UNIVERSITAT DE BARCELONA

Neurophysiological signatures of the body representation in the brain using Immersive Virtual Reality

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Submitted to the

Doctorate Program in Clinical Psychology

Facultat de Psicologia, UNIVERSITAT DE BARCELONA

Neurophysiological signatures of the body representation in the brain using Immersive Virtual Reality

Thesis submitted by

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for the degree of

Doctor (PhD) in Clinical Psychology

with the distinction of International PhD after her research stay at the

Massachusetts Institute of Technology (MIT)

presented at

Universitat de Barcelona, 2014

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ACKNOWLEDGEMENTS

First of all, I would like to thank my supervisor Prof. Mel Slater for giving me the opportunity to start this long journey in which I've not only been able to learn about many new concepts regarding the body and the brain, but also about how to overcome obstacles while being creative and enthusiastic. Mel has always been supportive when necessary and his experience and thoughts have greatly influenced me and this thesis. He has also taken me to the next level by empowering me to visit other institutions and to apply for grants. As a result I have received a three years FI-DGR grant to fund my PhD; a BE-DGR travel grant to do a research stay at the Massachusetts Institute of Technology (MIT); and I researched at the University College London (UCL) and at Microsoft Research. After the PhD I hope Mel's good advice and vision will continue influencing my future.

Second, I would like to thank Prof. Antoni Rodriguez-Fornells, who has contributed to my greater understanding of many aspects in neuroscience and more particularly of the field of human electrophysiology. He has been a key advisor in most of my EEG analysis, supervising and providing new ideas and insights on the meaning of the brain activity in my experiments. His calming personality and wide experience have proved vital throughout all the work that I present in this thesis.

I have especial thanks also for my proof readers and colleges who have patiently contributed to significant parts of this thesis by providing useful comments: Adam Sedó, Sameer Kishore, Dr. Bernhard Spanlang, Dr. Antonella Maselli and Dr. Laurence Lachamp.

Finally, I want to mention some other researchers that in one way or another have contributed to my work and helped me going through my PhD: Prof. MV Sanchez-Vives, Dr. T Peck, Dr. G Padrão, Dr. J Llobera, Dr. D Perez-Marcos, Dr. D Borland, Dr. K Kilteni, Dr. P Chou, Dr. J Moore, Dr. K Blom, Dr. J Arroyo Palacios, Dr. C Groenegress, Dr. I Bergstrom, Dr. JM Normand, Dr. A Antley, Dr. D Zhang, Dr. X Pan, Dr. D Friedmann, Dr. M Martini, Dr. I Kastanis, A Bellido, E Kokkinara, E Giannopoulos, D Banakou, S Gilroy, C Crusafon, R Pizarro, B Nierula, A Pomes, A Rovira, R Carbonell, I Sanjuan. My family: Adrián González, Dr. M Teresa Franco, Eki González, Elisa González, Mercé Galí, Pere Sedó, Bruna Sedó and (again) Adam Sedó who has constantly remained my link to rationality keeping me from frustration.

This doctorate was funded by the European Union Future and Emerging Technologies (FET) project VERE: "Virtual Embodiment Robotic Re-Embodiment", grant agreement number 257695. Also supported by the three years FI-DGR 2011 pre-doctorate grant, given by the Agència de Gestió d'Ajuts Universitaris i de Recerca of the Generalitat de Catalunya (AGAUR-Gencat) co-funded by the European Commission - European Social Fund (EC-ESF).

CONTENTS

LIST OF PUBLICATIONS

The work presented in this thesis has the objective to be a useful contribution to the scientific community; to enhance dissemination it has been compiled into several publications. In this section I will list all the publications that have been published as a result of my work in the EVENT Lab, including all the work related with my PhD.

Chapter 4

M Gonzalez-Franco, TC Peck, A Rodríguez-Fornells, M Slater (2014) *A Threat to a Virtual Hand Elicits Motor Cortex Activation*. Experimental Brain Research 232: 3. 875-887 March 2014 DOI: 10.1007/s00221-013-3800-1

Chapter 5

G Padrão[+], **M Gonzalez-Franco**[+], MV Sanchez-Vives, M Slater, A Rodríguez-Fornells (2016) *Violating body movement semantics: neural signatures of self-generated and externally-generated errors.* NeuroImage 124:A. 147-156 January 2016 DOI: 10.1016/j.neuroimage.2015.08.022

Chapter 6

M Gonzalez-Franco, AI Bellido, KJ Blom, X Alvarez Blanco, V Orvalho, A Rodriguez-Fornells, M Slater. *The neural basis of self-recognition in computer generated faces: An Event-Related Potential study.* (in submission)

Other publications

S Kishore, **M Gonzalez-Franco**, C Hintermüller, C. Kapeller, C Guger, M Slater, K J Blom (2014) *Comparison of SSVEP BCI and Eye Tracking for controlling a humanoid robot in a social environment*. Presence: Teleoperators and Virtual Environments 23:3. MIT Press

B Spanlang, JM Normand, D Borland, K Kilteni, E Giannopoulos, A Pomes, **M Gonzalez-Franco**, D Perez-Marcos, J Arroyo-Palacios, X Navarro-Moncunill, M Slater (2014) *How to build an embodiment lab: achieving body representation illusions in virtual reality* Frontiers in Robotics & AI/Virtual Environments 1:9 DOI: 10.3389/frobt.2014.00009

[+] Both authors *contributed equally* to the present study

M Gonzalez-Franco, PA Chou (2014) *Non-linear modeling of eye gaze perception as a function of gaze and head direction.* Quality of Multimedia Experience 2014, QoMEX 2014. IEEE. Singapore

M Gonzalez-Franco, SJ Gilroy, JO Moore (2014) *Empowering Patients to Perform Physical Therapy at Home.* Engineering in Medicine and Biology Society, EMBC 2014 Annual International Conference Chicago, IL, USA: IEEE EMBS.

J Llobera, **M Gonzalez-Franco**, D Perez-Marcos, J Valls-Solé, M Slater, MV Sanchez-Vives (2013) *Virtual reality for assessment of patients suffering chronic pain: a case study*. Experimental Brain Research 225: 1. 105 117 March 2010 DOI: 10.1007/s00221-012-3352-9

M Gonzalez-Franco, P Yuan, D Zhang, B Hong, S Gao (2011) *Motor Imagery based brain-computer interface: a study of the effect of positive and negative feedback*. Engineering in Medicine and Biology Society, EMBC 2011 Annual International Conference Boston, MA, USA: IEEE EMBS. DOI: 10.1109/IEMBS.2011.6091560

M Gonzalez-Franco, D Perez-Marcos, B Spanlang, M Slater (2010) *The contribution of real-time mirror reflections of motor actions on virtual body ownership in an immersive virtual environment.* Virtual Reality Conference (VR), 2010 IEEE pp.111-114 Waltham, MA, USA: IEEE ComputerSocietyPress DOI: 10.1109/VR.2010.5444805

Poster presentations

M Gonzalez-Franco, AI Bellido, M Slater (2014) *Measuring neural traces of self-identification in look-alike avatars*. Proceedings of the 2nd International VERE PhD Symposium. Barcelona (Spain)

M Slater, **M Gonzalez-Franco**, TC Peck, A Rodríguez-Fornells (2013) *Motor cortex correlates of virtual body ownership*. SfN Society for Neuroscience 2013. San Diego (USA)

KJ Blom, **M Gonzalez-Franco**, J de la Vega, C Hintermüller, C Guger, M Slater (2012) *A robust brain computer interface with in situ stimuli in an stereoscopic head mounted display*. 8th FENS Forum of Neuroscience. Barcelona (Spain)

M Gonzalez-Franco, TC Peck, M Slater (2011) *Virtual Embodiment Elicits a Mu Rhythm ERD when the Virtual Hand is threatened*. 8th IBRO World Congress of Neuroscience. Florence (Italy)

M Gonzalez-Franco, S Kishore, J de la Vega, C Hintermüller, KJ Blom, C Guger, M Slater (2011) *Immersive robot control through SSVEP*. Proceedings of the 1st International VERE PhD Symposium. Barcelona (Spain)

D Pérez-Marcos, **M Gonzalez-Franco**, B Spanlang, M Slater, MV Sanchez-Vives (2010) *Control by Brain-Computer Interface of a Virtual Body*. 16th Annual Meeting of the Organization for Human Brain Mapping. Barcelona (Spain)

ABSTRACT

Several studies have shown that it is possible to substitute a person's body by a virtual one giving rise to illusions of ownership and agency with respect to the virtual body. The effects and traces of such body substitution can be measured using subjective reporting, behavioural and objective physiological measures. However, considerable work remains for uncovering the underlying neurological mechanisms that trigger those effects. In this thesis we aim to measure neurophysiological correlates of ownership and agency, and by doing so to contribute to a greater understanding of the functioning of the body representation in the brain. In order to address this question we carried out a series of studies where the representation of the human body and activity in which it was engaged were externally manipulated in various ways through multisensory stimulation, while measuring the corresponding electroencephalography (EEG) responses. Through this multisensory stimulation, healthy humans experienced full body ownership and agency illusions over virtual bodies – as if their real bodies were perceptually substituted by these bodies.

Specifically, Virtual Reality (VR) was used to give participants an egocentric view of a co-located virtual body, using a Head-Mounted Display. They could move this body through real-time motion tracking thus providing synchronous visuo-motor stimulation. The combination of the first person perspective and synchronous visuo-motor stimulation resulted in full body ownership and agency illusions over the virtual body, which we refer to as virtual embodiment. Under these circumstances we then explored the implications of such bodily perceptual manipulations in the brain with EEG.

A first study was intended to validate whether a virtual body can be effectively recognized as a feasible substitute to the self-body at the unconscious level. A motor cortex activation equivalent to what would be expected in a real scenario was found after exposing participants' virtual body to harmful stimuli. This particular result provides a measure of response-as-if-real indicating that participants tended to accept their given virtual bodies as their own.

In a second study, the consequences of the agency mechanisms that provide the sensation of control over our own body actions were explored through virtual embodiment. In this study participants underwent sporadic agency disruptions while performing rapid arm movements. In certain conditions, the virtual hand of participants moved autonomously in the opposite direction to the participants' real hand. Results provide evidence of specific neural processes responsible for detecting externally induced agency disruptions. Moreover, these neural processes were correlated with the strength of the subjective embodiment illusion. This study was also aimed at widening current perspectives on agency schemas, proposing and demonstrating the existing theory of re-afferent and feedback error mechanisms that are concurrently functioning in the brain to detect agency disruptions.

In a third study the implications of the external appearance of the substitute virtual body for self-recognition were explored. We designed an experiment in which healthy participants were exposed to self, familiar and unknown faces of look-alike avatars. Results showed shared underlying mechanisms for self-identification in real and virtual faces in the visual cortex. In particular, neurophysiological traces showed that virtual faces are classified as real faces – in contrast to what happens with the classification of other objects (cars, flowers, etc.). Furthermore, the visual cortex differentiated familiarity levels among virtual faces. These are novel insights contributing to the better understanding of why different looking avatars can have an impact on participants' performance or behaviour, thus being useful both for the fields of virtual embodiment and of self-recognition.

Overall the research in this thesis explores brain activity through EEG of the immediate experience of having and controlling a body. Empirical evidence is presented to validate the use of virtual reality for the research of the body representation in the brain. Additionally, novel neural signatures of the bodily perceptual manipulations are presented through a set of studies. Results are put into context with an in-depth review of literature on self-awareness, body perception, body ownership and agency theories at the beginning of this thesis.

RESUMEN

Múltiples estudios han demostrado que es posible sustituir el cuerpo de una persona por uno virtual produciendo ilusiones de posesión y agencia sobre este nuevo cuerpo. Los efectos y trazas de esta sustitución de cuerpos se pueden medir de manera subjetiva, a través del comportamiento del participante o a través de medidas fisiológicas objetivas. Sin embargo, restan por descubrir muchos de los mecanismos neurológicos subyacentes que provocan dichos efectos. Esta tesis pretende medir correlaciones neurofisiológicas de las ilusiones de posesión y agencia, y de esta manera contribuir al mayor conocimiento del funcionamiento de la representación corporal en el cerebro. Para ello realizamos una serie de estudios donde la representación del cuerpo humano y su actividad son externamente manipuladas de diversas maneras mediante estimulación multisensorial mientras se registra la correspondiente actividad cerebral mediante electroencefalografía (EEG). La estimulación multisensorial permite que humanos sanos puedan tener ilusiones de posesión y agencia sobre avatares (como si sus cuerpos hubieran sido perceptualmente sustituidos por cuerpos virtuales).

Más en concreto, mediante el uso de Realidad Virtual (RV) los participantes tienen una perspectiva egocéntrica de un cuerpo yuxtapuesto al suyo (a través de cascos de realidad virtual estereoscópicos). A la vez que pueden mover este cuerpo mediante sistemas de rastreo del movimiento en tiempo real produciendo una estimulación visuo-motora síncrona. La combinación de la perspectiva en primera persona con la estimulación visuo-motora da como resultado una ilusión de posesión y control total del cuerpo virtual, a la que nos referimos como encarnación virtual. En este escenario exploramos las implicaciones de estas manipulaciones perceptuales en el cerebro mediante EEG.

Planteamos un primer experimento con intención de validar si el cuerpo virtual se puede efectivamente reconocer como un sustituto viable del propio cuerpo a nivel del subconsciente. Tras exponer el cuerpo virtual a estímulos nocivos se halla una activación en la corteza motora de los participantes equivalente a la que sería de esperar en un escenario real. Este resultado-como-real hace indicar que los participantes ciertamente aceptan sus cuerpos virtuales dados como su propio cuerpo.

En un segundo experimento se estudian las consecuencias de los mecanismos de agencia que nos proporcionan la consciencia de nuestras acciones corporales y motoras, a través de tecnologías de substitución virtual del cuerpo. Los participantes se someten a disrupciones esporádicas de sus acciones mientras realizan movimientos rápidos con su brazo. En algunas ocasiones, la mano virtual del participante se mueve autónomamente y en dirección contraria a la mano real del participante. Los resultados proporcionan evidencias de procesos neuronales específicos responsables de detectar disrupciones de agencia inducidas externamente. Asimismo, estos procesos neuronales se correlacionan con la ilusión de posesión del cuerpo medida a través de cuestionarios. Este estudio profundiza en las perspectivas actuales de los esquemas de agencia, proponiendo y demostrando la teoría existente de mecanismos de errores re-aferentes y de retro-alimentación que funcionan concurrentemente en el cerebro para detectar disrupciones de agencia.

Se propone un tercer experimento para explorar las implicaciones de la apariencia externa del cuerpo virtual a la hora de auto-reconocerse. Diseñamos un experimento en el que los participantes se exponen a caras de avatares que se parecen a ellos, a un familiar o a una persona que no conocen. Los resultados muestran mecanismos subyacentes compartidos de auto-identificación de caras reales y virtuales en la corteza visual. En particular, las trazas neurofisiológicas muestran que las caras virtuales se clasifican igual que las reales (en contraste con lo que ocurre durante la clasificación de otros objetos como coches o flores). Además, la corteza visual diferencia niveles de familiaridad entre las caras virtuales. Contribuyendo así de manera novedosa a entender porque avatares con diferente apariencia tienen un impacto en el comportamiento de los participantes, y por ello siendo útil tanto para el campo de la realidad virtual como para el de la auto-identificación.

Globalmente, la investigación de esta tesis explora las trazas cerebrales mediante EEG de la experiencia inmediata de poseer y controlar un cuerpo. Se presentan evidencias empíricas para validar el uso de realidad virtual en la investigación de la representación del cuerpo en el cerebro. Asimismo, a través de varios estudios mostramos novedosas trazas neurofisiológicas relacionadas con las manipulaciones corporales y perceptuales. Los resultados y experimentos se contextualizan mediante una revisión en profundidad de la literatura existente en consciencia, percepción corporal y teorías de posesión y agencia del propio cuerpo.

