual hand as if it was part of my body
15	**Sense of agency – control**	Dynamic	I felt as if the virtual hand was controlling my hand
16	**Sense of agency – control**	Dynamic	I had the feeling of forgetting my own hand, focusing only on the movement of the virtual hand
17	**Sense of agency – control**	Dynamic	I felt as if the virtual hand caused the movement of my hand
18	**Outcome agency**	Dynamic	I felt as if the lights were obeying my will
19	**Outcome agency**	Dynamic	I felt that the movement of my hand was turning off the lights on the table
20	**Outcome agency – control**	Dynamic	I felt as if the lights changed at random
21	**Sense of location**	Static and Dynamic	It seemed like my hand was in the location of the virtual hand
22	**Sense of location**	Dynamic	It seemed as if the movement of my hand was located where the virtual hand was moving

2.6. *Questionnaires*

To assess the participant's subjective experience, we used two questionnaires adapted from previous studies (Botvinick & Cohen, 1998; Kalckert & Ehrsson, 2012), one for each type of condition (i.e. static or dynamic). The participants rated their subjective experience on a seven-point Likert scale (1 = totally disagree, 4 = neutral, 7 = totally agree).

For the static conditions, we used an eleven-item questionnaire that assessed ownership (statements 1–4), sense of agency (statements 8–9), and sense of location (statement 21). We also used control statements of ownership (statements 5–6) and agency for static conditions (statement 10). For the dynamic conditions, the questionnaire consisted of nineteen items that assessed sense of ownership (statements 1–4), sense of agency in dynamic condition (statements 11–14) and sense of location (statement 21–22). Additionally, we used control statements of ownership (statements 5–6) and agency for the dynamic conditions (statement 15–17). The dynamic conditions also contained items regarding the perceived agency over the consequences of the action (hereafter, outcome agency) (statements 18–19), and the respective control statement (statement 20). Statements assessing sense of agency were different between static and dynamic conditions, to avoid priming effects from the statements referring to an active control in the first static block. The control statements served as controls for task compliance and suggestibility effects. We also assessed the subjective similarity between the real and the virtual hand (statement 7) (Table 1).

The experimented manually recorded the responses on paper and using the Likert.m Matlab function, modified to present the statements in a counterbalanced order across all conditions and participants.

2.7. *Data handling*

All data were analyzed using Matlab 2014b.

The questionnaires included more than one statement for sense of ownership, sense of agency (static), sense of agency (dynamic), sense of agency (outcome), and their respective control statements (see Section 2.6). To avoid the artifacts related to pseudoreplication, for each participant we calculated the individual mean score for each category (e.g. sense of ownership) in each condition (e.g. *full arm static*). Thus, we obtained a total of 37 individual scores for each category and condition. Using the Shapiro-Wilk test, the individual ownership scores were not found to follow a normal distribution, while the individual agency scores did. Therefore, we used non-parametric tests for the remaining analysis. We used a Friedman ANOVA to compare across all the conditions and the Wilcoxon signed-rank test for pairwise comparisons.

We compared the sense of ownership and the sense of agency statements to their respective control statements in each condition to test for task compliance and suggestibility effects. Also, in accordance to our hypotheses, we compared the ownership scores in the following pairs of conditions: *full arm static* against *full arm dynamic* and *detached hand static* against *detached hand dynamic*, to assess the effect of active control; *full arm static* against *detached hand static* and *full arm dynamic* against *detached hand dynamic*, to assess the effect of morphological congruence; and *full arm dynamic* against *incongruent movement* to assess the importance of movement congruence. We also compared the following pairs of conditions for the sense of agency: *full arm static* against *detached hand static* and *full arm dynamic* against *detached hand dynamic*, to assess the effect of morphological congruence; and *full arm dynamic* against *incongruent movement* to assess the importance of movement congruence. Finally, to assess the effects of morphological incongruence and movement incongruence on outcome agency, we compared *full arm dynamic* against *detached hand dynamic* and *full arm dynamic* against *incongruent movement*. Thus, in total, we performed twelve pairwise comparisons, each with a Bonferroni corrected p-value of 0.004.

Additionally, we reasoned that participants might be affected differently by the manipulations depending on their basal level of ownership. For this reason, we analyzed the reported ownership separating the participants into three groups according to their individual ownership score: low (i.e. individual ownership score ≤ 3), medium (i.e. individual ownership score > 3 and < 5), and high (i.e. individual ownership score ≥ 5). We compared participants within each group in the following pairs of conditions using the Wilcoxon signed-rank test: *full arm static* against *full arm dynamic* and *detached hand static* against *detached hand dynamic*, to assess the effect of active control movement; *full arm static* against *detached hand static* and *full arm dynamic* against *detached hand dynamic* to assess the effect of morphological congruence; and *full arm dynamic* against *incongruent movement* to assess the importance effect of movement congruence. Each of these five pairs of conditions was tested for the three groups with different basal individual ownership scores, giving a total of 15 tests, each with a Bonferroni corrected p-value of 0.003.

Lastly, we assessed the correlation between the changes in sense of agency and sense of ownership in two conditions. To this end, we calculated the differences in the individual agency scores and ownership scores in two conditions and calculated the correlation in these differences using the Spearman ρ correlation coefficient.

3. Results

3.1. Sense of ownership and sense of agency over a virtual hand

We first assessed whether the statements for the sense of ownership and sense of agency (dynamic and static) were higher their respective control statements for each experimental condition (see Section 2.6).

Participants reported a sense of ownership after seeing the arm at rest connected to the body (*full arm static*) (median = 4.5 ± 1.45; see Table 2 for the median ownership scores in all conditions). In this condition, the reported sense of ownership was higher than the respective control statements (Wilcoxon signed-rank; Z = 4.56, $p < 0.001$). In the *detached hand static* condition, the median reported sense of ownership was below the neutral score (score = 4) (median = 3.25 ± 1.53) and was higher than the control statements (Wilcoxon signed-rank; Z = 3.02, p = 0.002). The *full arm static - post* condition (median = 4.25 ± 1.54) was also significantly different from the control statements (Wilcoxon signed-rank; Z = 5.15, $p < 0.001$) (Fig. 2A).