1. INTRODUCTION

Humans and animals are able to survive in part thanks to the primal reflexes that take place unconsciously when they respond to external stimuli automatically. These very rapid automatic responses have been a selection advantage for all species, yet as for many things in nature, the facts are clear, but the mechanisms responsible are complex and hard to isolate from other concurrent events. In the case of the automatic responses, the behavioural reactions are easy to predict: i.e. *if I accidentally put my hand over a fire,* with very high probability the outcome will be: *I will rapidly remove the hand from there*; however, the underlying neural mechanisms that trigger the responses to this and other stimuli are far more complex and quite unknown. Even less explored is the combination of the unconscious and the conscious processes in the brain: *I have removed the hand so fast* (unconsciously) that it isn't until later that *I am aware of the action undertaken* (consciously). We do know that both cognitive processes are based on very fast adaptive models through which the brain controls the body and the body sends signals to the brain [Chiel and Beer 1997]. However, given its multiple components –sensory input, pre-existing information, multiple effectors– and the fast cadence of the processes involved, this integration has traditionally been difficult to study. In this thesis we are interested in measuring some aspects of the body representation in the brain through to the temporal dynamics of the responses to different stimuli using electroencephalography (EEG).

Most of the previous and current research that explored how the brain integrates bodily signals has been based on responses to perceptual stimuli using, in some cases, several neuroimaging techniques to study the underlying processes of bodily illusions [Blanke 2012]. However, as in other scientific fields, sometimes processes need to be isolated or externally modified in order to be able to really understand them, which in our area of study would be highly complex since one cannot simply disconnect a part of the brain to study the effects of such manipulations for obvious ethical reasons. Therefore some of the most drastic investigation in the field has traditionally been carried out on other animals (rats) and primates that can be tested under laboratory conditions [Graziano 1999; Graziano et al. 2002; Ongür and Price 2000]. However humans, unlike primates, not only have the ability to report what they are conscious of, but also the capacity to focus their attention on demand while taking part in visual experiments. Furthermore, while exploring animals' responses can contribute to the basic research on the underlying mechanisms of the brain, when it comes to the study of the neural correlates of attention and consciousness, it is also necessary to directly study the functioning of the human brain.

In order to reproduce experiments that are ethically impossible in a real scenario with humans and where the intrinsic limitations of manipulating the bodily signals make impossible the alteration of spatiotemporal coherences of multisensory stimulations we turn to Virtual Reality (VR). Immersive Virtual Environments (IVE) can be used to systematically test particular stimuli in humans without compromising their integrity. Extensive research has proven that reactions in virtual environments are equivalent to the ones in the corresponding real scenario [Sanchez-Vives and Slater 2005; Meehan et al. 2002]. This is the major foundation that allows real experimentation with humans to take place inside virtual environments obtaining results similar to what would be expected if the experiments would take place in reality.

Additionally, in such technical setups we can "substitute" a human body by a virtual one, generating what is known as an embodiment illusion [Kilteni et al. 2012]. This substitution technology provides a reliable platform to study how humans represent their bodies in the brain and which are the brain responses to body changes, motor actions, and body perception in general. In fact, VR allows us to alter the virtual body in ways that would not be achievable in the real world, for example changing body sizes [Banakou et al. 2013; Normand et al. 2011], modifying limbs [Kilteni et al. 2012], altering the race [Peck et al. 2013] or gender and age [Slater et al. 2010] of experiment participants. Further studies have explored the circumstances in which the body substitution illusion can be experienced and beyond which thresholds it disappears [Kokkinara and Slater 2014; Maselli and Slater 2013]. This previous research has confirmed the high plasticity of the human brain and that humans are able to accept other bodies as their own even if they are subject to quite radical alterations of the body. A more in depth overview of these and other studies will be presented in the background section.

In this thesis we will leverage similar body "substitution" technologies to further explore how the brain and the body are connected.

1.1. Research Problem

Several studies have shown that it is possible to substitute a person's body by a virtual one and measure the effects and traces of such embodiment via experiments using subjective reporting, behavioural and/or objective physiological measures [Llobera et al. 2013; Maselli and Slater 2013; Kokkinara and Slater 2014]. However, the underlying neurological mechanisms that trigger those effects are not yet clear. In this thesis we aim (i) to measure aspects of the neurological responses to body ownership illusions, (ii) to contribute to the greater understanding of the functioning of the body representation in the brain and (iii) to explore how the perceptual system responds to external/internal stimuli that affect the self-body perception, also known as minimal self-awareness [Gallagher 2000; Blanke and Metzinger 2009].

To address these three propositions we will dissociate conscious from unconscious reactions to the stimuli. While conscious responses in human experimentation are easier to measure as they can be reported subjectively, unconscious responses are much more difficult to detect but are more objective variables. Physiological measures such as heart rate deceleration, respiration rate, galvanic skin response, etc. have been used as reliable objective outputs of the autonomic system [Llobera et al. 2013; Maselli and Slater 2013; Slater et al. 2010; Meehan et al. 2002]. The challenge is not only dissociating unconscious from conscious but also finding some of the brain processes that trigger the autonomic system responses. Checking the physiological outputs to a stimulus is just the first step to comprehend how the signals are processed, to fully understand how these sensory signals from the body are integrated in the brain it is necessary to study the neurological temporal dynamics.

1.2. Research Questions

This thesis addresses the following three hypotheses under the initial proposition that changes to the embodied virtual avatar can be measured through EEG as responses to instantaneous stimuli.

Hypothesis 1: *A stimulus directed to the embodied virtual body will result in a brain response equivalent to what we would expect if the stimulus happened to the participant's real body*. This will be true if people accept their given virtual bodies as if they were their own, meaning that virtual body substitutes (avatars) are integrated as the own body also at an unconscious level. Chapter 4 of this thesis will focus on an experiment that assesses this hypothesis by providing a harm stimulus to the virtual body and measuring the brain processing and reaction of the participants. This particular study shows that virtual bodies can be effectively integrated as the own body; providing evidence of unconscious motor activity in the motor cortex as a response to a threat to the virtual body.

Hypothesis 2: *When somebody is embodied in a virtual avatar and experiences agency of that body, any break in that agency (such as hijacking in the movements of the virtual body) would be clearly perceived as an externally generated error.* The expectation is that a higher feeling of embodiment would lead to a stronger perception of the break in agency. Chapter 5 will present a second study describing a set of experiments that explore the implications at a neurological level of such an experience of control over the body and the agency of the actions performed. This second study widens the current knowledge on agency schemas, proposing and demonstrating the existing theory of re-afferent and feedback error mechanisms that are concurrently working in the brain to detect agency disruptions. It is also proposing a new way to differentiate among internal versus external errors by means of EEG.

Hypothesis 3: *Given a virtual body we can potentially measure different levels of self-identification: an avatar that looks like the participant is interiorized unconsciously to a different level than an avatar that does not look alike*. During the embodiment illusion avatars are accepted as the self-body through multisensory stimulation. This illusion can be induced to avatars of different races and genders that share more or less similarities to the participant [Peck et al. 2013]. However, studies have shown that the more the avatar looks like the participant the stronger the identification is [Bailenson and Segovia 2010]. In Chapter 6 we present an approach to study the underlying mechanisms of such self-identification with the avatar's appearance using EEG. This third study enhances the current perspectives of self-recognition in avatars and shows how exteroceptive components may affect the embodiment illusion.

In the following chapters different experiments specifically developed to address the central concern of this thesis are presented. All the different experimental setups exploit electroencephalography recording in order to explore and measure the traces of the underlying neurological mechanisms that trigger the full-body illusions.

1.3. Scope

In the current thesis we are investigating how the brain and the body integrate at a neurological level by exploiting IVE and EEG recording. Several experiments are presented to widen current perspectives on how humans identify the body as their own and how they integrate its sensory signals in the brain. We limited our measures of the EEG to the study of Event Related Potentials (ERPs) as response to repeated stimuli observation. The setup limited natural movements of the participants in some cases to reduce noise on the EEG. Significant findings on the EEG levels were associated to underlying mechanisms. Although it is true that some people can learn to control their brain activity in real time using Brain Computer Interfaces we will not address such cases [Guger et al. 2003]. Subjective questionnaires have been used as dependent variables to assess the relationship between conscious and unconscious mechanisms, but in general the subjective evaluations are not the focus of this thesis.

During the experimentation, the real bodies of the participants were substituted by avatars using Head Mounted Displays (HMDs) and real time tracking devices when necessary. This thesis is based on prior studies on embodiment where the same technologies have already demonstrated significant embodiment illusions [Kokkinara and Slater 2014; Maselli and Slater 2013; Banakou et al. 2013]. Here we mainly focused on novel research rather than replicating previous embodiment results. I.e. if synchronous visual motor correlations have been shown as a good method to induce the embodiment illusion we will use it as starting point and tweak the motor control to study sudden breaks in the agency of the movement.

All of the experiments presented in this thesis focused on the virtual body that substitutes the participant's own body. In all of the setups the substituting avatar is the only virtual body present in the scene, and since no other avatars are present, the scope of the study will not focus on topics such as the interaction with other virtual avatars or empathy towards others. Furthermore since the embodiment illusion requires a first person perspective, other IVE technology such as the CAVE systems will not be used for the purposes of this thesis.

1.4. Contributions

This thesis aims to contribute to a better understanding of how the brain and the body are connected. We used IVE and novel surrogate technologies to induce strong illusions of embodiment in avatars [Slater et al. 2010; Maselli and Slater 2013; Kokkinara and Slater 2014]. We then explored the extent to which these new virtual bodies were accepted by the participants and found that:

(i) Neurophysiological traces demonstrated that the virtual body is integrated as a feasible substitute for the real one at the unconscious level. These effects were tested on healthy participants who were first embodied in a collocated avatar and subsequently exposed to a harmful stimulus to their virtual body. Evidence shows that when a sudden instantaneous stimulus threatens their embodied virtual avatar there is an unconscious motor preparation equivalent to the one that would be expected if the threat were to happen to the real body. We introduce an objective measure of response-as-if-real based on cortical activation that determines that if an embodied virtual avatar is integrated as the participant's real body, the responses to external stimuli will be processed by natural unconscious mechanisms. Yet another evidence that surrogate bodies can be effectively integrated as the self-body [Lenggenhager et al. 2007; Slater et al. 2009; Petkova and Ehrsson 2008]. Additionally, the results represent another validation that humans behave realistically in virtual scenarios when they have the illusion of presence [Sanchez-Vives and Slater 2005; Meehan et al. 2002].

(ii) As part of the full body experience, visual motor correlations create a strong illusion of control over an avatar's motor actions. We demonstrate that this illusion is also integrated at an unconscious level and that any disruption in agency is rapidly interpreted in the brain as a violation in the body semantics. These effects were tested on healthy participants that were first embodied on a collocated avatar through synchronous visual motor correlations while performing an Eriksen flanker task [Rodriguez-Fornells et al. 2002]. This kind of motor action task is usually executed to study fast decision making and error monitoring. Through a series of experiments, participants were exposed to correct trials, internal errors – in which the participant made a mistake in the decision making –, and externally induced errors – in which the avatar moved the hand incongruently with the participants intended movement. We present new neural traces of how the agency mechanisms on surrogates work when related to motor actions. These new results provide a new insight on the error monitoring systems that match the efferent (intended movement) and re-afferent (execution result) signals, providing new evidence to the theories that support the existence of a re-afferent feedback model in the brain that compares the executed action to an efferent copy to detect incongruences [Grüsser 1995; Tian and Poeppel 2010; Sommer and Wurtz 2002].

(iii) The external appearance of the surrogate influences the self-recognition and possibly affects the exteroceptive part of the embodiment illusion. An observational experiment was carried out in which healthy participants were exposed to self, familiar and unknown faces of look-alike avatars. Neurophysiological traces showed that different familiarity levels are processed in the visual cortex. These effects replicated the findings on real faces [Keyes et al. 2010]. Results also showed that virtual avatar faces are classified in the visual cortex as real faces after a fast adaptation phase, indicating that avatar faces are just as real to the brain as any other face; in contrast with what happens with other object classifications (cars, flowers, etc.) that have different voltages than faces [Bentin et al. 1996]. These results contribute to the virtual embodiment science that uses avatars to substitute bodies, as it not only shows that extereoceptive self-identification of participants with their virtual counterparts is possible but also that look-alike avatars may enhance the embodiment illusion.

These new findings are consistent with the literature on full body ownership illusions, agency, consciousness, minimal self-awareness, and body ownership theories. An in-depth review of all of these concepts is provided in the background section.

2. BACKGROUND

2.1. The body representation in the brain

R. Descartes described in 1641 the dualism between the mind and the body, proposing that the mind controls the body but the body also influences the mind. Although this declaration derives from a philosophical standpoint, it can also be described from a physiological perspective since the brain and the body are known to interact both ways through the Central Nervous System (CNS) – the brain receives signals from the receptors (afferent path) and sends actions to the effectors (efferent path).

As introduced in Chapter 1 this thesis aims to explore how the body is represented in the brain, therefore the study of the bodily perception and its theories are of great importance for the development of the thesis. This section will first discuss the perceptual processing of stimuli in the brain, explaining the top-down and bottom-up theories of stimuli driven systems and presenting the basics of multisensory integration. We will discuss the implications of external appearance, body ownership, and agency for self-awareness. A detailed review exploring the phenomenology of owning a body and controlling it including relevant experiments from the literature to illustrate the different concepts will follow. Models for motor control will also be introduced. Additionally, several pathologies such as Schizophrenia, Somatoparophrenia and Alzheimer will be reported at different points for illustration of dysfunctional singularities.

In summary, "The brain and the body" section will introduce several neuroscience concepts necessary for understanding the experiments proposed in further Chapters. Some of them are of more relevance to the study of the body representation in the brain and the minimal self-awareness [Gallagher 2000; Blanke and Metzinger 2009]: i.e. *this is me*. At the end of this section the reader will have a better understanding of the difference between having an experience vs. being aware of having an experience.

2.1.1. Perceptual processing

In all of the experiments of this thesis we provide several stimuli to the participants, being a major factor the perceptual processing of such. A in detail description of the different senses and how they may influence the participants is discussed in this section.

There are multiple sensor modalities that contribute to the afferent inputs of the CNS. Some are capable of measuring the environment status (exteroceptive modalities), generally known as senses – taste, sight, hearing, smell, touch. Others that remain less known provide information about internal aspects of the body such as the proprioception that senses the relative position of the parts of the body, or the interoception that senses the normal functioning of the body [Berlucchi and Aglioti 2010].

The brain combines all these measures to get a global overview of the external and internal status of the body and to evaluate complex scenarios. This combination of modal inputs is known as multisensory integration and it is believed to be widespread in cortical and subcortical regions of the brain [Bavelier and Neville 2002]. Some single neurons also related with multisensory integration have super additive firing rates that are modulated by two or more sensory inputs, when one sensor modality provides information the cell fires at different rates than when two sensor modalities deliver coherent information regarding the same stimuli. Therefore, these cells are not only contrasting the input but are also enhancing resolution and likeliness of the perceived stimuli when multiple coherent inputs are delivered [Stein and Stanford 2008].

Generally sensors give coherent and synchronous information, which allows for a correct interpretation of the stimuli and the environment. However when one or more sensors give incoherent, missing or asynchronous information the interpretation of the signals may incur into a breach in perception. For example auditory manipulations have been shown to modify the tactile perception of a textured surface: while performing a blind tactile exploration on a constant surface, participants estimated smoother surfaces when listening to higher frequencies, whereas lower frequencies induced rougher perceptions on the same surface [Guest et al. 2002].

Furthermore, the incoherence between different inputs is likely to induce bodily hallucinations. In fact, it is believed that some patients suffering somatoparophrenia, asomatognosia or schizophrenia have a reduced multisensory integration in a number of sensor modalities, for example during target detection tasks [Williams et al. 2010]. Even if the inputs are coherent, the literature has described multiple cross-modal effects when one sense influences the others. Sometimes, this influence may be strong enough to generate synaesthesias – e.g. between vision and sound: provided only sound as the input some people are able to see colours [Ward et al. 2006].

Additional studies on sensory deprivation on monkeys and cats showed that these cross-modal effects are also plastic and malleable. Under deprivation, areas predominantly visual are recruited by tactile modalities in monkeys, while in cats an improvement in auditory localization was found in such circumstances [Bavelier and Neville 2002]. There is evidence that any sense could influence others [Ghazanfar and Schroeder 2006], however humans are visual animals and in many situations the visual input tends to dominate other modalities [Posner et al. 1976]. This visual predominance has been exploited largely for body ownership manipulation research as we will see during this Chapter. Besides, it will have major implications for the hypothesis testing in the present work.

When no perceptual incoherencies are found, both the multisensory integration and its processing usually develop into rapid responses, most of the times automatic and unconscious.

Unconscious automatic mechanisms can potentially be used as objective measures of the reaction to stimuli in experimental conditions. Since these kinds of processes cannot be manipulated easily by participants, subjectivity is reduced to the minimum in the results obtained.

Typically, automatic mechanisms influence heart rate, respiration, electrodermal conductance and other physiological measures. All of them have been extensively used to account for human responses to experimental stimuli through the field of psychophysiology [Andreassi 2000]. Most of the times they are used to measure arousal or stress: a heart rate deceleration has been found to be triggered by sudden unpleasant stimuli [Maselli and Slater 2013; Bradley et al. 2001; Slater et al. 2010]; while electrodermal conductance, also known as galvanic skin response (GSR), generally increases for given stressful situations [Meehan et al. 2002; Slater et al. 2006]. Although these are clear measures of the unconscious processing of stimuli, they are only physiological outputs that tell very little about how the perceptual processing works in the brain. Therefore, to better understand how these automatic responses are triggered we have to explore the processing of the original stimuli at a neurophysiological level.

There are two main approaches that simplify the functioning of the brain as a stimuli-driven system: the bottom-up and the top-down models [Connor et al. 2004]. In many occasions both models work together and may be hard to dissociate from each other.

During a pure bottom-up experience the brain behaves as a one-way stimuli-driven system. One or more of the receptors send signals to the CNS, which coordinates the information and sends a reaction to the effectors. This model responds to classical theories of perceptual processing where interactions between the brain and the body are carried through automatic mechanisms that remain at the unconscious level. In this approach, the responses are driven in a reflex-like manner and can be validated through single cell recordings in vitro conditions [Connors et al. 1982].

Nevertheless, sometimes the input cannot be processed by a simple bottom-up model since the output is not only influenced by the current information from the receptors but is also based on previous experience. Those cases that require an intelligent behaviour to the processing are well explained by the top-down models. During a top-down, an active and selective brain influences the processing of stimuli [Engel et al. 2001].

Visual detection tasks have been used to address the validation of both models. Usually these tasks present one singleton (the target to be detected) together with other identical stimuli with either different colour or shape (Figure 2-1). Participants are asked to perform a basic detection in which the singleton has to be dissociated from the rest. In this context, the first instinct is valid since there are no other concurrent confounding factors and there is no need of a top-down selection (the so called active brain). This scenario generates an oddball paradigm in which the bottom-up mechanisms dominate [Folk et al. 1992].

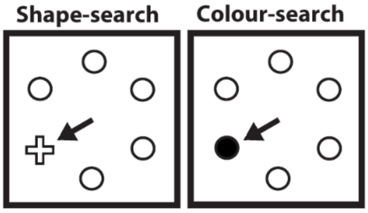

Figure 2-1 Visual attention tasks that involve only bottom-up mechanisms with two different search conditions and only one singleton: Shape-search condition; Colour-search condition. The arrow points at the singleton. Adaptation from [Connor et al. 2004].

More complex visual detection experiments include two or more different singletons within the same dissociation task e.g.: one colour singleton vs. one shape singleton in the same scenario. Participants are previously asked to distinguish only for either colour or shape. In this case the task performance involves making a decision based on prior knowledge: the bottom-up mechanisms have to be controlled by a top-down system that finally decides which one of the singletons is the real target (Figure 2-2). In the case of the experiment with two singletons it is clear that in order to decide between colour and shape there is previous knowledge required on the objective of the trial.

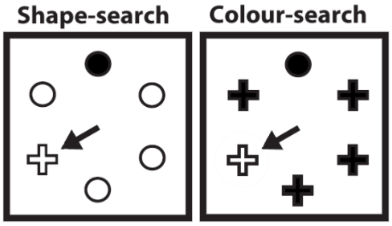

Figure 2-2 Visual attention tasks that involve not only bottom-up but also top-down mechanisms with different search conditions and a number of different singletons. The arrow points at the target singleton. Adaptation from [Connor et al. 2004].

While doing the same visual attention task on monkeys, Ogawa & Komatsu (2004) recorded the V4 area of the brain and found a clear modulation of the signal intensity depending on the number of singletons, finding electrophysiological signatures of a top-down modulation.

Indeed, the effects of the top-down mechanisms are believed to be even greater than a simple input modulation. Engle et al. (2001) proposed that the active brain is also able to predict forthcoming events, which explains part of the anticipatory nature of the neural activity. This theory assumes that the actions are guided through knowledge even before they actually occur, which, for instance, is the main reason why humans cannot tickle themselves [Blakemore et al. 2000].

Sometimes these top-down predictions can be erroneous and generate perceptual illusions: *often we feel the mobile phone vibrating in the pocket, but after checking it we realize that it really wasn't* [Rothberg et al. 2010; Lin et al. 2013]. While the feeling of the vibration seems to be very real, it turns out to be hallucinatory. There are many of these top-down illusory sensations happening concurrently in our brain: usually the prediction is contrasted with the real sensory input to check whether it is really happening or not, and then discarded if it is an illusion. However, schizophrenic patients for example are not always able to make this discrimination and therefore suffer from hallucinations.

The mentioned cell phone example is not only of interest to this Chapter for the top-down triggered illusion, but also because it shows how the perceptual illusion has become a conscious experience: *we are aware of this hallucination*. Having an experience and being aware of having an experience are two different things – unconscious processes can become conscious.

Although the mechanisms by which an unconscious experience becomes conscious are yet to be explored in depth, significant theories exist in this field. The most relevant one was presented by Crick & Koch in 2003. In their framework for consciousness, they predict that a consciousness threshold has to be reached in order to transform an unconscious neural process into a conscious one. According to Crick & Koch this threshold can be achieved via positive feedback loops in the neurons, firing of pyramidal cells, activating essential nodes, generating neural coalitions and other mechanisms in the brain.

Crick & Koch's framework not only highlights the projections to the frontal cortex where much of the experience seems to take place – recent empirical evidences have found that it is possible to disrupt consciousness through electrical stimulation of a small area at the anterior-dorsal insula region [Koubeissi et al. 2014] –, but also looks at the thalamus, the organ of attention, thus emphasizing the importance of attention for a conscious experience. They propose a revealing analogy by which attention determines our conscious experiences in a similar way to how the media or the polls influence a given political election – they will not choose the winner but with their action they can modulate the results [Crick and Koch 2003]. Attentional processes are therefore important for the conscious experience and they can either be originated by a bottom-up mechanism or by a top-down one (more volitional).

Interestingly, humans are able to focus their attention outwards or inwards: we can both be consciously aware of events happening around us as well as become objects of our own attention through self-consciousness [Gallup 1977].

2.1.2. Self-awareness

When do we develop self-awareness? Is it a uniquely human quality? These and other questions have long been discussed among philosophers and scientists when studying consciousness. *Cogito ergo sum*, the well-known philosophical proposition by R. Descartes, tried to describe self-consciousness by the capacity to think. But *how can self-*

consciousness be tested? In this context, self-recognition has been exploited as an empirical technique to validate the existence of self-awareness [Gallup 1977].

In this thesis theories related with self-awareness are exploited in several occasions to unveil the limitations and implications of the external appearance and/or functioning of the body in the scope of Chapter 1. More in particular one of the hypothesis is dedicated into the observation of avatar faces that look alike the participant, thus exploiting self-recognition theories.

Back in 1877, Charles Darwin conducted a report on one of his own infants, where he learnt that by the age of 9 months his child was capable of recognizing himself in a mirror [Darwin 1877]. In 1931 a more standardized study quantified that 67% of 2-year-old children identify themselves in a mirror [Stutsman 1931]. However, a large number of children react to mirrors as if the mirrored image is a playmate, not revealing a self-recognition behaviour and therefore biasing the results. In order to address this issue, researchers placed a red spot on the child's nose. The red spot served as a point of reference: self-recognition was assumed if the child touched the actual spot or used the mirror to examine his nose [Amsterdam 1972]. Self-awareness has been proven to be shared with other primates through similar experiments: chimpanzees are also capable of recognizing the red dye mark in their reflection on a mirror; while monkeys do not appear to have this capacity [Gallup 1970]. Other animals such as pigs can learn what a mirror image represents and use it to obtain information even though those animals lack self-awareness [Broom et al. 2009]. Additional attempts have been carried out training non-organic entities, such as robots, to self-recognize and pass the mirror test, however this does not represent a real self-awareness behaviour [Takeno et al. 2005].

But the more revealing characteristics of self-awareness are actually observed in patients with neurodegenerative diseases such as Alzheimer. Patients suffering this pathology have deficits to perform self-recognition tasks, related with their loss of self-awareness. 25% of patients in GDS stage 6 (with a severe cognitive decline) did not recognize themselves in a mirror, the percentage being significantly higher when shown in a video [Biringer and Anderson 1992].

This difference between the real-time and the off-line observation indicates that self-recognition resides not only in the external appearance (picture/video observation), but also in the internal corporeal experiences of own motor actions and behaviours in real time (mirror observation). Therefore we can assume that one can potentially distinguish the self from the others by external appearance as well as by the experience of owning a body and having agency of this body.

In fact, the neural mechanisms involved in self-recognition have different underlying origins: they are believed to have a strong contribution of both afferent (the incoming signals to the brain, such as the sensorial information: vision, proprioception etc.), as well as efferent information (outgoing signals: motor actions etc.) [Tsakiris et al. 2005]. As mentioned before, those afferent and efferent inputs are combined through multisensory integration, always modulated with prior knowledge (the experience is controlled by the top-down mechanisms). The top-down mechanisms are especially used when there is no efferent information, for example while observation [Bar et al. 2006; Bar 2003].

2.1.3. Exteroceptive part of the self-recognition

Humans are able to identify pictures of themselves, play-backs of self-generated actions, and determine authorship from kinematic displays based on prior knowledge and action-planning structures [Knoblich and Prinz 2001]. Some call this effect a re-efferent mechanism [Tays et al. 2011].

More precisely, whereas in real time the congruence between the afferent and efferent channels modulates the experiences of self-awareness, in the picture/video observation there is only one functional channel (afferent visual input), which is combined with the prior knowledge (re-efferent mechanisms). In the case of the Alzheimer patients the re-efferent channel is clearly affected, thus their self-recognition and self-awareness is significantly reduced during off-line observation.

With the arrival of new neuroimaging techniques the underlying mechanisms for external self-recognition have been widely explored. Using pictures of faces and objects and leveraging EEG techniques, researchers have been able to discover the neurophysiological processes that classify faces differently from other objects in the visual and frontal cortex [Bentin et al. 1996]. Further research has found that those processes are also involved in self-recognition [Liu et al. 2002; Keyes et al. 2010].

Studies with magneto-encephalography (MEG) have revealed that the categorization of faces is done via a two stage process: an early mechanism facilitates the discrimination of faces from other objects (at approximately 100ms), a later process is in charge of identifying the owner of the face (after 170ms) [Liu et al. 2002]. A growing literature has documented similar effects taking place when observing self vs. other people's faces using EEG and ERPs. A reduction on the P2 component voltage in the occipito-parietal areas of the brain was detected during self-face observation [Sui et al. 2006; Keyes et al. 2010].

These neurophysiological traces will be leveraged in Chapter 6 of this thesis to study self-identification in look-alike avatar faces. One of the challenges of the proposed study is the lack of prior exposure to computer generated faces, especially since identification mechanisms require extensive experience: children of various ages elicit different ERPs during observation of faces [Taylor et al. 2004]. Therefore, the processing evolves with time and requires exposure and training (for an extended review [de Haan et al. 2003]).

However, some people seem to have an impaired ability to recognize faces. Patients with disorders such as prosopagnosia cannot identify faces, while their skills for object discrimination or decision making remain intact [Damasio 1985]. Prosopagnosia patients have a healthy sense of self-awareness even though they do not recognize their own face, in contrast to patients with severe Alzheimer. Yet, another clear indication that self-recognition is not uniquely triggered through external appearance: other human characteristics are also key for self-awareness.

2.1.4. Corporeal part of the self-recognition

As we have seen in the previous section, self-recognition can be generated through mere exteroceptive modalities (i.e. observation) but other components such as the proprioception and the interoception also contribute to it through corporeal self-awareness. More precisely the experience of having and perceiving the body while in real time (body ownership) or the control of our own motor actions and kinematics (agency) are two related phenomena of the minimal self-awareness [Gallagher 2000].

According to Gallagher (2000) the minimal self-awareness refers to the consciousness of one-self as the immediate subject of an experience. A minimal self-awareness (*this is me*) involves two related aspects: ownership (*I am the one undergoing an experience*) and agency (*I am the one causing the action*). In this thesis the concept of minimal self-awareness will always refer to the above description, even though minimal self-awareness is not yet a fully agreed term among all authors, e.g. other authors refer to different but related terms such as the minimal phenomenological self [Blanke and Metzinger 2009].

2.1.4.1. Body ownership

While perceiving the own body may seem an obvious experience for a human since we integrate our bodies naturally, it is rather complex to study how body ownership works in the context of corporeal self-awareness: i.e. *how do I accept that this is my body?* This body acceptance mechanisms are of great interest to this thesis, since we are trying substitute participants bodies by virtual ones as stated in Chapter 1.

Disorders affecting the natural somatognosia – i.e. self-awareness of one's own body parts – produce hallucinations of reduplication or rejection of the owned body that include a variety of short lasting illusory experiences about the seen and felt location and position of one's body or body parts in the space [Blanke and Mohr 2005]. Bodily experiences influencing body ownership have been reported in patients with dysfunctional multisensory integration or brain damage in the temporo-parietal junction [Blanke and Mohr 2005].

Similar illusory experiences can be produced in healthy participants by manipulating the multisensory input and integration for the induction of these states. The stimulation of several afferent sensory signals together can generate body ownership illusions in mannequins, avatars or other body parts to better explore the functioning of body ownership [Botvinick and Cohen 1998; Petkova and Ehrsson 2008; Lenggenhager et al. 2007; Slater et al. 2009].

This approach was first proven to work through visuo-tactile synchronous stimulation with a rubber hand (Figure 2-3) where an illusion of ownership towards a fake arm was generated [Botvinick and Cohen 1998]. In the rubber hand illusion, tactile stimulation (tapping and stroking) was applied synchronously on the real arm (out of the participant sight) and on a visible rubber arm (placed in a feasible anatomical position in front of the participant). When the experimenter stroked both the real and the rubber arms synchronously the participant experienced the illusion that the fake arm was his real arm: i.e. the participant had an illusion of ownership over the rubber hand (Figure 2-3). When the same stroking was provided asynchronously participants did not experience any ownership illusion.

Figure 2-3 The rubber hand illusion. Tactile stimulation (tapping and stroking) is applied on a visible rubber arm placed in a feasible anatomical position in front of the participant, while the real arm rests hidden out of the participant's sight. When the experimenter stroked both the real and the fake arms synchronously the participant had the illusion of ownership over the rubber hand [Botvinick and Cohen 1998].

The illusion, which can be elicited in less than 15 seconds in approximately 80% of the people [Lloyd 2007], results in shifts of the real limb's felt location towards the fake limb. The bias between the real location and the felt location is known as the proprioceptive drift [Tsakiris and Haggard 2005]. Furthermore if the rubber hand is subjected to sudden harm and the participant has interiorized it as its own, a physiological reaction may be found – e.g. GSR increase [Armel and Ramachandran 2003] or a brain activation [Ehrsson et al. 2007].

The rubber hand illusion has been reproduced in VR through visuo-tactile stimulation [Slater et al. 2008], and more recently also through visuo-motor correlations [Sanchez-Vives et al. 2010] where the illusion was induced through a synchrony between the virtual hand movements and the participants' movements. The rubber hand experiment has been replicated extensively with multiple variations, for a broad review check [Makin et al. 2008].

Parallel studies have shown that the rubber hand illusion can also be generated on amputated patients by administering synchronous touches to the stump as well as to a fake hand [Ehrsson et al. 2008]. Related research with amputee patients that suffer from phantom limb pain has used similar body ownership illusions to reduce their pain by direct observation of their intact arm through a mirror. The mirror is precisely located creating a symmetry such that when patients view it, they have the illusion that their missing arm has been resurrected (Figure 2-4) [Ramachandran et al. 1995]. When a miscorrelation among multiple inputs is provided the brain disembodies the phantom limb. Subsequently, the brain relays strongly in the visual input to recalibrate and accepts that the phantom limb is not anymore in a painful posture [Ramachandran and Altschuler 2009].