The agency scores in the *full arm static* (median = 6 ± 1.45; see Table 2 for a summary of the median agency scores) were higher than the respective control statements (Wilcoxon signed-rank; Z = 3.12, $p < 0.001$). In the *detached hand static* condition, agency scores (median = 5 ± 1.83) showed no significant difference compared to the control statements (Wilcoxon signed-rank; Z = 1.14, p = 0.15). In the *full arm static - post*, participants reported agency scores (median = 6 ± 0.84) that were significantly different from the control statements (Wilcoxon signed-rank; Z = 3.66, $p < 0.001$) (Fig. 2C).

In the dynamic conditions, participants reported feeling ownership over the virtual hand in *the full arm* (median = 4.75 ± 1.39) and in the *detached hand* (median = 4.25 ± 1.34). In both conditions, ownership scores were higher than in the control statements (Wilcoxon signed-rank; Z = 4.65, $p < 0.001$, and Z = 4.92, $p < 0.001$). In the *incongruent movement* condition, the median ownership score was below the neutral score (score = 4) (median = 3.5 ± 1.62). The scores in this condition were higher than in the respective control statements (Wilcoxon signed-rank; Z = 3.73, $p < 0.001$) (Fig. 2B).

Participants also reported a sense of agency over the virtual arm movements in the *full arm dynamic* (median = 6.25 ± 0.85) and *detached hand dynamic* (median = 6.25 ± 0.72), which were higher than in their respective control statements (Wilcoxon signed-rank; Z = 5.30, $p < 0.001$; and Z = 5.28, $p < 0.001$, respectively). In the *incongruent movement* condition, the sense of agency (median = 5.5 ± 1.12) was higher than the control statements (Wilcoxon signed-rank; Z = 5.18, $p < 0.001$) (Fig. 2D).

The subsequent analyses are aimed at understanding whether the different manipulations caused a difference in the reported ownership and agency scores in the different conditions.

Table 2

Median scores for each condition and for each category of statements. Means of all the statements of a category (e.g. sense of ownership) were calculated for each individual. Using these individual scores, we calculated the median scores of the sample for each category in each condition.

	Full arm static	Detached hand static	Full arm dynamic	Detached hand dynamic	Full arm static - post	Incongruent movement
Ownership	4.5	3.25	4.75	4.25	4.25	3.5
Ownership Control	3	2.5	2.5	2.5	2.5	2.5
Agency (static)	6	5	n/a	n/a	6	n/a
Agency (static) Control	5	4	n/a	n/a	5	n/a
Agency (dynamic)	n/a	n/a	6.25	6.25	n/a	5.5
Agency (dynamic) Control	n/a	n/a	3	3	n/a	3
Outcome Agency	n/a	n/a	6	6	n/a	6
Location	7	6	6.5	6	7	6

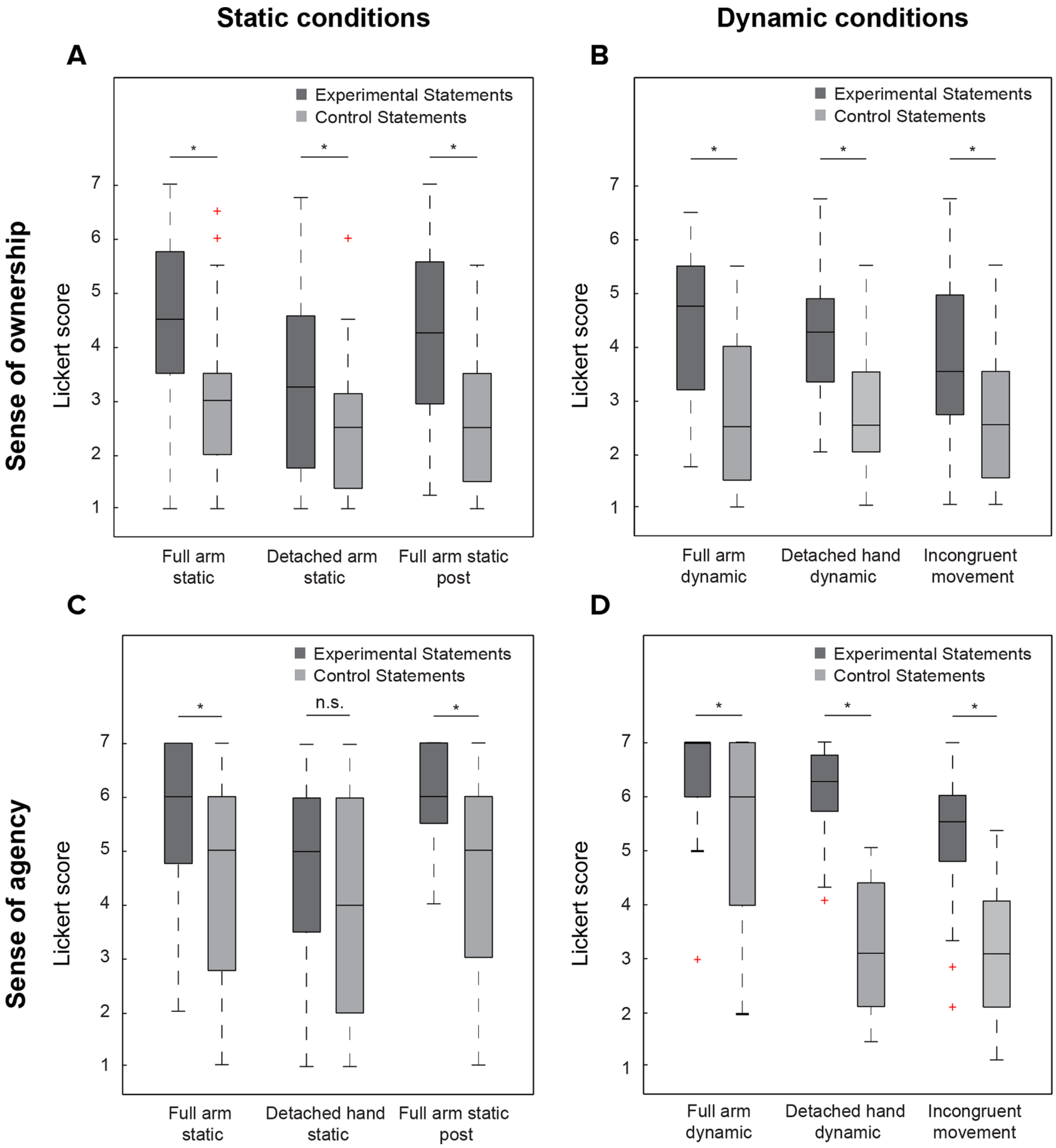

Fig. 2. Reported sense of ownership and sense of agency scores and their respective control scores. (A) Ownership scores in the static conditions (B) Ownership scores in the dynamic conditions (C) Agency scores in the static conditions (D) Agency scores in the dynamic conditions. The middle quartile indicates the median value and the whiskers indicate the most extreme values that are not considered outliers. $^{*}p < 0.05$.