Figure 2-4 Looking at a mirror reduces the phantom pain on an amputated limb. Figure adapted from [Ramachandran and Altschuler 2009].

Recently, ownership experiments have also been oriented to generate full-body ownership illusions with mannequins. Using HMDs, cameras as well as synchronous visuo-tactile stimulation participants had a full-body ownership illusion and reacted when a knife was directed towards the mannequin [Petkova, Khoshnevis, et al. 2011] (Figure 2-5).

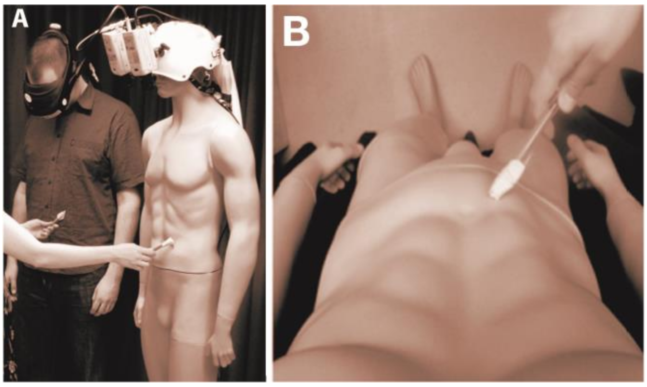

Figure 2-5 (A) The participant looks down with an HMD and sees a mannequin body instead of his own body. (B) The participant experiences a full body ownership of the mannequin from a first person perspective through synchronous tactile stimulation. Figure adapted from [Petkova, Khoshnevis, et al. 2011].

The full-body ownership illusion can also take place within virtual reality exploiting both visuo-tactile and visuo-motor correlations [Slater et al. 2009; Maselli and Slater 2013; Banakou et al. 2013; Normand et al. 2011; Kilteni et al. 2012; Kokkinara and Slater 2014; Slater et al. 2010]. Using VR technology participants have the feeling that their body has been substituted by a virtual body. Chapter 4 of this thesis provides new evidences about the integration of the illusion at the unconscious level measuring the brain activity to sudden harming stimuli rendered in the virtual environment while exploring the limits of the body representation in the brain.

Interestingly, the technology to generate body ownership illusions has also been exploited to produce out of body illusions in healthy participants. Literature has described out of body hallucinatory experiences in patients with dysfunctional multisensory integration that suffer from autoscopic phenomena. Such patients feel they are outside their own body being able to see it from a distanced perspective [Blanke and Mohr 2005].

Displaying a real-time video stream – recorded 2 meters from the back of the participant – in a stereo HMD, healthy participants can experience the detachment from their own body [Lenggenhager et al. 2007]. The proposed setup induces the illusions through synchronous tactile stimulation (Figure 2-6).

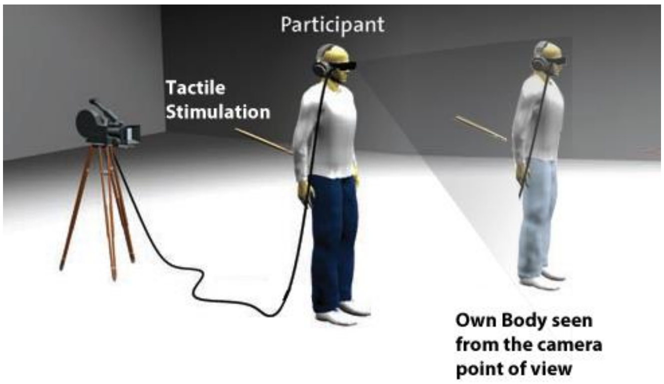

Figure 2-6 Out of body experience. The participant sees through an HMD his own virtual body standing 2 m in front. The illusion is generated with a synchronous stroking at the participant's back. Illustration adapted from [Lenggenhager et al. 2007].

In these illusions participants recognize the body they see as their own, however, the body is significantly displaced from the self-perspective (camera position).

Experimenters have shown that this illusion can also be induced using virtual avatars [Pomés and Slater 2013].

Even though there are multiple variations and experiments on body ownership and out of body experiences, two findings arise in all of them: i) some kind of multisensory stimulation is needed to produce the illusions and ii) the illusions are modulated by the visual perspective – being inside or outside the body. More precisely, first person perspective (1PP) has been found a necessary condition for a full virtual body substitution [Petkova et al. 2011; Slater et al. 2010; Maselli and Slater 2013].

2.1.4.2. Agency

Most of the experiments presented involving full body ownership illusions on virtual bodies and mannequins rely on passive stimulation provided by the experimenter: the stimulation of the afferent signals induces the feeling of owning a body – e.g. *my body is the one being touched, or being moved*. However, as remarked before, to have a complete experience of a body integration participants need to be controlling the new body – e.g. *I'm the initiator of the action*. In fact, the body ownership illusion can be generated leveraging active stimulation through synchronous match of the participant's movements to the ones of the virtual body (providing visuo-motor correlations) [Kokkinara and Slater 2014; Gonzalez-Franco et al. 2010].

The Hypothesis 2 of this thesis explores the implications of such visuo-motor correlations and the effects of a break in the agency mechanisms that control the movements of the virtual body. In this context, neuroscience relevant concepts such as agency, volition and motor control schemas are presented in this section.

In essence, having a body (body ownership) is naturally combined with an active control of the body (agency), especially since humans are the initiators of many of their own movements, being the source of the efferent signals [Gallagher 2000]. In this context, agency is a closely related phenomenon to minimal self-awareness – i.e. *this is me* – that depends on the processing of sensory and motor signals involved in almost every body activity.

But, *how do we recognize ourselves as initiators of our movements?* Tsakiris et al. (2005) studied the role of the efferent signals in self-recognition through a rather complex experiment in which participants experienced a passive extension of the right index finger. This stimulation was triggered in two different ways: either directly by the participants moving a lever with their left hand ('self-generated action') or induced by the experimenter ('externally generated action'). At the same time, their visual feedback (a video streamed in real time) was manipulated and subjects saw either their own hand or someone else's hand that was being extended with the same lever (Figure 2-7). Both hands were covered with identical gloves and the discrimination on the basis of morphological differences was not evident in their setup. The task for the participants was to judge whether the hand they saw was theirs or not. Participants were significantly more accurate in the self-generated condition – when they were the authors of the stimulation –, while the performance dropped near chance levels in the externally generated condition. With this experiment Tsakiris et al. were able to determine the specific contribution of afferent (vision and proprioception) and efferent information in self-recognition, showing that the mechanisms to produce agency and self-recognition are highly dependent on the efferent information [Tsakiris et al. 2005], in contrast to body ownership that is more frequently modulated by the afferent information [Tsakiris, Schütz-Bosbach, et al. 2007].

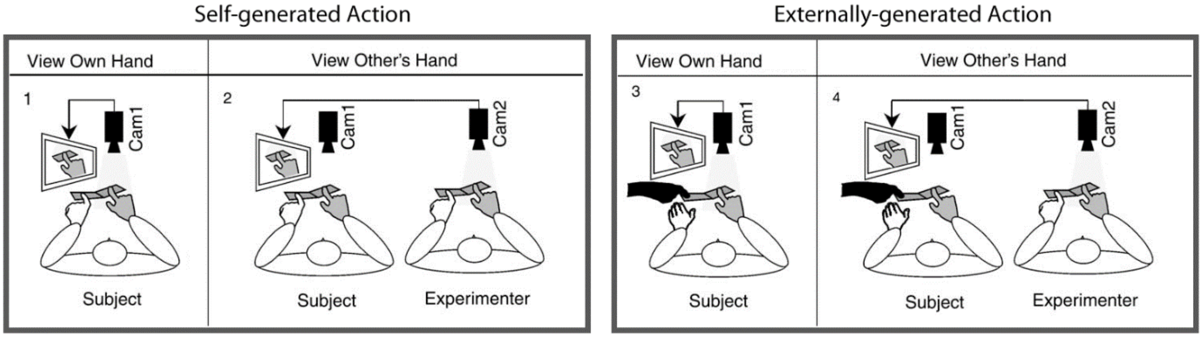

Figure 2-7 Participants have to judge whether the hand they see moving through a video stream is theirs or not. The participants' hand is passively extended via a lever triggered by the participant ('self-generated action') or by the experimenter ('externally generated action'). Illustration adapted from [Tsakiris et al. 2005]

Volition remains a parallel question to agency: *when is a movement considered voluntary?* In order to study the underlying mechanisms of motor intentions, Libet et al. (1983) proposed an experiment using Readiness-Potentials (RP)[1]; the conscious appearance of the intention to act was compared to the time at which the RP originated [Libet et al. 1983]. More specifically, participants were asked to stop a round running timer whenever they wished. Then participants reported the clock position at which they felt they wanted to stop the clock – i.e. their initial awareness of intending to move. Libet et al. compared the electrophysiological data – origin of the RP – against the reported awareness, finding that the movement was actually initiated 800ms prior to the participant reported awareness (Figure 2-8).

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[1] RPs are measured through scalp EEG, being a lateralization of the voltage between the hemispheres that appears in the motor cortex preceding voluntary hand movements [Kornhuber and Deecke 1965].

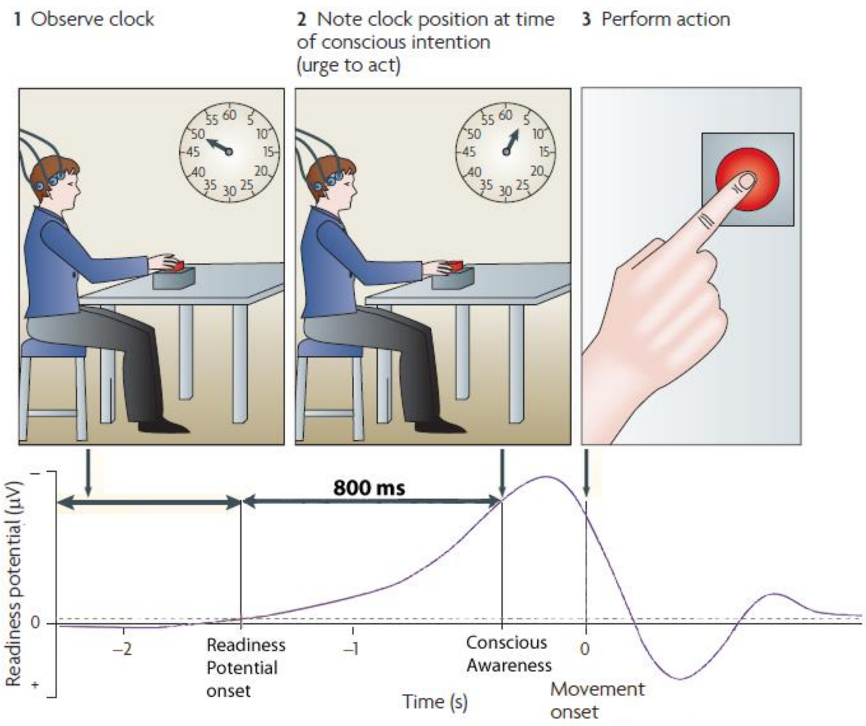

Figure 2-8 Libet et al. experiment. Top: the sequence of the Libet experiment. Bottom: the corresponding readiness potential (RP) taking place in the brain. The time when the RP starts is 800ms ahead to the participant reported awareness of his urge to act. Illustration adapted from [Haggard 2008].

Libet et al. results indicate that free voluntary acts are indeed originated unconsciously: the cerebral initiation of spontaneous acts begins prior to the subjective awareness that a decision has been taken to start an action. This discovery has major implications not only for the free will theories but also for the fields of agency, consciousness and self-awareness.

Consequently, being aware of, initiating and controlling actions is a major component of the conscious experience even though many aspects involved actually occur without awareness [Blakemore and Frith 2003]. This order of causality is in accordance with Crick & Koch (2003) framework for consciousness mentioned previously in the perceptual processing section.

Some theories in line with the findings of Libet et al. (1983) proposed that humans must have mechanisms oriented towards intentional inhibition of involuntary movements [Haggard 2008]. Some specific kinds of pathologies that alter significantly the sense of agency are precisely associated with failures to perform such movement inhibition. E.g. patients suffering the anarchic hand syndrome may perform simple actions (like grasping something) that are not intended [Sala 1998]. The non-controlled movements by this hand are due to a lesion in the contralateral hemisphere of the supplementary motor area. The affected hand may even interfere with the actions that the patient tries to perform with the healthy working hand. The existence of this rare pathology can be considered tangible evidence supporting the theories of active motor inhibition mechanisms that prevent involuntary movements in healthy humans.

While anarchic hand patients recognize their body as the one performing the action – they have a completely functional body ownership –, and they are fully aware that the movement was not intended – they do not report agency over the hand [Sala 1998]. On the contrary, schizophrenic patients that suffer from delusions of control are not sure whether their hand was controlled externally or not [Frith et al. 2000]. Clearly, volition is a necessary condition for an experience of agency and thus for a conscious experience of the self: *This is me, I'm the one performing the action*.

Interestingly, the consequences of events occurring after voluntary and involuntary actions are also crucial to better understand the agency of our actions.

On those lines, Haggard et al. (2002) studied volition and agency reproducing the Libet et al. (1983) setup. Haggard et al. asked participants to press a button whenever they wanted; a tone would be triggered 250ms later. Meanwhile they would watch a clock and judge the onset of both events: the action and the tone. Results showed that participants overestimated the time of the action and underestimated the time of the tone, perceiving as if the action and the event were closer in time, thereby demonstrating the existence of a mechanism that binds agency of actions to intentions. In a second condition magnetic brain stimulation (TMS) was applied in the motor cortex to trigger involuntary movements so the participant would press the button involuntarily. In this condition the time estimation between the action and the tone was divergent: participants perceived as if the action and the tone were more distant in time. During involuntary actions the binding mechanism was opposed to it of voluntary actions, when the mechanism attached the event from the action [Haggard et al. 2002].

The objective in Chapter 5 is to exploit the capabilities of VR and body substitution to better study these agency and volition mechanisms. We propose an experimental study where an Eriksen flanker motor task was performed by healthy participants. In random trials a hijack to the avatar introduced some incoherent movements. Brain activity was recorded to measure the effects of such breaks in the agency in the minimal self-awareness experience.

2.1.4.3. Model for Motor Control

A neurocognitive model (Figure 2-9) has been proposed to describe immediate self-awareness during motor actions through forward and feedback comparators [Gallagher 2000]. Gallagher's model connects several components that contribute to the minimal self of motor control and cognition – from the intention to the actual action. Interestingly, the model is not only based on the afferent input (sensory feedback), but also on efferent signals. In this context the comparators and the efferent signals from the model have also been strongly related to the functioning of the whole motor system being responsible for motor learning, motor prediction and motor correction [Wolpert 1997].

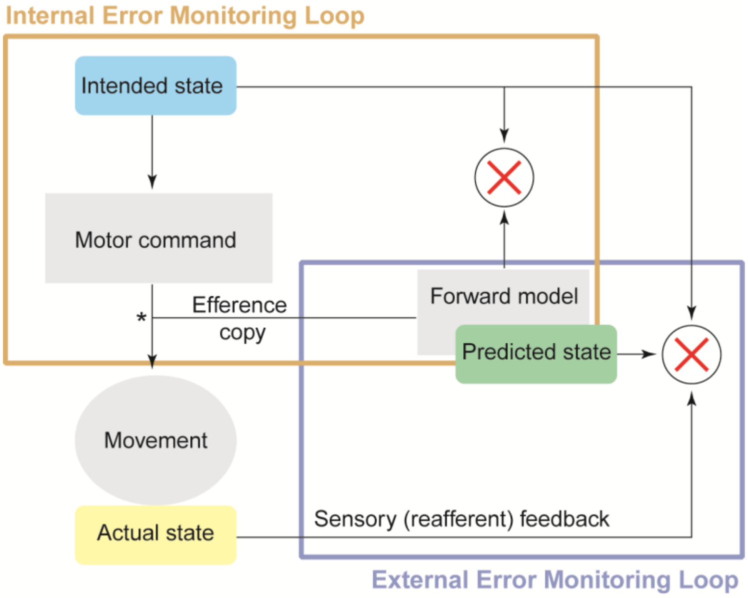

Figure 2-9 Motor control model including the internal and external error monitoring loops. Adapted from [Gallagher 2000].

During the execution of most of our actions an internal error-detection loop and a prediction based external system (also known as the external error-monitoring loop) constantly monitor the correctness of our own behaviour and motor commands (Figure 2-9). The internal forward model computes the correctness of the efferent action whereas the external loop checks for the final output of the action: it contrasts whether the afferent input of the executed action is equivalent to the original efferent output and predicted state.

Specifically, the forward part of the model is an incredibly fast error-detection system that computes error deviations from our on-going actions even before they have been completed. This mechanism generates constant predictions of the consequences of one's actions using an internal copy of the on-going motor command (also called efference copy) [Kawato 1999; Frith et al. 2000; Holst and Mittelstaedt 1950].

Researchers have associated an Error-Related Negativity (ERN) signal that originates in the anterior cingulate cortex with the forward comparator [Rodriguez-Fornells et al. 2002]. When a participant makes a mistake during a decision making task, such as the Eriksen flanker task [Eriksen and Eriksen 1974], ERN components are elicited [Rodriguez-Fornells et al. 2002]. If an error signal is triggered in the forward comparator the brain can implement fast inhibitory processes and error correction commands.

While the internal error-monitoring loop helps the organism to adapt in a fast and flexible way in the ever-changing environment, the external error-monitoring loop plays an important role in the agency of our actions. The external loop integrates new sensory incoming information about the real consequences of our current action through the re-afferent feedback. This mechanism helps to *attribute the agency of the action to ourselves* [Frith et al. 2000]. However, even though this external monitoring loop has been predicted the brain traces associated to it are yet unknown.

The model can be adapted to account for the multiple variations on the minimal self-awareness in psychiatric patients affecting agency and ownership, when one or other components of the model are not functioning well. I.e., no match of the forward or feedback comparators can deprive the system of a sense of agency or ownership [Blakemore et al. 2002].

In Chapter 5 we explore the agency and ownership mechanisms in the context of this minimal self-awareness model. A fast Eriksen flanker motor task was implemented to generate internal errors, whereas hijacks to the avatar were used to induce external errors – hijacks were avatar performed animations that did not originate from the users tracked body. The study’s objective was to measure the brain activity for the two comparators in the model, searching for the agency and ownership mechanism related with the minimal self-awareness experience.

2.1.5. Summary

In “The brain and the body” we have explored several neuroscience concepts relevant to the study of the body representation in the brain both at unconscious and conscious levels. A number of experiments and theories around the perceptual processing of stimuli, or self-awareness exteroceptive and corporeal parts have been presented together with a detailed review exploring the phenomenology of owning a body and controlling it. Models for motor control and minimal self-awareness were also introduced.

Furthermore, the three main hypotheses to be defended in Chapters 4, 5, 6 have been contextualized not only among a review of similar experiments but also with several pathologies producing similar effects for dysfunctional illustration.

In conclusion, the conceptual roots upon which this thesis will gravitate have been introduced: agency, body ownership, volition, self-recognition, unconscious mechanisms, proprioception, afferent and efferent signals, and multisensory integration.

2.2. Virtual Reality

2.2.1. Presence

Real time Computer Graphics together with advanced tracking technologies can generate IVE in which participants find themselves in a totally new location or scenario.

Under such circumstances participants experience a “presence illusion”, the feeling of being there (Place Illusion) while also behaving realistically (Plausibility Illusion) [Sanchez-Vives and Slater 2005]. People immersed in virtual environments have realistic responses to external stimuli: the reactions in virtual environments are equivalent to the ones expected if the stimuli were to happen in a real scenario [Sanchez-Vives and Slater 2005]. For this reason VR provides a great platform to systematically test particular stimuli in humans without compromising their integrity.

Presence has traditionally been measured via questionnaires [Slater et al. 1994]. However surveys alone may not be sufficient for evaluating presence effects, making more objective measures necessary [Slater 2004]. Researchers have monitored physiological responses to account for objective presence measures and found that people exposed to stressful situations in an immersive environment – e.g. walking on the edge of a virtual cliff – register strong increases in their heart and respiratory rate or galvanic skin response [Meehan et al. 2002].

Additionally, participants not only respond realistically to the environment but also behave genuinely when interacting with avatars. A virtual reprise of the Milgram’s obedience to authority study, in which participants are asked to provide electric shocks to a virtual learner whenever he answers incorrectly to a question, found that people behaved as if the situation was real [Slater et al. 2006]. In another example of social psychology inside IVE people immersed as bystanders during violent incidents were likely to intervene following realistic behavioural patterns [Rovira et al. 2009; Slater, Rovira, et al. 2013].

Furthermore, the presence illusion can be generated exploiting different modalities of immersive technologies – HMDs or CAVEs. The evaluation of the effectiveness of the different systems producing presence is not trivial. Some research has focussed on a single characteristic of the technology in order to do so; such as the quality of the image, the time delay, the depth perception (3D stereo, vs mono), the head tracking or the field of view (FoV), etc. [Chen et al. 2007]. Overall, there is a major agreement that stereo rendering with head tracking is necessary to consider an immersive VR effective [Slater et al. 2010; Sanchez-Vives and Slater 2005].

2.2.2. Virtual Embodiment

IVE with real-time tracking devices not only transport participants to a totally different location or scenario, but also provide a platform in which participants can have their body substituted by a virtual body.

Being inside a virtual body that moves as you move (with real-time tracking) can generate a strong full-body illusion. More precisely, the embodiment in a 1PP virtual body causes a combination of the previously described phenomena of body ownership illusion and agency over the virtual body [Kilteni et al. 2012]. Therefore embodiment produces an advanced full body ownership illusion in which the participant not only has an egocentric perspective of the body but also has control over it [Slater et al. 2010].

Using HMDs researchers have shown that is possible to produce functional body substitutions in VR [Banakou et al. 2013; Slater et al. 2010]. In those experiments the HMD is combined with real-time head tracking that produces a 1PP where the virtual view position and orientation is constantly updated according to the participant's tracked head position and orientation [Maselli and Slater 2013]. Simultaneously, full body tracking systems provide real-time motor control of the rest of the virtual body generating strong multisensory correlations. Synchronous tactile stimulation through vibrators (passive) or touch (active) can also help in inducing visuo-tactile correlations. The combination of various kinds of synchronous multisensory correlations strengthens the embodiment illusion over the virtual body.

In fact, studies have shown that both synchronous visuo-motor and visuo-tactile correlations can be used to induce the embodiment illusion by providing strong virtual body ownership [Kokkinara and Slater 2014]. Kokkinara et al. examined the relative contribution and mutual interaction of both stimulations (tactile and motor) on the full-body ownership illusion. Results show that the illusion is more strongly and positively influenced by congruent visuo-motor correlations than visuo-tactile stimulation, however the illusion can be broken to the same extent by incongruent stimulation of both kinds. Previous research had found that virtual body ownership illusions can be enhanced when the participant sees his/her virtual body moving synchronously in a mirror [Gonzalez-Franco et al. 2010]. Interestingly, the embodiment illusion may even exist when the virtual body and the real body are not perfectly co-located [Blom et al. 2014; Pomés and Slater 2013].

Ultimately, the embodiment illusion provides the means to further explore how the brain and the body integrate, especially since computer graphics programming allows researchers to alter the virtual bodies beyond what would be physically feasible on a real body.

Experimenters have shown that people embodied in avatars whose hand was elongated up to three times the length of the real arm can still perceive the virtual arm as their own [Kilteni et al. 2012]. In that experiment participants underwent visuo-tactile and visuo-motor multisensory stimulation, which enhanced the ownership illusion and resulted in a proprioceptive drift. Kilteni et al. not only showed how virtual bodies can be manipulated to this extreme, but also contributed to the field of brain plasticity.

Similar proprioceptive drifts were produced in adult males when they experienced a larger belly after self-induced visual tactile stimulation, resulting in an overestimation of their real belly size after synchronous tactile self-stimulation [Normand et al. 2011]. Without doubt, modifications in virtual bodies have contributed to a greater understanding of the neuroplasticity and the quick adaptation of the brain to changes in the body.

Further experiments have shown that embodying adults in bodies of children not only produces proprioceptive drifts and overestimations of object sizes but also implicit attitude changes [Banakou et al. 2013]. Attitude changes were found after embodiment exposure to black skinned avatars, in this case participants' racial bias was significantly reduced [Peck et al. 2013]. Interestingly, behavioural responses have also been related to the virtual body appearance when in a music scenario, showing that embodiment can help modify behaviours [Kilteni et al. 2013]. More intriguing effects have been found in participants embodied in look-alike avatars where their behaviour was also modified [Bailenson and Segovia 2010]. Even though this is not the focus of this thesis it is important to note that there are great implications of these attitude changes induced during embodiment experiences used for therapy. Nevertheless the understanding of how the self-identification with avatars works will be further explored in Chapter 6.

2.2.3. Summary

This section has reviewed a series of experiments that use IVE to study not only human behaviour or social psychology but also the body representation in the brain. Such experiments in VR have been possible because participants perceive and respond to the virtual stimuli as if the events happening were real. Inside VR participants can be embodied in a virtual body while experiencing an illusion of presence.

The technologies used to generate body substitutions for the hypothesis testing will be similar to those exploited in many of the experiments presented in this thesis; HMDs with head tracking and body tracking devices.

In this thesis we are interested in exploiting embodiment to explore how the brain and the body are integrated and the underlying brain mechanisms that take place during virtual body ownership illusions as well as the nature of virtual body agency.

More precisely, Chapter 4 is dedicated to explore how the virtual body is integrated in the brain. An instantaneous harmful stimulus is presented to the virtual body of the participant to measure the brain activity that processes such event. In theory similar motor cortex activation would be expected were the threat happen to their real body. This Chapter will provide new evidence of the unconscious mechanism that regulate the body ownership illusion.

Chapter 5 will explore how human motor control mechanisms work and how we achieve minimal self-awareness and agency of our own bodies. Participants will perform a motor task while embodied in a virtual avatar and sporadically experience agency breaks in which their virtual body performs some incongruent movement (simulating what happens during anarchic hand episodes). This Chapter will provide new evidence on the brain mechanisms that control the agency of our own actions.

Finally Chapter 6 will look at the effects of the virtual body appearance for self-recognition, presenting an experiment where participants have their brain activity recorded while observing virtual look-alike avatar faces. This research is particularly motivated by the studies that find attitude changes when embodied in different looking avatars [Peck et al. 2013; Kilteni et al. 2013; Bailenson and Segovia 2010] which may also have great implications for the self-recognition field.

2.3. Measuring the brain activity

Nowadays, there are several techniques available that can measure the brain activity in non-invasive ways, and it is usual that scientists use different techniques for different purposes as one may provide a good spatial resolution, whereas another may have a good temporal one. At the same time many researchers specialize in more than one modality of brain functioning in their research: vision, language, learning, sensory integration, motor control, decision making, etc., but try to avoid combining many modalities in the same experimental setup, as one may interfere with others.

2.3.1. Techniques

In this section we present some of the most common non-invasive brain activity recording techniques, to evaluate their compatibility with the use of VR as well as their temporal and spatial resolution.

2.3.1.1. Functional Magnetic Resonance Imaging

Functional Magnetic Resonance Imaging (fMRI) detects changes in the blood flow exploiting the magnetization of the blood when the oxygenation level changes. It is quite an expensive technology that comprises of a very big magneto-generator device (Figure 2-10). This technology creates magnetic fields that can localize activity anywhere in the brain within millimetres of spatial resolution, which is very good for research focus on human brain mapping.

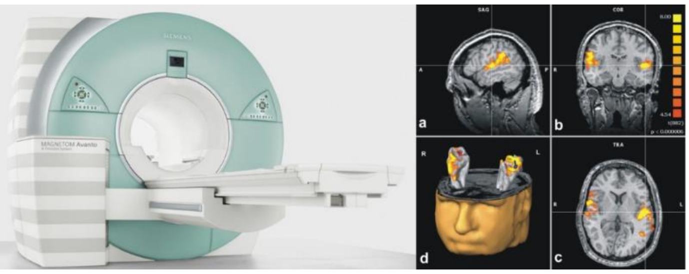

Figure 2-10 Left: an fMRI machine from Siemens. Right: results adapted from an auditory perception study with fMRI [Wengenroth et al. 2010].

However this technique does not provide much information about the temporal dynamics since the minimum time window for the fMRI is about a few seconds, which also means that since the head has to remain restrained fMRI cannot be used during complex motor action scenarios. It is therefore un-efficient to test temporal dynamics of instantaneous stimuli or motor control with fMRI.

Furthermore, given its magnetic fields it is very hard to integrate with other technologies such as the HMDs necessary for the VR. However there have been attempts towards creating a magnet-friendly VR, where the screens of the HMD were successfully replaced with a fiberoptic delivery system [Hoffman et al. 2003] that can be now found commercially.

2.3.1.2. Near Infrared Spectroscopy

Using Near Infrared Spectroscopy (NIRS) researchers can focus on a specific area of the brain. NIRS is based on a source that irradiates infrared light paired to a detector that measures the diffused light from the volume of tissue beneath. Different blood oxygenation levels have different light diffusion properties, so the light measured at the detector depends on the activity of the area (Figure 2-11). NIRS is a widely used technology for pulse-oximeter devices but it can also be used for functional neuroimaging.

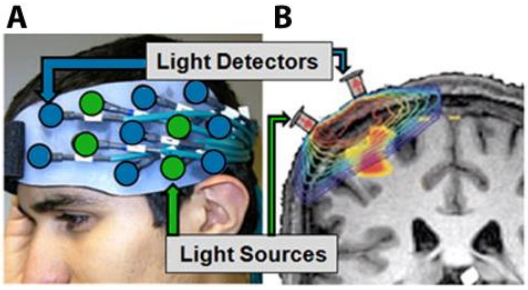

Figure 2-11 (A) A grid of fiber optic-based light sources and detectors mounted on a participant. (B) The model of light propagation (in log-scale). Figure adapted from [Karim et al. 2012].

This technology combines a good temporal resolution (millisecond scale) with a reasonable spatial resolution (centimetres). The light can reach approximately 5-8mm into the brain cortex at a source-detector spacing of 3.2cm.

Although NIRS uses infrared exposition instead of magnetic fields it can be considered similar to the fMRI since it is based on the detection of blood oxygenation, hence it is sometimes used as a partial replacement for fMRI since it offers a much cheaper and portable solution. Even though it is a more limited technology it can provide decent measures for cortical exploration in specific areas. Furthermore, NIRS can be used with VR setups, as it does not interfere with other electronic equipment.

2.3.1.3. Transcranial Magnetic Stimulation

It is also possible to explore the functioning of a specific area of the brain (mostly cortical) using Transcranial Magnetic Stimulation (TMS) that triggers depolarizations or hyperpolarizations of neurons by rapidly changing the magnetic field (Figure 2-12).

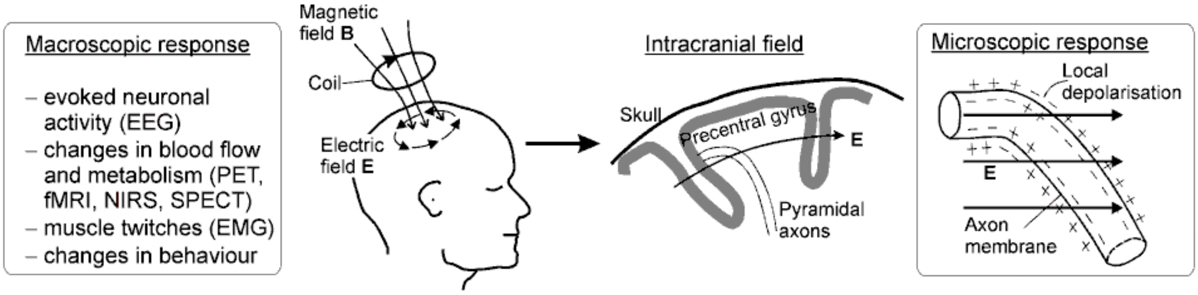

Figure 2-12 Principles of transcranial magnetic stimulation. The current in the coil generates a magnetic field (B) that induces an electric field (E). At the microscopic level, the electric field (E) affects the transmembrane potentials and may lead to local membrane depolarization and subsequent neural activation. Macroscopic responses can be detected with functional imaging tools, with surface electromyography (EMG), or as behavioural changes. Adapted from [Ilmoniemi et al. 1999].