3.2. *Morphological incongruence decreases reported sense of ownership and agency in static, but not in dynamic conditions*

We assessed whether seeing the hand detached from the body affected the reported sense of ownership and the sense of agency and if active control made a difference in this effect. Previous studies had already reported a decrease in sense of ownership and vicarious agency over a static discontinuous limb (Tieri et al., 2015b). We hypothesized that, if active control is relevant the reported sense of ownership, this decrease in reported ownership and agency would be absent when participants actively controlled the movements of the virtual hand.

Ownership scores were significantly different across all the conditions (Friedman test; $\chi^2 = 31.45$ (df = 5, n = 37), $p < 0.001$). To test for our hypothesis, we compared the ownership scores between the *full arm* conditions and their corresponding morphological incongruent conditions (i.e. *detached hand*). In the absence of movement, the ownership scores in the *detached hand* were lower than the scores in the *full arm static* condition (Wilcoxon signed-rank; Z = 4.21, $p < 0.001$) (Fig. 3A). However, we found no significant difference between the ownership scores in the *full arm dynamic* and the *detached hand dynamic* (Wilcoxon signed-rank; Z = 2.02,

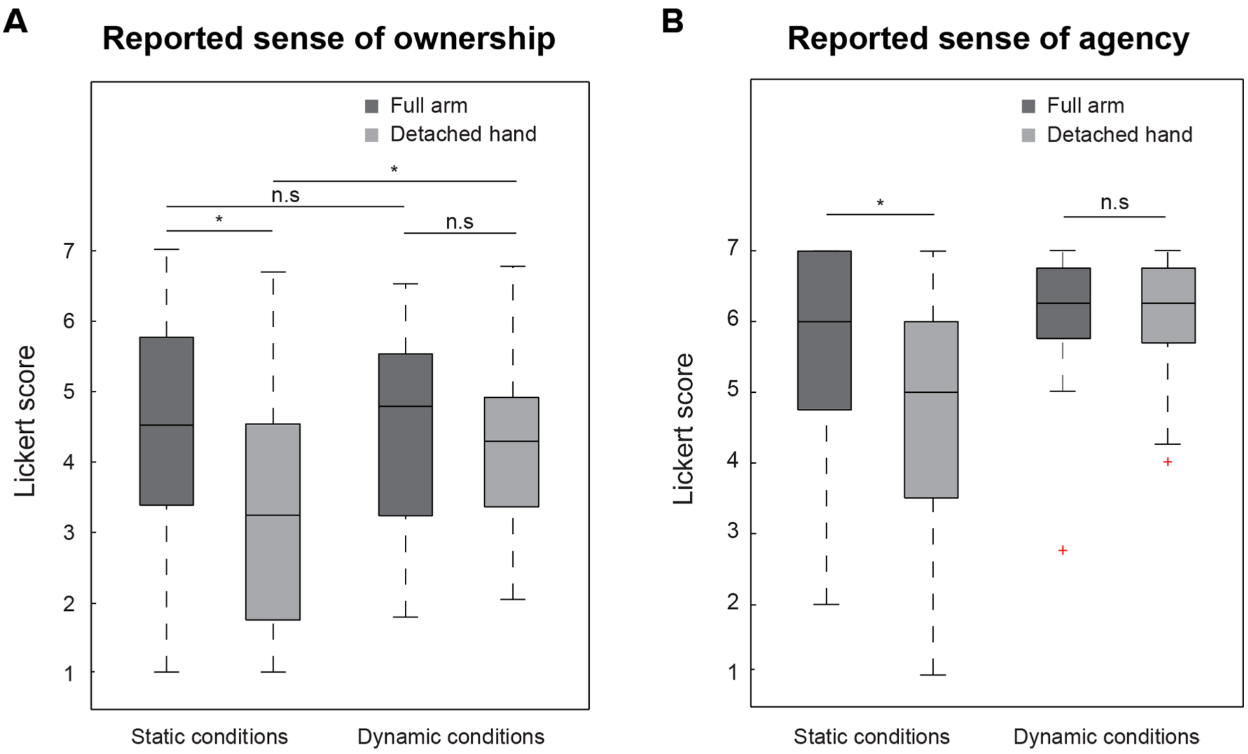

Fig. 3. Effect of movement and morphological incongruence in reported ownership and agency scores. (A) Active control did not increase reported ownership when comparing the full arm static and the full arm dynamic conditions ($p = 0.51$, Wilcoxon signed rank test). Seeing the hand detached caused a decrease in reported ownership scores in the static conditions ($p < 0.001$, Wilcoxon signed rank test), but not in the dynamic conditions ($p = 0.04$, (not significant with Bonferroni correction), Wilcoxon signed rank test). Active control increases reported ownership scores in detached hand conditions ($p < 0.001$, Wilcoxon signed rank test). (B) Seeing the hand detached decrease reported perceived agency in the static conditions ($p = 0.002$, Wilcoxon signed rank test), but it did not decrease agency scores in dynamic conditions ($p = 0.44$, Wilcoxon signed rank test). The middle quartile indicates the median value and the whiskers indicate the most extreme values that are not considered outliers. * The Bonferroni corrected p-value for these comparisons was 0.004.

$p = 0.04$; not significant with Bonferroni correction) (Fig. 3A).

Agency scores were different across the three static conditions (Friedman test; $\chi^2 = 25.29$ (df = 2, n = 37), $p < 0.001$) and the three dynamic conditions (Friedman test; $\chi^2 = 21.53$ (df = 2, n = 37), $p < 0.001$). We tested for differences in the agency scores according to the planned pairwise comparisons (see Section 2.7). In static conditions, the agency scores in the *detached hand* condition were lower than in the *full arm* condition (Wilcoxon signed-rank; $Z = 3.03$, $p = 0.002$) (Fig. 3B). However, under congruent active control (i.e. dynamic conditions), the agency scores in the *full arm dynamic* condition were not found to be significantly different to the *detached hand dynamic* agency scores (Wilcoxon signed-rank; $Z = 0.77$, $p = 0.44$) (Fig. 3B).