This technology is considered non-invasive even though it can cause activity changes in the affected area of the brain. Its effects are instantaneous and the brain recovers its normal functioning after the controlled pulse.

TMS has been widely used to evaluate cortical functioning, especially in the study of the primary motor cortex, where it produces Motor Evoked Potentials (MEP) that can be recorded through EMG. More specifically it can be used to study agency and motor control by triggering involuntary movements [Haggard et al. 2002], making it an interesting tool to understand how the brain and the body interact.

2.3.1.4. Magneto Encephalography

Other technologies are purely measuring devices that do not interact at all with the natural activations of the brain by creating magnetic fields (fMRI, TMS) or by infrared exposition (NRSI), but rather take direct measurements of the activity voltage or the magnetic field created during the synapses. One of these technologies is the Magneto Encephalography (MEG).

MEG consists of a very precise magnetometer based on superconducting quantum interference devices (SQUID) that is able to measure the extremely subtle magnetic fields created by the brain currents, its working principles are explained in detail here [Hämäläinen et al. 1993].

This technology has a satisfactory spatial and temporal resolution. However, MEG devices are very expensive, relatively big and non-portable (Figure 2-13). Additionally, they are also incompatible with other electronic devices such as HMDs or similar that can create strong interferences in the magnetic fields. In fact MEG recordings usually take place inside magnetically shielded rooms.

Figure 2-13 MEG machine by Elekta Nuromag.

2.3.1.5. Electroencephalography

The electroencephalography (EEG) is an innocuous technology based on direct voltage recording with electrodes placed in standard positions all over the scalp connected to the skin through gel.

EEG is often used as it is the cheapest portable system for cortical activity recording. With a very good temporal resolution (milliseconds) it is a great platform to evaluate instantaneous stimuli processing in the brain while remaining reasonably robust to interferences of HMDs or other equipment.

However, the acquired signal tends to be very noisy and the experimentation requires multiple repetitions of each stimulus in order to really isolate the underlying processing – about 40 to 60 repetitions are necessary in order to record the average brain response. The resulting signal of the average response is known as the Event Related

Potential (ERP), which is associated with the processing of the specific stimuli in the brain (Figure 2-14). Using offline EEG analysis one can extract the ERPs to different stimuli or conditions and answer questions of broad interest in cognitive neuroscience and also explore the temporal dynamics of the body representation in the brain.

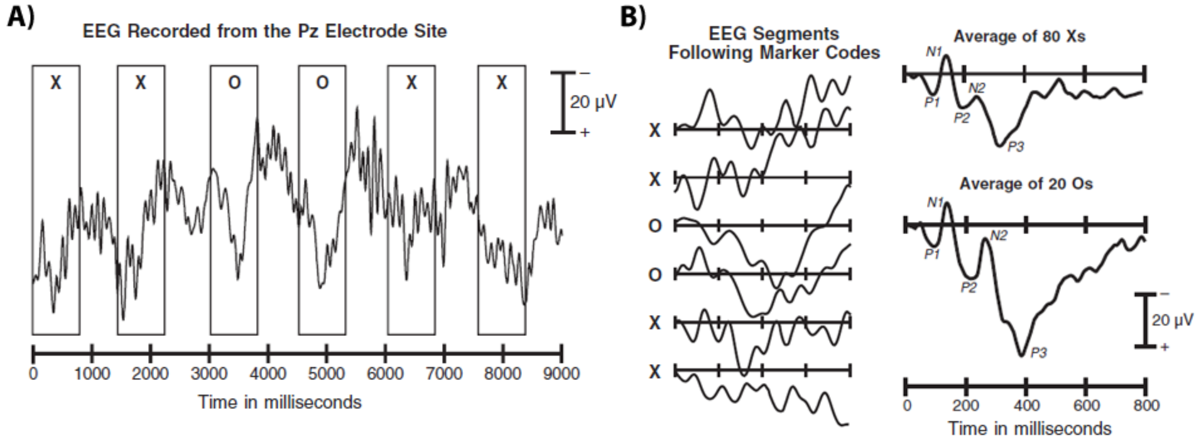

Figure 2-14 ERPs of a classic oddball paradigm rare stimuli 'O' get stronger P3 component amplitudes than more frequent stimuli 'X'. Adaptation from [Luck 2005].

2.3.1.6. Summary

This section has presented several non-invasive technologies for measuring the brain activity. In Table 2-1 we present a short summary of the different technologies and their features.

Table 2-1 Review of the technologies for non-invasive measuring the brain activity.

Technology	Spatial resolution	Temporal resolution	Compatibility with VR	Size/Price
fMRI	Whole brain (millimetres)	Few seconds	High interference. Magnets interfere with electronic equipment.	Very big/Expensive(more than 1 million €, plus high operational costs)
NIRS	Specific area of the cortex (centimetres)	Milliseconds	Low interference.	Portable/Up to 400.000€
TMS	Specific area	Milliseconds	Possible interference. Magnets	Small/Approx. 30.000€

	of the cortex (centimetres)		can interfere with electronic equipment in the range of action.	
MEG	Whole cortex (centimetres)	Milliseconds	High interference in both directions, magnets interfere with electronic equipment, while the electronic equipment interferes with the recording.	Big/ Expensive (more than 1 million €, plus high operational costs)
EEG	Whole cortex (centimetres)	Milliseconds	Low interference.	Portable/Approx. 30.000€ for 64 channel device

* Cost extracted from manufacturers websites.

While some of the technologies have better temporal resolution other provide better spatial scales. There are also significant differences in interference sensitivity, sizes and prices among them. More importantly, some of the devices are very difficult to combine with HMDs, such as the fMRI and the MEG, and for this reason these technologies will be discarded for the implementation of our work.

On one hand the objective of this thesis is also to explore the responses to stimuli by measuring the whole brain activity, rather than focusing on a specific area, thus NIRS will also be discarded since it can only focus on specific parts of the scalp. On the other hand we want to interfere as little as possible with the natural stimuli processing, TMS will also be rejected as it induces external activations in the brain.

Consequently, only EEG seems suitable for the aim of this thesis. Even though this technology also has limitations, such as its low signal to noise ratio, its sensitivity to muscle activity near the head or its limited spatial resolution, it provides a sensible platform to explore the temporal dynamics of the external stimuli integration for our three hypothesis without incurring into high operational costs (as it would be the case with MEG or fMRI). Therefore Chapters 4, 5, 6 will only present brain activity recorded with EEG.

2.3.2. Brain traces of the body representation in the brain

In this section recent research on neurophysiological traces of bodily experiences is presented. In most of the cases the techniques previously described are employed to measure the brain traces for both healthy and clinical populations. However there are several limitations and possible errors derived from the use of current measuring techniques that need special attention before continuing this section. It is important to highlight that not well defined conditions combined with certain measuring techniques can make for ridiculous results: see Bennet et al. who using brain imaging (fMRI) found significant traces of brain activation on a dead salmon [Bennett et al. 2009].

Therefore, and in order to avoid these sort of issues, most of the research on brain mapping requires strong conditions and hypothesis. More in particular studies on the body representation in the brain usually try to reproduce previous designs by comparing two or more conditions showing coherent vs. ambiguous multisensory stimulation. This sort of research on body perception with brain activity recording provides a unique platform to ultimately study the immediate experience of one's own body, often considered the most fundamental aspect for generating self-consciousness [Gallagher 2000; Blanke and Metzinger 2009; Blanke 2012].

Various research has been able to trace brain activation in regard to bodily signals that generate the experience of owning and controlling a body. However different authors link bodily experiences to multiple areas of the brain. Certainly it is reasonable to believe that such a complex task involving from the processing of multiple sensorial modalities to its interpretation requires the implication of several brain areas.

Essentially the brain mapping of body ownership experiences has been done mostly using fMRI and Positron Emission Tomography (PET), and it has found that many areas are implicated: the bilateral premotor cortex (PMC) [Ehrsson et al. 2004; Ehrsson et al. 2005], the insula [Tsakiris, Hesse, et al. 2007], the somatosensory cortex [Tsakiris, Hesse, et al. 2007], the anterior cingulate cortex (ACC)[Ehrsson et al. 2007], the posterior parietal cortex [Kammers et al. 2009], the intra parietal sulcus (IPS) [Ehrsson et al. 2004], the cerebellum [Ehrsson et al. 2005], and even with some specific gamma band oscillations over the sensorimotor area [Kanayama et al. 2009]. All of these areas (Figure 2-15) seem to be associated with the illusory limb ownership produced during experimentation with the Rubber Hand Illusion.

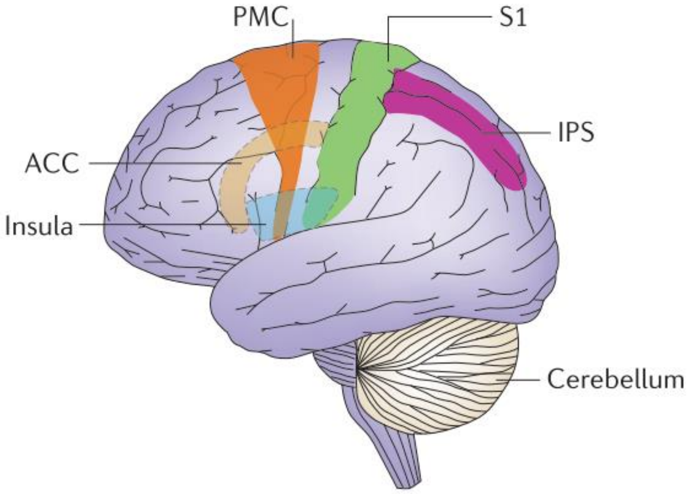

Figure 2-15 Schema of the brain areas that have been identified as relevant for the generation of body ownership experiences. ACC: Anterior Cingulate Cortex, S1: Primary Somatosensory Cortex, IPS: Intraparietal Suculus, PMC: Premotor Cortex. Figure adapted from [Blanke 2012].

In order to make some sense of how all the different parts of the brain implicated on the body perception really work, further research has concentrated on finding both the connectivity and the functionality behind. Research focused mainly on localizing and understanding the multimodal integration of the tactile, visual and proprioceptive signals showed that the multisensory integration happens in the IPS and PMC neurons, as these areas are able to respond both to tactile and visual stimuli. For example, those areas (IPS and PMC) get activated both when tactile stimulation is applied on the contralateral arm as well as when a visual stimuli approaches the same arm [Makin et al. 2008]. Furthermore, similar multisensory integration mechanisms have also been described in other primates [Bremmer et al. 2001].

In terms of the connectivity of the different areas, studies on clinical populations that are not able of experiencing the RHI have shown the importance of the network, as for example the damage of the pathways between the PMC, the prefrontal and the parietal cortex seems to prevent experiencing body ownership illusions [Zeller et al. 2011], showing that these areas must be connected for a proper functioning.

Overall studying the brain mechanisms that enable ownership of body parts contributes to the fundamental understanding of the unitary experience of self-consciousness through the corporeal awareness: this is my body, thus this is me [Blanke 2012]. However, as we have mentioned previously in the self-awareness section, there are other phenomena crucial for a complete bodily experience that include self-recognition in base to the self-location and the viewing perspective.

Up to date, not many studies have been carried out to map the brain areas that reflect self-identification on a body. However some research manipulating visual-tactile stimulation while measuring fMRI during a full-body illusion found the PMC and IPS areas to increase their activity consistently with the reported self-identification with the virtual body [Petkova, Björnsdotter, et al. 2011]. As we just mentioned before these areas also play a major role in the ownership illusions of body parts [Ehrsson et al.

2004], showing a clear link between the different phenomena related to bodily experiences.

Further experimental studies with EEG have altered participants' self-location and perspective finding alpha band oscillatory modulations in the sensorimotor cortex and PMC [Lenggenhager et al. 2011], the alpha power was significantly suppressed during visuo-tactile conflict manipulations, i.e. asynchronous stimulation to the virtual body.

In the current thesis the focus is not so much into the brain mapping but rather on the study of the temporal dynamics and early processing in the brain of different sensorial inputs, i.e. stimuli perception, (Chapters 4, 5, 6). Further Chapters also dedicate to the multisensory integration (Chapter 5), and to the higher level cognitive processes that produce self-consciousness and self-recognition: the experience that "this is me" through external visual appearance (Chapter 6).

2.4. Summary

Firstly, this Chapter has contextualized the current work within previous research presenting a set of neuroscience theories and experiments in areas including bodily perception, agency, body ownership, volition, self-recognition, unconscious mechanisms, proprioception, afferent and efferent signals, and multisensory integration. This Chapter is therefore meant to aid the readers throughout this Thesis as a theoretical reference.

Besides, the use of Virtual Reality as a platform to study these and other neuroscience topics has also been introduced not only by presenting concepts such as presence or embodiment but also by reviewing previous experiments that draw similarities to the approaches taken in Chapters 4, 5, 6.

Further review has focused on the different brain activity measuring techniques, and their adequacy for the purpose of the hypothesis testing. A throughout state of the art analysis of non-invasive techniques was presented including a summary of the different uses that those technologies have had in the past in the context of body ownership and self-recognition.

In the forthcoming Chapters different experimental designs that employ Virtual Reality and EEG are presented in order to validate the hypothesis presented at the beginning of the Thesis. Even though, each of the experimental Chapters has a different aim, the common materials and methods are summarized in the following Chapter to emphasize the shared concepts behind them.

3. MATERIALS AND METHODS

This Chapter describes the technologies used to validate the hypothesis of this Thesis. Even though each experiment has its own characteristics they all have some materials and methods in common. For example some experiments in this Thesis create an embodiment illusion of an avatar, and all of them record the brain activity through EEG.

3.1. Generating the Embodiment Illusion

In order to place participants inside a virtual body, they were fitted with a stereo NVIS nVisor SX111 HMD. This HMD with a refresh rate of 60 Hz provides stereoscopic view through dual SXGA displays with 76°H × 64°V degrees FoV per eye. In total the field of view is 111° horizontal and 60° vertical, with a resolution of 1,280 × 1,024 per eye (Figure 3-1).

Figure 3-1 A participant wearing the NVIS nVisor HMD

HMDs are capable of producing very immersive experiences [Slater et al. 2010]. On one hand, the wide FoV provides a strong feeling of immersion, with its corresponding Presence illusion (see background section) [Sanchez-Vives and Slater 2005; Slater et al. 2010]. On the other hand the resolution enhances the quality of the experience by making pixels very tiny [Slater and Wilbur 1997]. Thus, the real-time rendering at such high resolution also augments the Presence illusion [Slater et al. 1994]. Once put on, the HMD “transports” participants to a new environment with high fidelity [Slater et al. 2010].

The combination of this HMD with real-time head tracking produced a 1PP where the FoV was constantly updated according to the participant’s head position and orientation. To do so, a 6-Degrees of Freedom (DoF) Intersense IS-900 device with an update rate of 180Hz was used for the head tracking; allowing participants to look around the virtual environment just as they would do in a real environment (Figure 3-2).

Figure 3-2 An array of Intersense IS-900 at Brown University. Figure adapted from [Tarr and Warren 2002].

This technology comprises of a source device fixed to the top of the HMD, and a receiver which is usually attached to the ceiling of the laboratory. Its working principles, based on inertial and ultrasonic technology, provide very smooth, robust and precise position and orientation stream, while remaining immune to both occlusions and metallic interferences. The steadiness of the head-tracking has been considered a major factor to avoid motion sickness and dizziness among participants while in VR [Cobb et al. 1999]. Indeed during the experiments carried out in this Thesis none of the participants reported to experience such effects.

In our setup participants experienced an authentic egocentric perspective of the virtual body[2]. When looking towards their own body participants saw a virtual body placed in the same location and pose as theirs. Provided that participants would not move other parts of their body, besides their head, they could experience the illusion that their real body had been substituted by the virtual one. The real-time motor control of the head plus the proprioceptive and visual coherent inputs of their virtual body generated strong multisensory correlations.

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[2] See http://youtu.be/029XNWctb4A

In order that the virtual body would move synchronously with the real body movements when participants were asked to move during the experimentation (as in Chapter 5) a full body tracking system had to complement the head-tracking.

Body movements can be tracked using an optical infrared system (12 camera Natural Point OptiTrack setup). A set of reflecting markers placed on different parts of the participants' body were triangulated – from the information recorded by the available cameras – in order to find the position and rotations of every join of regard. When whole body tracking is necessary participants usually wear a suit with the markers already on to facilitate the calibration. However, when only one part of the body needs to be tracked an inverse kinematics technique is enough to reproduce the participant movements. For example, in the case of Chapter 5 the whole arm kinematics (hand, elbow and shoulder positions and rotations) were computed from the hand position using Inverse Kinematics. This setup supports the real-time display of the avatar with 4 DOF in the arm giving the participant strong visuo-motor coherence.

The virtual environment was programmed in the XVR system [Tecchia et al. 2010] and the virtual character rendered using the HALCA library [Gillies and Spanlang 2010].

3.2. Electrophysiological recording

Continuous EEG was acquired for all the experiments with electrodes located according to the standard 10-20 positions [Jurcak et al. 2007], although different amplifiers and electrodes were used depending on the equipment available for each experiment.

Trials that were contaminated, i.e. exceeding amplitudes of ±100 µV by any electrode or with eye movements (electrooculogram, EOG) were rejected off-line in all of the experiments.

In Chapter 4 EEG and EMG were recorded with a g.USBamp amplifier connected to Matlab at a sampling frequency of 512 Hz. For this experiment the electrodes were set to cover the motor cortex area and surrounding: FC3, FC4, C3, C4, CP3 and CP4; the reference was set with an ear clip on the left ear lobe; the ground was positioned on the forehead. Further electrodes in the face measured ocular activity (EOG). Besides, three EMG electrodes were placed in the flexor carpi ulinaris muscle of the right arm to measure whether participants moved their hand. All the electrodes were kept to impedances below 10 kΩ and the signals were filtered with band-pass of 0.5–100 Hz and a 50Hz notch filter.

In Chapter 5, EEG was recorded at 250Hz from tin electrodes mounted in an elastic cap and located at 27 standard positions (Fz, F7/8, F3/4, Fc1/2 Fc5/6, Cz, C3/4, T7/8, Cp1/2, Cp5/6, Pz, P3/4, P7/P8, Po1/2, O1/2). All scalp electrodes were referenced offline to the mean activity of the left mastoid and the ground was located on the forehead. Vertical eye movements (EOG) were monitored with electrodes located above and below the right eye. Horizontal EOG was collected from electrodes located at the outer canthus of each eye. Both vertical and horizontal EOG were used for artefact rejection and corrected with automated ICA-based methods [Joyce et al. 2004]. Impedances were kept below 5 kOhm. The electrophysiological signals were filtered with band-pass of 0.1–70 Hz (half-amplitude cutoffs) and an AC notch filter.

In Chapter 6, 64 active electrodes were connected to a g.HIamp multichannel amplifier. Active ring electrodes (g.LADYbird) were used in a standardized cap (g.GAMMAcap), both from g.tec Medical Engineering. The activity was referenced to the earlobe and the ground electrode was located in the frontal area of the head. Signals where digitized at

256 Hz frequency rate, a notch Butterworth filter 4th order from 48-52Hz was used to eliminate the AC. Ocular movements were detected from FP1, FP2, AF7 and AF8.

3.3. Procedures

In all three experiments the experimental protocol was approved by the Universitat de Barcelona Ethics Committee (Spain), all the participants gave written informed consent according to the declaration of Helsinki and were paid for their participation.

In the experiments Chapters 4 and 5, participants entered the virtual reality and saw a virtual body (avatar) from 1PP that was consistent with their gender and skin colour. In both cases the virtual scene consisted of the avatar seated on a chair with its virtual right hand placed on a desk. In the laboratory, the participant was seated with his/her real right hand collocated with the avatar's hand and resting on a table. The left hand was placed comfortably on the participant's lap (Figure 3-3).

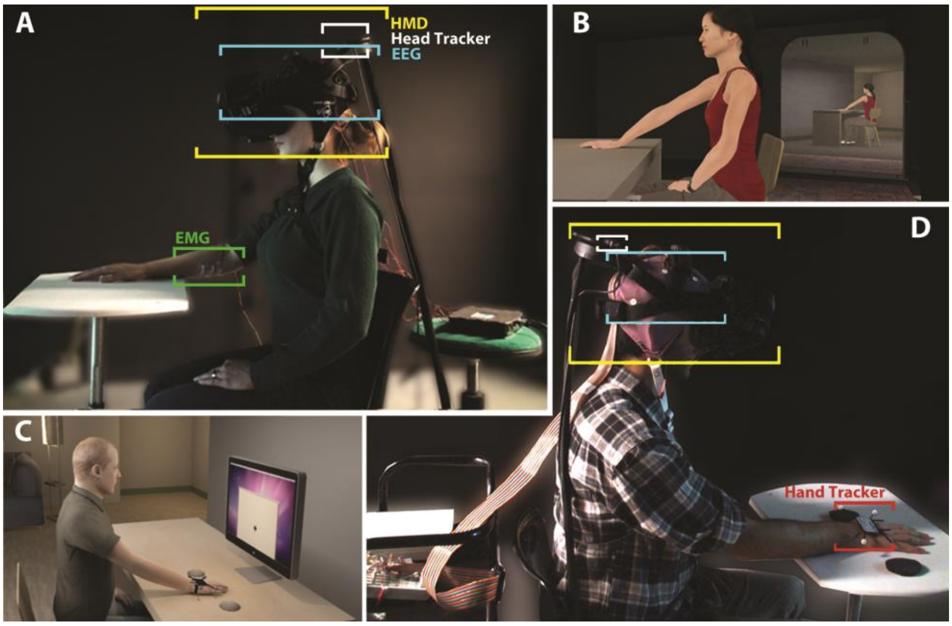

Figure 3-3 Setup of the participants in the experiments of this Thesis. A, B correspond to the participant and its virtual counterpart in Chapter 4, where the participant had EEG and EMG recordings. C, D correspond to the setup for Chapter 5 where the participants performed a motor task.

In the experiment of Chapter 4 participants were asked to remain still, i.e. not to move their hand throughout the whole experiment. An EMG setup controlled that the hand was indeed not moving during the observation experiment, contrary to the experiment of Chapter 5 where participants were asked to perform a motor task with their hand. In this case the real hand position was tracked using an optical infrared system (12 camera OptiTrack). The whole arm kinematics were computed from the hand position using Inverse Kinematics.

In both experiments participants were encouraged to freely look around for 60 seconds to familiarize themselves with the environment. After the familiarization time, in Chapter 4 we told participants to fix their gaze on the virtual hand resting, while in Chapter 5 a guided motor task started.

In the experiment of Chapter 6, related with self-recognition on faces, there was no embodiment of avatar, instead the stimuli were shown on a regular screen.

3.4. Stimuli and EEG analysis

In order to study the brain response to the different stimuli, participants repeatedly experienced the stimuli (minimum 40 times) in each of the experiments while their brain activity was being recorded. EEG was segmented offline into epochs starting before the stimulus onset. Traditionally in order to overcome the issues derived from the nature of EEG, with a very bad signal to noise ratio, researchers have used stimuli response averages, also called ERPs. Given a sufficient number of trials time-locked to the onset of the stimuli, the averaging technique cleans the noise from the response, leaving only the common components that occur as a result of the stimuli. In all of the experiments the ERPs were calculated for each condition. Mean amplitudes of components of the ERP waveform were studied at different parts of the cortex relevant in each of the experiments. Trials in which ocular movements were found or where the absolute amplitude of the signal at any electrode was greater than 150μV were rejected.

In cases where motor cortex activation was to be expected, the lateralization part of the readiness potential (RP) was studied (for example in Chapter 4). The RP has been previously related to movement preparation, and it is generally calculated as the double subtraction of C3–C4 [Eimer 1998], considering right and left hand movements. Frequency bands evolution was also evaluated in experiments involving motor cortex activation. To account for variations, the short-time power spectra was calculated as described in [Pfurtscheller and Lopes da Silva 1999]. Power spectral density (PSD) consisted in the superimposed 1-second power spectra calculated over the event-related EEG for both the reference and activity periods.

In the case of self-recognition experimentation (Chapter 6) the occipito-parietal areas of the brain were considered. Particularly the amplitude of N170 and P2 components was studied, where previous research has found significant activation [Keyes et al. 2010].

For the experiments looking for traces of self-generated errors and decision making responses clear ERN components were expected [Rodriguez-Fornells et al. 2002]. The search of the agency mechanisms in Chapter 5 was exploratory, therefore a large number of electrodes was used.

In some cases the original ERPs for each subject were transformed into reference-free Current Source Density (CSD) estimates (μV/cm2 units) using a spherical spline surface Laplacian Matlab-based CSD toolbox [Kayser and Tenke 2006] to better explore the topographical maps of the brain activation.

3.5. EMG data analysis

EMG data described in Chapter 4 was filtered with a band pass of 20–250 Hz selected according to the recommendations of [Fridlund and Cacioppo 1986] and keeping the frequency range where the primary energy in the surface EMG signal is located. As is common practice, the root mean squared (RMS) processing technique was used [Fridlund and Cacioppo 1986]. The RMS of the signal was computed with a sliding window of 500 ms in order to detect whether right arm muscles were activated at any moment. For the purpose of this experiment, subjects were asked not to move their hand under any circumstance, and the plan was that trials showing EMG activation would be discarded.

3.6. Summary

This Chapter has tried to summarize the materials and methods common to all of the forthcoming experimental Chapters 4, 5, 6.

Furthermore, most of the materials utilized in the hypothesis testing in this thesis are also shared with other research that was presented in the Virtual Reality section of the Background chapter.

4. A THREAT TO THE VIRTUAL BODY

When someone anticipates that a knife might stab their hand that is resting on a table they would be likely to attempt to move the threatened hand out of the way. They would expect to feel considerable pain should the knife stab it. In this Chapter we consider what happens when a person's real body is visually substituted by a life-sized virtual body, and they see a threat or attack to a hand of this virtual body.

This Chapter addresses the first hypothesis of this thesis. *A stimulus directed to the embodied virtual body will result in a brain response equivalent to what we would expect if the stimulus happened to the participant's real body*. This will be true if people accept their given virtual bodies as if they were their own, meaning that virtual body substitutes (avatars) are integrated as the own body also on an unconscious level.

Our work contributes to the growing field of body representation, how the brain integrates the body, as well as presenting results on pain observation. It does so by providing a harm stimulus to the virtual body and measuring the brain processing and reaction of the participants. This particular study is an important contribution to the field, since it shows that virtual bodies can be effectively integrated as the own body; providing real evidences of unconscious motor cortex activity as a response to a threat to the embodied virtual body. Furthermore, this Chapter provides new evidences of the unconscious mechanism that regulates the virtual body ownership illusion.

The results of this Chapter have been shared with the community in form of presentations at the 8th IBRO World Congress of Neuroscience [Gonzalez-Franco et al. 2011], at the Society for Neuroscience 2013 [Slater et al. 2013], and in form of journal publication in Experimental Brain Research [González-Franco et al. 2014].

4.1. Background

This section will present previous research that has focused on brain activity in response to events that would cause pain to the observer were they to occur in reality. Introducing novel techniques such as the body substitution in the IVE we can further the study of pain observation, and use it as a measure to account for levels of embodiment. Furthermore, exploring the underlying mechanisms of the thread processing also contributes to the field of body representation.

Several brain imaging techniques have been used in pain observation experiments to understand the associated mental processes. Methods that employ fMRI have found that the anterior cingulate cortex and the right insula brain regions are associated with nociceptive processing [Jackson et al. 2005; Gu and Han 2007]. Furthermore, ERP temporal dynamics involved in empathy, measured as the response to observation of pain in others, are especially prominent in the motor cortex area. Researchers have found greater P450 responses for painful images compared to neutral images in the motor cortex [Fan and Han 2008; Li and Han 2010; Meng et al. 2012; Meng et al. 2013]. These effects were modulated by the realism of the presentation and were stronger with greater realism [Fan and Han 2008].

Similarly, in studies using TMS, participants showed a reduction in Motor Evoked Potentials (MEPs) when watching a hand undergoing a painful situation [Avenanti et al. 2005]. Experiments combining both pain observation and electrical stimulation have shown modulations in the Somatosensory Evoked Potentials (SEP), particularly prominent in the centroparietal locations, with larger amplitudes for the P450 component when observing a painful situation [Bufalari et al. 2007].

This automatic empathy response is elicited involuntarily [Preston and de Waal 2002] through a bottom-up process. However it can also be modulated consciously (top-down), for example under instructions of subjective pain estimation, generating stronger P450 responses [Fan and Han 2008].

Interestingly, pain observation studies that have focused on Frequency Power Spectra (FPS) decomposition have shown a depression in the mu-rhythm during painful conditions, using MEG and EEG [Cheng et al. 2008; Yang et al. 2009]. This abolition or suppression of the mu-rhythm when observing painful situations has been interpreted to be in agreement with previous observations about the involvement of this oscillatory activity in the execution of voluntary movements [Neuper et al. 2005]. The mu-ERD is described as a circumscribed desynchronization in the upper alpha frequency band (in the range of about 9-12Hz) when a participant performs a motor action [Pfurtscheller and Lopes da Silva 1999] or motor action observation [Muthukumaraswamy and Johnson 2004]. Moreover, previous studies have found that mu-ERD can also be triggered as an unconscious mechanism to avoid painful events [Babiloni et al. 2008]. When a sound alerted participants 2.5 seconds prior to an electrical painful stimulation at the left index finger, a suppression of the mu-rhythm was elicited, as if the participant had tried to move the hand to avoid harm. This effect was not elicited during non-painful stimulation [Babiloni et al. 2008].

In this Chapter we present a pain observation experiment in the context of a whole body illusion in IVR. The IVR was delivered through a wide field-of-view head-tracked stereo HMD. This setup substitutes a person's own body by a virtual body seen from a 1PP, such that when participants look down towards their body they would see a virtual body replacing their own (Figure 4-1).

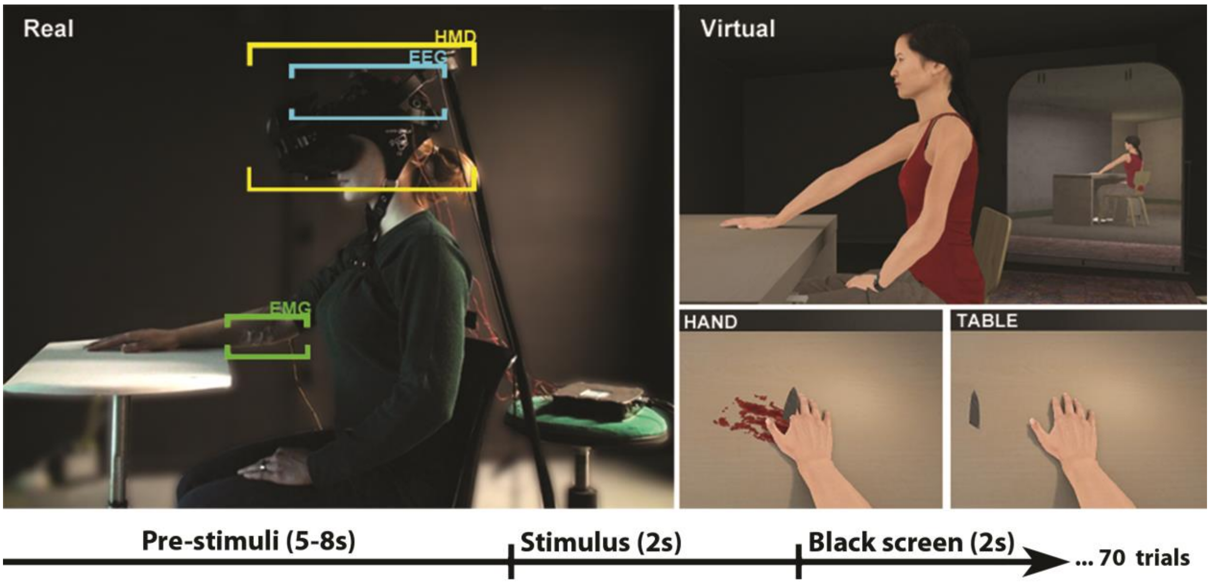

Figure 4-1 Real: the participant wearing the HMD and EEG cap. Virtual: the IVR with the gender-matched collocated virtual avatar. And the two experimental conditions seen by the participant when looking towards his hand from the 1PP: HAND) virtual hand stabbed by the knife; TABLE) virtual table stabbed by the knife (control condition).