These findings are consistent with the idea that active control over the virtual hand movement plays a differential role in the effect of morphological incongruence in the reported sense of ownership and sense of agency.

3.3. Congruent active control does not increase reported sense of ownership in full arm, but it does in detached hand conditions

To assess the effect of active control on reported sense of ownership, we compared the ownership scores between the static and dynamic conditions. We hypothesized that if active control contributes to the sense of ownership, we would see an increase in the reported ownership scores for both *full arm* and *detached hand* conditions.

Sense of ownership scores were significantly different across all six conditions (Friedman test; $\chi^2 = 31.45$ (df = 5, n = 37), $p < 0.001$). To test for our hypothesis, we compared the ownership scores between the static conditions and their corresponding dynamic condition. We found no significant differences in reported sense of ownership when comparing *full arm static* and *full arm dynamic* (Wilcoxon signed-rank; $Z = 0.66$, $p = 0.51$). However, active control resulted in an increase in the ownership scores in the morphological incongruent conditions (*detached hand static* vs *detached hand dynamic*) (Wilcoxon signed-rank; $Z = -3.38$, $p < 0.001$) (Fig. 3A).

These results show that active control can increase the reported sense of ownership, but this effect occurs only in conditions when controlling a morphological incongruent virtual limb.

3.4. Participants respond differently to each manipulation depending on their reported ownership

So far, our results suggest that the effect of active control on reported sense of ownership is affected by the morphological

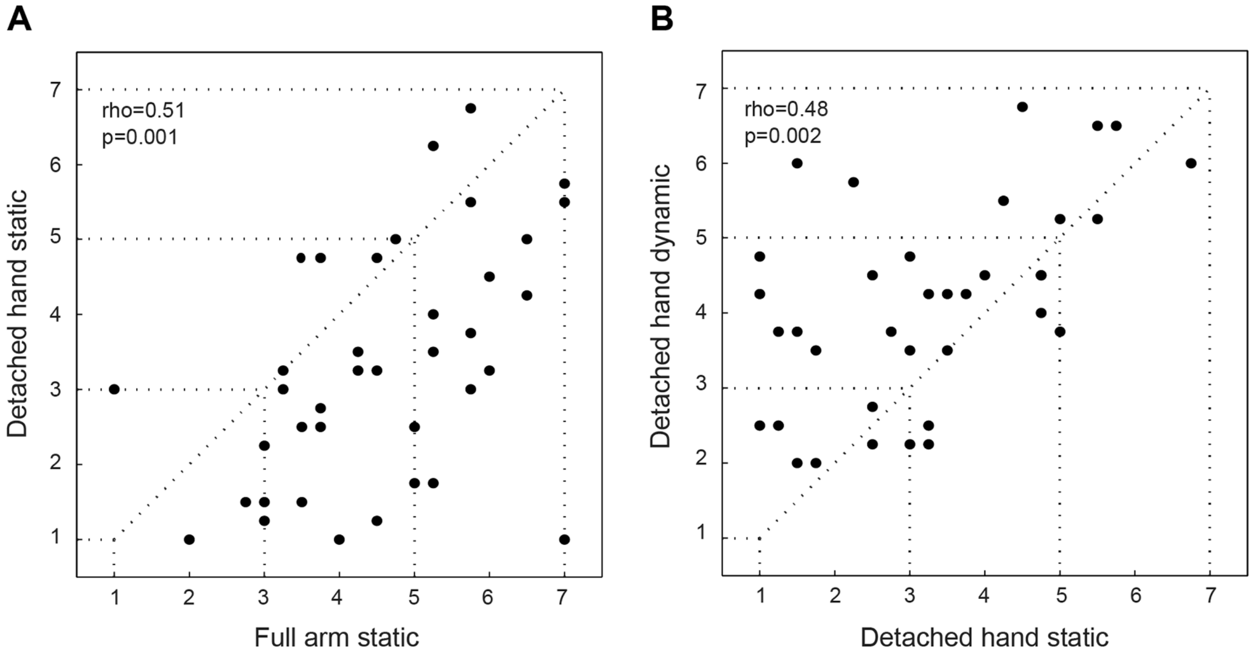

Fig. 4. Correlations of reported ownership scores. (A) Reported ownership in the full arm static and detached hand static were significantly correlated (Spearman $\rho = 0.51$, $p = 0.001$). Participants in the high ownership group ($n = 16$) were significantly different in the medians between both conditions ($p < 0.001$, Wilcoxon signed rank test), while participants in the medium ($n = 15$) and low ownership ($n = 6$) did not show any significant difference ($p > 0.4$, Wilcoxon signed rank test) (B) Reported ownership in the detached hand static and detached hand dynamic were significantly correlated (Spearman $\rho = 0.48$, $p = 0.002$). Participants in the low ownership group ($n = 18$) were significantly different between both conditions ($p < 0.001$, Wilcoxon signed rank test), while participants in the medium ($n = 13$) and high ownership ($n = 6$) groups did not show a significant difference ($p = 0.03$ (not significant under Bonferroni correction) and $p = 0.49$, respectively).

appearance of the limb. We tested whether participants responded differently to the manipulations depending on their ownership levels. For this purpose, we divided the participants into three groups according to a different baseline in each pairwise comparison (see Section 2.7), and tested for differences within each group.

In the static conditions, reported ownership was significantly different in the *full arm* and *detached hand* conditions (Fig. 3A). Individual ownership scores showed a positive correlation between these two conditions (Spearman $\rho = 0.51$, $p = 0.001$) (Fig. 4A). When comparing reported sense of ownership in the different subgroups of participants, using the *full arm static* as a baseline, seeing the hand detached from the body caused a decrease in the high ownership individuals (Wilcoxon signed-rank; $Z = 41$, $p < 0.001$, $n = 16$), but not the medium and low (Wilcoxon signed-rank; $p = 0.04$, not significant under Bonferroni, $n = 15$ and 0.53, $n = 6$, respectively) (Fig. 4A).

Active control only showed an effect in sense of ownership in morphologically incongruent conditions (*detached hand static* against *detached hand dynamic*) (Fig. 3A). These conditions were also correlated (Spearman $\rho = 0.48$, $p = 0.002$) (Fig. 4B). Furthermore, the analysis of the subgroups, using the *detached hand static* condition as the baseline, revealed that active control caused a significant increase in low (Wilcoxon signed-rank; $Z = -3.37$, $p < 0.001$, $n = 18$), but not in medium or high ownership groups (Wilcoxon signed-rank; $p = 0.03$, not significant under Bonferroni correction, $n = 13$ and $p = 0.49$, $n = 6$, respectively) (Fig. 4B). The remaining comparisons can be found in the Supplementary Materials (Fig. S1).

These results show that active control and morphological incongruence have different effects in different subgroups of participants, depending on the experimental conditions that are used as the baseline.

3.5. *Incongruent active control decreases sense of agency and sense ownership*

Up to this section, we have shown that active control is relevant in the sense of agency and the sense of ownership. We further hypothesized that, for active control to be relevant for the sense of ownership, the movement needed to be congruent to the participant's real movements. We thus used the *incongruent movement* condition as a manipulation in which noise is added to the mean trajectory of the virtual hand (see Section 2.5.4).

Sense of ownership was significantly different across all six conditions (Friedman test; $\chi^2 = 31.45$ ($df = 5$, $n = 37$), $p < 0.001$) and for sense of agency in the three dynamic conditions (Friedman test; $\chi^2 = 21.53$ ($df = 2$, $n = 37$), $p < 0.001$). Reported agency scores in the *incongruent movement* condition were significantly reduced when compared to the *full arm dynamic* condition (Wilcoxon signed-rank; $Z = 4.09$, $p < 0.001$). This was also the case for the reported ownership scores (Wilcoxon signed-rank; $Z = 3.64p < 0.001$) (Fig. 5A). These results are consistent with the idea that the movement needs to be congruent to the movement of the real hand is needed to elicit a sense of agency and ownership over the virtual hand.

We also measured the correlation of the change in individual ownership scores and the change in individual agency scores

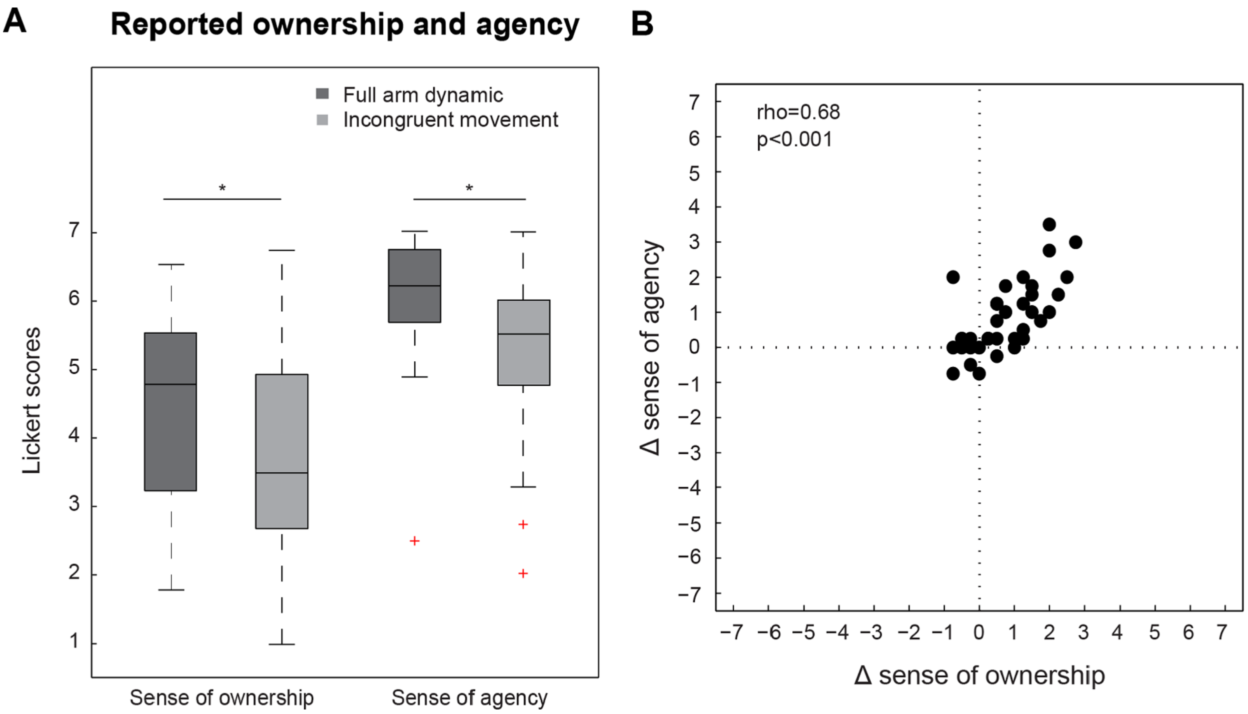

Fig. 5. Effect of incongruent movement in reported sense of ownership and sense of agency. (A) There is a significant decrease in reported sense of ownership ($p < 0.001$, Wilcoxon signed rank test) and in reported sense of agency ($p < 0.001$, Wilcoxon signed rank test). The middle quartile indicates the median value and the whiskers indicate the most extreme values that are not considered outliers. * The Bonferroni corrected p-value for these comparisons was 0.004. (B) Correlation between the difference in ownership and the difference in agency scores, when comparing full arm dynamic and incongruent movement conditions. These show a strong correlation (Spearman $\rho = 0.68$, $p < 0.001$).

between the *full arm dynamic* and *incongruent movement* conditions. The changes in both categories are strongly correlated within participants (Fig. 5B). This suggests that incongruent hand movement, in each participant, has a similar detrimental effect on both the senses of ownership and agency. This correlation is less clear when comparing the *full arm* conditions to the *detached hand* conditions in static and dynamic scenarios (Fig. S2).

4. Discussion

We here report two main findings on the effect of visuomotor information on the sense of ownership in the moving Virtual Hand Illusion (mVHI) paradigm. First, we show that morphological incongruence did not change the reported sense of ownership under active control, contrary to what is seen in static conditions. Secondly, we found that active control increased the reported sense of ownership, but only when participants controlled a detached form of the hand, in which sense of ownership was significantly lowered. Taken together, our results show that active control of the movements of the virtual hand enhanced and maintained reported ownership over the virtual hand. However, this effect was contingent on the available sensory information in favor of sense of ownership.

Seeing a static hand with the missing forearm has been reported to negatively affect the reported sense of ownership in the absence of any additional sensory information (Tieri et al., 2017, 2015a, 2015b) or after visuotactile stimulation (Perez-Marcos et al., 2012). In the absence of active control, we also found a significant decrease in the reported sense of ownership over the hand appears detached from the body (i.e. *detached hand static*) compared to *full arm static* condition. The integration of all available sensory information is critical for eliciting a sense of body ownership and is not restricted to visuotactile information (Kalckert & Ehrsson, 2012), as visuomotor information can also add evidence of feelings of ownership (Synofzik, Vosgerau, & Newen, 2008). Here, we found no significant change in the sense of ownership between the *full arm* and the *detached hand* while performing a goal-directed task. Thus, active control circumvents the decrease in reported ownership caused by seeing a morphological incongruent limb. This suggests that, when available, visuomotor information plays a critical role in maintaining a sense of ownership over a limb that appears detached from the body. To our knowledge, this is the first study to report this effect.

In this study, we also tested whether active control could enhance sense of ownership over a virtual limb. While some studies have reported that active control increased the sense of ownership (Dummer et al., 2009; Kalckert & Ehrsson, 2012), others failed to see this effect (Kalckert & Ehrsson, 2014; Walsh et al., 2011). We hypothesized that this could result, in part, from the differences in the morphological appearance of the hand, since it is known to play a crucial role in the RHI paradigm (Kilteni et al., 2015). We used the morphological incongruent form of the hand (*detached hand*) to test for this hypothesis. In our setup, the information provided to the participants in *full arm static* condition (i.e. first-person perspective, anatomical plausibility, realistic appearance of the hand) was sufficient to drive the illusion of ownership (Costantini & Haggard, 2007; Ehrsson, Spence, & Passingham, 2004; Haans et al., 2008;

Maselli & Slater, 2013; Slater et al., 2010). In this scenario of relatively high ownership, active control did not further enhance the sense of ownership (*full arm static* compared to *full arm dynamic*). However, in conditions of morphological incongruence (i.e. *detached hand static*), in which evidence of the sense of ownership was lowered, active control provided evidence in favor of the sense of ownership in the *detached hand dynamic* condition. The results reported here suggest that there is interplay between the existing level of ownership and the effect of active control. The analysis of the subgroups further strengthens this idea. Since subjects with low individual ownership scores in the *detached hand static* condition (individual mean ownership score ≤ 3) reported significantly higher scores in the *detached hand dynamic* condition.

We also assessed the interplay between visual appearance and visuomotor information on sense of agency. In the absence of visuomotor information, a sense of ownership has been shown to elicit a weak sense of agency (Kalckert & Ehrsson, 2014), as a result of congruent morphological, proprioceptive, and visuotactile information. However, when body continuity is broken, the vicarious agency significantly decreased in the absence of voluntary motor commands (Tieri et al., 2017; 2015a, 2015b). We here report the same finding in the static conditions: the reported sense of agency was significantly lower in *detached hand* compared to the *full arm static* condition in the absence of movement. However, this is not the case under active control of the movements of the virtual hand, as we found that participants did not change agency scores over the morphologically incongruent limb (i.e. *detached hand*) compared to the *full arm dynamic* condition. The presence of active control, through voluntary control of the movements of the virtual hand, plays a differential role on the effect of incongruent morphological appearance in the reported sense of agency.

A limitation of this study is that we did not present the subjects with a condition where they passively observed the moving virtual hand without performing any movement themselves. Previous studies found that visual information is sufficient to elicit the sense of agency when passively observing a moving virtual limb (Pezzetta et al., 2018; Tieri et al., 2015b). Furthermore, a break in the body continuity negatively affects reported vicarious agency when participants passively observe the moving virtual arm moving with a missing forearm (Tieri et al., 2015b). Our results indicate that, when active control is present, visuomotor information is weighted more heavily than visual information. The presence of active control could explain the difference found between our findings and what has been previously reported using passive observation of movement. The data from our *incongruent movement* condition can further support this hypothesis. In this condition, the mismatch between the performed and seen action is accompanied by a decrease in the reported sense of agency and the sense of ownership compared to the *full arm dynamic* condition. Interestingly, the difference in the individual ownership scores between the *full arm dynamic* and the *incongruent movement* conditions strongly correlates with the difference in the individual agency scores in the same conditions (Fig. 5B). The result shown in this figure suggests that congruent movement is important to maintain both a sense of agency and a sense of ownership over the virtual limb. On the other hand, manipulating morphological appearance does not present this correlation, especially in the static conditions (Fig. S2).

The primary goal of this study was to understand the effect of active control on the sense of ownership. Thus, we did not want to disclose to the participants that they would actively control the hand in the dynamic trials. Therefore, statements for the sense of agency needed to be different between the static and the dynamic conditions. As a result of this, another limitation in this study is that we could not compare the sense of agency between static and dynamic conditions. This comparison could help us further understand the interplay between morphological and visuomotor congruence in the sense of agency.

The outcome of the action has also been suggested to play a crucial role in the sense of agency (Caspar et al., 2015) and the sense of ownership (Wen et al., 2016). We labeled as outcome agency those questions that referred to the feeling of control over the consequence of the action (i.e. target lights turning off). We found no main effect for the statements assessing the outcome agency (Friedman test; $\chi^2 = 0.25$ (df = 2, n = 37), p = 0.88), and neither morphological (Wilcoxon signed-rank test; Z = −0.44, p = 0.65) nor movement incongruence (Wilcoxon signed-rank test; Z = 0.35, p = 0.72) affected outcome agency compared to the *full arm* condition (Fig. S3). The reported feeling of authorship over the consequence of the action in the environment is resistant to manipulations in the visual appearance of the limb or noise in the performance of the action. However, the relation between the role of congruent information of the outcome of the task and the morphological appearance of the limb in reported ownership needs to be further explored.

The results reported here are consistent with a Bayesian framework previously proposed to explain the mechanisms underlying the RHI paradigm (Kilteni et al., 2015; Samad et al., 2015). In this model, the sensory information is integrated to estimate whether the sensory information originates from one common source (i.e. virtual hand, which leads to the illusion of ownership) or two (i.e. virtual and real hands). We propose a similar model to qualitatively explain the results reported in this study. In our scenario, the probability that there is a single hand is estimated given the following information: morphological appearance of the virtual hand (i.e. shape of arm, body continuity, texture, color), proprioceptive information from the real hand and congruent static position of the virtual hand, and consistent information from motor feedback of the real hand and visual input of the virtual hand during movement (see Supplementary Text 1 for mathematical formulation).

In the absence of visuomotor information (i.e. *full arm static* condition), the probability that there being single hand is estimated based on the morphological appearance and proprioceptive information. With a realistic appearance of the hand and consistent proprioceptive information, we expect a high probability of estimating that there is a single hand. The results reported in the *full arm static* condition are consistent with this prediction. By introducing a break in body continuity, we expect the probability that there is a single hand to decrease. This is consistent with a reduction of reported ownership in the *detached hand static* condition. This prediction changes when the subject actively controls the movements of the virtual hand in the dynamic conditions. The additional evidence, provided by the visuomotor information, increases the probability of integrating all the information as arising from the virtual hand when compared to the static case. This is consistent with what we observe in the dynamic conditions, as the comparison between *full arm dynamic* and *detached hand dynamic* did not yield a significant decrease in the reported ownership. According to the model, the highest probability of sensory input corresponding with a single hand should take place without a break in the body continuity and under active control of the arm. Experimentally, however, in our results, we did not find an increase in the *full arm* conditions. One possible explanation is that there is a saturation effect in which ownership scores cannot be manipulated to be higher given the experimental conditions.

An analogous reasoning can be applied to compare model and experimental results for the sense of agency. The belief that the participant caused the movements of the virtual arm can also be estimated from these sensory inputs. In the absence of any motor information, we would expect congruent morphological appearance and the proprioceptive information to elicit a strong sense of agency. This is what we report in the *full arm static* condition. When a break in the continuity of the arm is introduced, we expect the probability of all the information arriving from one hand to be reduced, as we see in the *detached hand static* condition. As in the predictions for sense of ownership, this is not the case in the presence of active control. Further support for this model comes from the *incongruent movement* conditions. We would expect that the noise added to the trajectory of the virtual hand would decrease evidence in favor of a single hand, consistent with a reduction of ownership and agency scores in the *incongruent movement* condition. While at this point the model does allow for a more quantitative test, there is a qualitative agreement that suggests further tests might be fruitful.

Taken all together, our results suggest that the contribution to the sense of ownership and sense of agency from each sensory modality varies depending on the experimental context and the available information in each condition.

Author contributions

VBR and GGdP designed the project; VBR, IC, and GGdP designed the experiment; GGdP supervised project; IC and VBR programmed the experimental software; VBR collected the data; VBR and GGdP analyzed the data; VBR and GGdP wrote the manuscript.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.concog.2019.04.003.

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Supplementary Material

Supplementary Text 1

We extend the model in Samad, M., Chung, A. J., & Shams, L. (2015). Specifically, we consider action control of a virtual limb as further evidence in favor that perception is compatible with a scenario with one hand (i.e. the virtual hand) and not of two hands (i.e. real and virtual hand) as being the source of all sensory information. The evidence in our virtual scenario has the following elements: semantic information,m_v (shape of arm, attachment to body, texture, color), proprioceptive information, x_p, action control as measured by a function comparing the intended trajectory, x_I, and the observed trajectory, x_O, with the form $\varepsilon(x_I, x_O)$; and any priors. As in our experiments we manipulated semantic information (i.e. attachment or not to body) and the observed trajectory, we are considering only m_v and $\varepsilon(x_I, x_O)$ in the following. The estimated probability that the scenario corresponds to a single hand, $h = 1$, can be written using Bayes' theorem as

$$P\big(h = 1\big|m_v, \varepsilon(x_I, x_O)\big) = \frac{P(m_v, \varepsilon(x_I, x_O)|h = 1)P(h = 1)}{P(m_v, \varepsilon(x_I, x_O)|h = 1)p(h = 1) + P(m_v, \varepsilon(x_I, x_O)|h = 2)P(h = 2)}$$

Assuming for simplicity that semantic and control information are independent, and comparing the probabilities for the one hand ($h = 1$) and two hands ($h = 2$) scenarios we get

$$\frac{P(h = 1|m_v, \varepsilon(x_I, x_O))}{P(h = 2|m_v, \varepsilon(x_I, x_O))} = \frac{P(m_v|h = 1)P(\varepsilon(x_I, x_O)|h = 1)P(h = 1)}{P(m_v|h = 2)P(\varepsilon(x_I, x_O)|h = 2)(1 - P(h = 1))}$$

We further model that an illusion occurs when this ratio is above a certain threshold, or equivalently when the logarithm of the ratio is above a threshold

$$\log\frac{P\big(h = 1\big|m_v, \varepsilon(x_I, x_O)\big)}{P\big(h = 2\big|m_v, \varepsilon(x_I, x_O)\big)} > \theta$$

giving

$$\big[\log\big(P(m_v|h = 1)\big) - \log\big(P(m_v|h = 2)\big)\big] + \big[\log\big(P(\varepsilon|h = 1)\big) - \log\big(P(\varepsilon|h = 2)\big)\big] > \theta$$

where we have absorbed the priors into a new threshold constant.

For a comparison between *full arm static* and *full arm dynamic*, note that the first term in square brackets is the same in both cases. For the second term in square brackets, note that the *full arm static* is compatible with a single hand but even more so the dynamic one, giving a higher value for the dynamic case. The *dynamic* case might then have a higher total value sum of the two terms but both static and dynamic can be above threshold and therefore give similar ownership illusions. It is interesting to speculate that experimental differences among different groups might then arise because the priors are set-up differently and therefore in how easy subjects might go above threshold.

The situation is different in the case of a *detached arm*. Here, the first term in square brackets is much smaller than before, if not negative, both for static and dynamic scenarios, going against the illusion. However, in the dynamic case, the second square bracket has a much higher value than in the static case because the intended and observed trajectories coincide many times making it less likely to come from two hands. The sum of the two terms is then much more likely to be above threshold in the dynamical case.

Other results might also be explained using a similar logic. For example, in the incongruent arm trajectory scenario, the first term in square brackets is the same than in a no noise scenario. However, the second term has a lower value as the situation is now more compatible with a two hands scenario. This gives a smaller total sum of the two terms and more likely below threshold

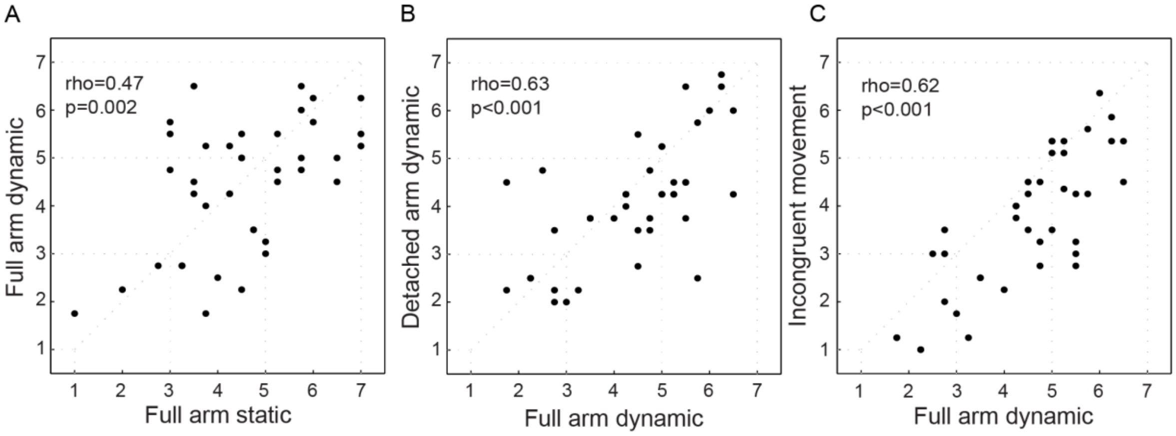

Figure S1. Correlations and subgroup comparison in different pairs of conditions. (A) Comparison of the *full arm static* and *full arm dynamic* conditions. Participant responses were correlated (Spearman ρ=0.47, p=0.003). In the subgroup comparison, movement caused a decrease in the medians of high ownership (p<0.001, n=16), but not in medium (p=0.91, n=15) nor low ownership groups (p=0.03 (not significant under Bonferroni correction), n=6). (B) Comparison of the *full arm* and *detached hand dynamic* conditions, participants responses were correlated (Spearman ρ= 0.63, p<0.001). None of the subgroup comparison showed a significant difference (p=0.022 (not significant under Bonferroni correction), n=17, p=0.09, n=11, and p=0.48, n=9, for high, medium and low ownership score respectively). (C) Comparison of the *full arm dynamic* and *incongruent movement* conditions showed a strong correlation in the responses (Spearman ρ=0.62, p<0.001). Only the medium ownership groups showed a significant decrease in the ownership scores group (p=0.002, n=15), but not in high (p=0.03 (not significant under Bonferroni correction), n=17), or low (p=0.14, n=6).

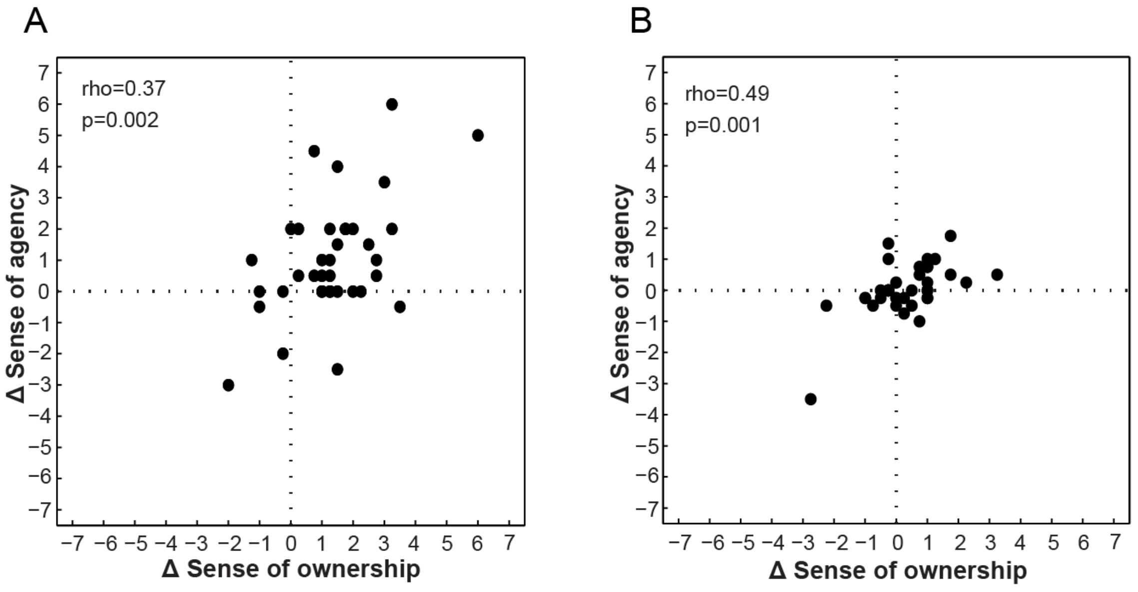

Figure S2. Correlation between changes in ownership scores and changes in agency scores in (A) full arm static and detached hand static (Spearman ρ=0.37, p=0.002), and (B) full arm dynamic and detached hand dynamic (Spearman ρ=0.49, p=0.001).

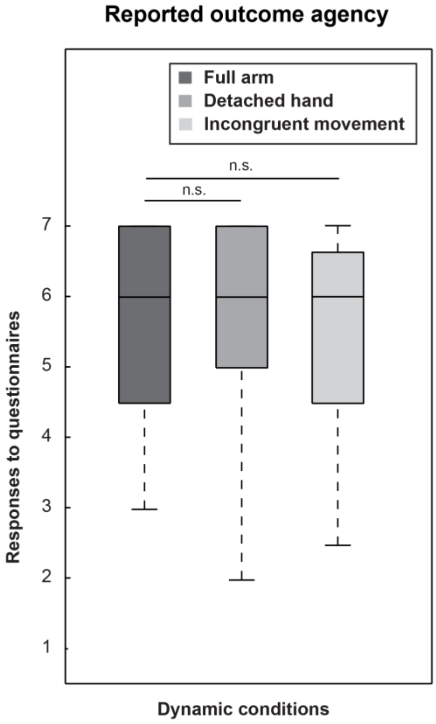

Figure S3. Reported outcome agency scores in the dynamic conditions. Morphological and movement incongruence did not change reported ownership over the outcome of the actions. The middle quartile indicates the median value and the whiskers indicate the most extreme values that are not considered outliers. * The Bonferroni corrected p-value for these comparisons was p=0.004.