In the experiment the participant's stationary right virtual hand, which was collocated with the real right hand resting on a table, was repeatedly threatened by a virtual knife, thereby reproducing in IVR previously conducted pain observation experiments [Avenanti et al. 2006; Bufalari et al. 2007; Gu and Han 2007; Fan and Han 2008; Li and Han 2010; Meng et al. 2012; Meng et al. 2013; Ehrsson et al. 2007]. The painful stimulation was compared to a control where the same knife attacked only the virtual table that was spatially registered with the real table on which the hand was resting (Figure 4-1). In short we measured EEG responses, which resulted in similar ERPs compared to previous experiments, with greater P450 effects in CP3 for the painful condition compared to the control condition [Bufalari et al. 2007; Fan and Han 2008; Li and Han 2010; Meng et al. 2013].

We used IVR for the study of pain observation due to recent results that show that virtual reality can be used to induce an illusion of ownership over a virtual body. This work has its origin in the rubber hand illusion, where it has been shown that synchronous tactile stimulation of a visible rubber hand and the experimental subject's corresponding hidden real hand, results in an illusion of ownership over the rubber hand [Botvinick and Cohen 1998; Armel and Ramachandran 2003; Ehrsson et al. 2004; Tsakiris and Haggard 2005]. Here the rubber hand is placed on a table in front of the subject in an anatomically plausible position, with the corresponding real hand out of sight behind a screen. When the real and rubber hand are synchronously brushed in the same location on each hand then there is typically and quickly an illusion of ownership over the rubber hand. This result has been extended to a virtual hand in virtual reality [Slater et al. 2008] including, but less strongly, a table-top projection of a hand [IJsselsteijn et al. 2006], and the illusion is also reproduced when visuomotor synchrony is used rather than visuotactile [Sanchez-Vives et al. 2010; Kalckert and Ehrsson 2012].

Similar multisensory techniques have been used for whole body ownership illusions – both illusions of displacement (or out of the body illusions) [Ehrsson 2007; Lenggenhager et al. 2007], and illusions of body substitution [Petkova and Ehrsson 2008]. Evidence suggests that the dominant factor in such whole body illusions may be first person perspective [Slater et al. 2010; Petkova et al. 2011; Maselli and Slater 2013], though it is likely that additional multisensory stimulation such as visuotactile and visuomotor synchrony would also play a role. For a review of the field see [Blanke 2012].

Typically, however, pain observation experiments present a series of pictures with hands or other extremities undergoing painful situations, and they compare the brain response of the participants to the activation produced by pictures where the same extremities do not undergo painful situations [Avenanti et al. 2006; Bufalari et al. 2007;

Fan and Han 2008; Li and Han 2010]. Many of these experiments present scissors and needles perforating the extremities as painful stimuli. A potential advantage of IVR, however, is that greater ecological validity can be enabled, going beyond the presentation of two-dimensional, static stimuli. With IVR there is a life-sized, three dimensional virtual body seen in stereo, that visually substitutes the obscured real body of the participant, which can be virtually attacked. Hence the level of realism can be greatly enhanced. In the present study participants saw a knife attacking the hand of their virtual body, the virtual body therefore acting as a surrogate for the real body in the context of pain observation.

4.2. Materials and Methods

Most of the materials for this experiment are common with the rest of the experiments of this thesis, which have been previously described in Chapter 3. More precisely the Apparatus, Procedures and EEG recording of this experiment have been already described in the mentioned Chapter.

4.2.1. Procedure

Nineteen healthy volunteers – 9 male, 10 female; aged 25 ± 4.0(S.D) years – all right-handed participated in the experiment.

Participants entered the virtual reality, and saw a virtual body (avatar) from 1PP that was consistent with their gender and skin color. The virtual scene consisted of the avatar seated on a chair with its virtual right hand placed on a desk. In the laboratory, the participant was seated with his/her real right hand collocated with the avatar's hand and resting on a table. The left hand was placed comfortably on the participant's lap. Participants were asked to relax and keep their arms and hand still throughout the experiment (Figure 4-1).

Participants were encouraged to freely look around for 60 seconds to familiarize themselves with the environment while keeping their arms still and collocated with those of the virtual body. After the familiarization time, we told participants to fix their gaze on the virtual hand resting on the table and to keep their real hand still. We did not ask them to perform any other task at all, such as pain judgment, but only to fixate on the virtual hand.

4.2.2. Stimuli

Participants repeatedly experienced two conditions in a within-group design[3]: condition HAND where the knife stabbed the virtual hand, and condition TABLE where the knife stabbed the table, 15 cm away from the participant's hand (Figure 4-1). The experiment consisted of 70 trials repeating the HAND and TABLE conditions (30 HAND and 40 TABLE). A trial consisted of three parts:

1. Pre-stimulus: the participant looked at the virtual hand (5-8 seconds).
2. Stimulus: a knife appeared in the HAND or TABLE (2 seconds).
3. Black screen: a black screen appeared (2 seconds).

During the first 10 trials only the TABLE condition was presented to acclimatize participants to the trial evolution and the black screen. Then, there were 6 predefined blocks of 10 trials each; each block had 5 HAND and 5 TABLE, with the order randomized within each block. The order in which these blocks were presented to the

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[3] See supplementary movie http://youtu.be/029XNWctb4A

participants was randomized for each participant. After the 70 trials the screen went black and the experiment ended. This virtual reality exposure lasted for 15 minutes.

4.2.3. Questionnaire

Participants then completed a questionnaire about their virtual experience, in which they answered the following questions:

1. *Ownership*: I felt as if the hand I saw in the virtual world might be my hand.
2. *Harm Hand*: I had the feeling that I might be harmed when I saw the knife inside the hand.
3. *Harm Table*: I had the feeling that I might be harmed when I saw the knife outside the hand.
4. *No Ownership*: The hand I saw was the hand of another person.
5. *Body Threat*: I saw the knife as a threat to my body.

Responses to these statements were on a 5-point Likert-scale where 1 was anchored to strong disagreement and 5 to strong agreement. Questions 1 and 4 were related to the sense of ownership of the hand, with question 1 expected to record high scores while question 4 expected to record low scores. These two questions are similar to those used in previous studies to measure ownership illusions [Banakou et al. 2013; Llobera et al. 2013] for example: “How much did you feel that the virtual body was your body” for the ownership question, and “How much did you feel that the virtual body was another person?” as a control for the no ownership, or “How much did you feel that the virtual body you saw when you looked down at yourself was your own body”, versus “How much did you feel as if you had two bodies”. Moreover question 1 is similar to that used by the original Botvinick and Cohen (1998) paper “I felt as if the rubber hand were my hand”. Questions 2 and 3 were to examine whether there was any feeling of harm in response to the knife being in the condition HAND or TABLE. Question 5 was a consistency check to control questions 2 and 3; we expect similar responses to *Harm Hand*.

4.2.4. EEG Analysis

In order to study the effects of the stimuli on the pain sensitivity, ERP components were analyzed as in [Fan and Han 2008; Li and Han 2010; Meng et al. 2012]. The stimulus locked ERP helped us determine the pain related levels of the participants with respect to the HAND condition, where a higher P450 activity was expected in case of a pain response.

The ERPs in both conditions HAND and TABLE were averaged separately for each subject. The ERPs were also used to better study the lateralization part of the Readiness Potential in order to detect which hemisphere was more active. As in our case we only used right hand manipulations we report only one side C3 - C4 subtraction. An increase in negativity is expected when a movement is prepared with the contra lateral hemisphere. Thus, negative amplitude might reflect a right hand movement preparation.

Apart from the ERPs, frequency bands were also evaluated. To account for variations we used short-time power spectra as described in [Pfurtscheller and Lopes da Silva 1999]. Power Spectral Density (PSD) was calculated as the superimposed 1-s power spectra calculated over the event-related EEG for the HAND and TABLE conditions for both the reference and activity periods.

4.3. Results

4.3.1. Hand Movements

A critical question for this experiment was whether participants did actually move their threatened hand or not. Real hand movement had to be negligible otherwise it would increase activation in the motor cortex. This was assessed using the EMG data. The RMS was calculated for the pre-stimuli reference period (-1 to 0 seconds) and the post-stimuli activation period (0.7 to 1.7 seconds), these periods correspond to the time when the motor cortex was found activated. Using a repeated measures ANOVA comparing (HAND-BASELINE vs. TABLE-BASELINE) no significant difference nor effects were found in the RMS, F(1,18)=2.685, P=0.119. Other timings also did not show any activation, and the same ANOVA analysis was later used to analyze the mu-ERD. These results suggest that the participants did not move their real hand during the experimental period.

4.3.2. Questionnaire

Here we consider whether the setup did induce an illusion of ownership over the virtual hand, and whether the stabbing knife was subjectively experienced as a threat. Figure 4-2 shows the box plot (n = 19) for the questionnaire responses that were designed to assess this. It is clear that the illusion of ownership was high (the median level of ownership is 5), and the no ownership score was comparatively low (the median is 2). The Wilcoxon matched pairs sign-rank test (two-sided) comparing *Ownership* with *No Ownership* shows that this difference is significant ($z = 3.89$, $P < 0.0001$). The illusion of harm to the hand (*Harm Hand*) has median 3, and *Harm Table* has median 1. The paired sign rank test again shows these to be significantly different ($z = 3.74$, $P < 0.0002$). The threat to the body as a whole (*Body Threat*) also has median 3, and is significantly different from *Harm Table* (z = 3.59, P < 0.0003). Although the medians of *Harm Hand* and *Body Threat* are the same, the greater range of the former leads to it being significantly greater overall (z = 2.36, P < 0.018).

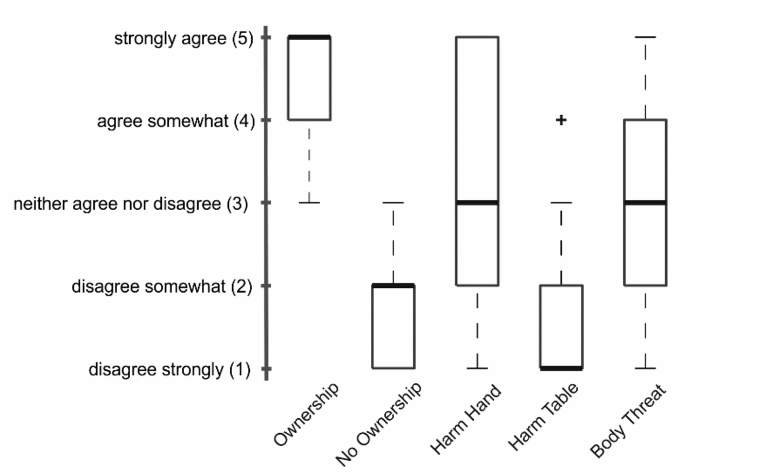

Figure 4-2 Box plots showing the responses to the questionnaire. The thick lines are the medians, and the boxes are the interquartile ranges (IQR). The whiskers follow the standard convention of extending to 1.5 times the IQR or the maximal/minimal data point

Table 4-1 shows that *Ownership* is positively correlated with *Harm Hand* which is positively correlated with *Body Threat*. *Body Threat* is also positively correlated with *Ownership*. There are no other significant correlations. This is important since illusory ownership of the hand should go along with the feeling of threat to that hand or to the body, since without illusory ownership there is no actual threat. These results are consistent with the original hypothesis that the stronger the illusion of ownership the greater the tendency of participants to give higher ratings to the Harm questions. We consider these relationships in greater depth in Section 3.6.

Table 4-1 Spearman Correlation Coefficients Between the Questionnaire Scores

	Ownership	*Harm Hand*	*Harm Table*	*No Ownership*	*Body Threat*
Ownership	1.000				
Harm Hand	0.726	1.000			
	(0.000)				

Harm Table	0.162	0.302	1.000		
	(0.508)	(0.209)			
No Ownership	-0.048	0.079	-0.125	1.000	
	(0.844)	(0.749)	(0.611)		
Body Threat	0.481	0.774	0.418	-0.179	1.000
	(0.037)	(0.000)	(0.075)	(0.463)	

(P values for test of 0 correlation). P = 0.000 means P < 0.0005, n = 19

4.3.3. ERP Stimulus-locked activity

The pain sensitivity levels of the participants for the HAND and TABLE conditions were assessed using stimulus-locked ERPs depicted in Figure 4-3. A repeated measures ANOVA P450 [condition (HAND/TABLE) · electrode (Frontal/Central/Centro-parietal) · hemisphere (Left, Right)] in the time window 420 to 620 ms on the original real voltage data showed a significant main within subjects effect for Condition (F(2,18)=6.977, P=0.017) and for Electrode position (F(2,36)=21.401, P<0.001). A centroparietal distribution was observed for the P450 component as reflected by the significant interaction between Condition and Electrode (F(2, 36)=7.640, P=0.002) (the peak value was observed at CP3, see Figure 4-3.

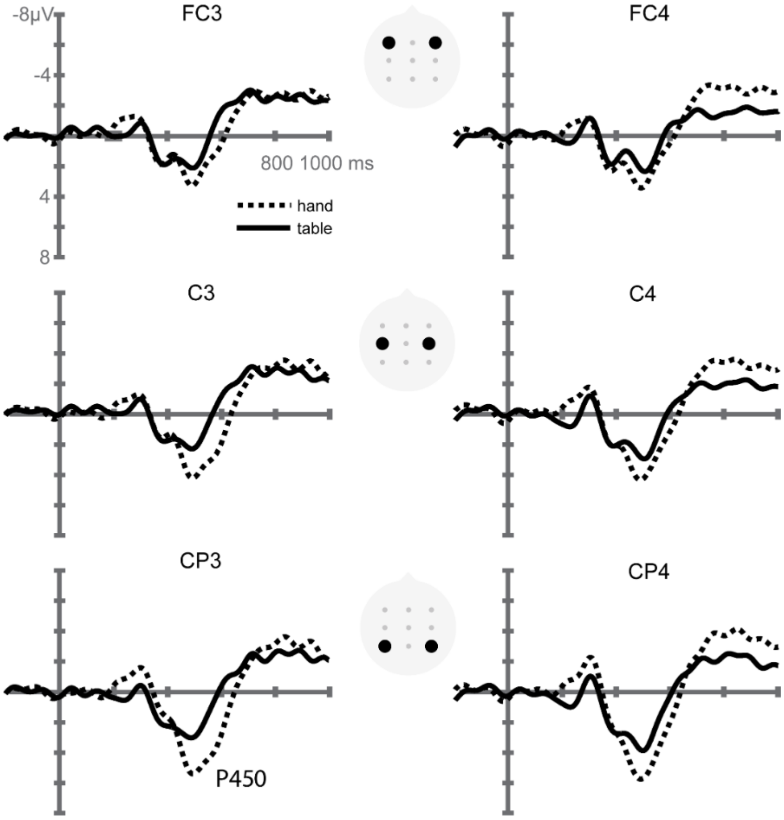

Figure 4-3 Grand averaged stimulus-locked ERPs for six representative front, central and parietal electrode locations. A significant increase in the amplitude of the P450 is observed in the HAND condition mainly at C3 and CP3 locations. Baseline from −200 to 0 ms, time 0 indicates the stimuli onset; a low pass filter 12 Hz half-amplitude cut-off was applied.

We conducted further post-hoc pairwise comparisons between both conditions (hand and table) at parietal and central electrodes; the paired samples t-tests were significant for the P450 at C3 and CP3 electrodes (t(18)=3.438, P=0.003 and t(18)=3.637, P=0.002, respectively). These results are consistent with the P450 effects induced when a pain estimation task was performed in previous studies [Fan and Han 2008; Li and Han 2010; Meng et al. 2012].

4.3.4. Frequency Power Spectral Density

To determine whether participants showed a different frequency response to the attack (HAND) versus the control stimulus (TABLE), we performed a 1-s power spectra analysis (see Figure 4-4abc).

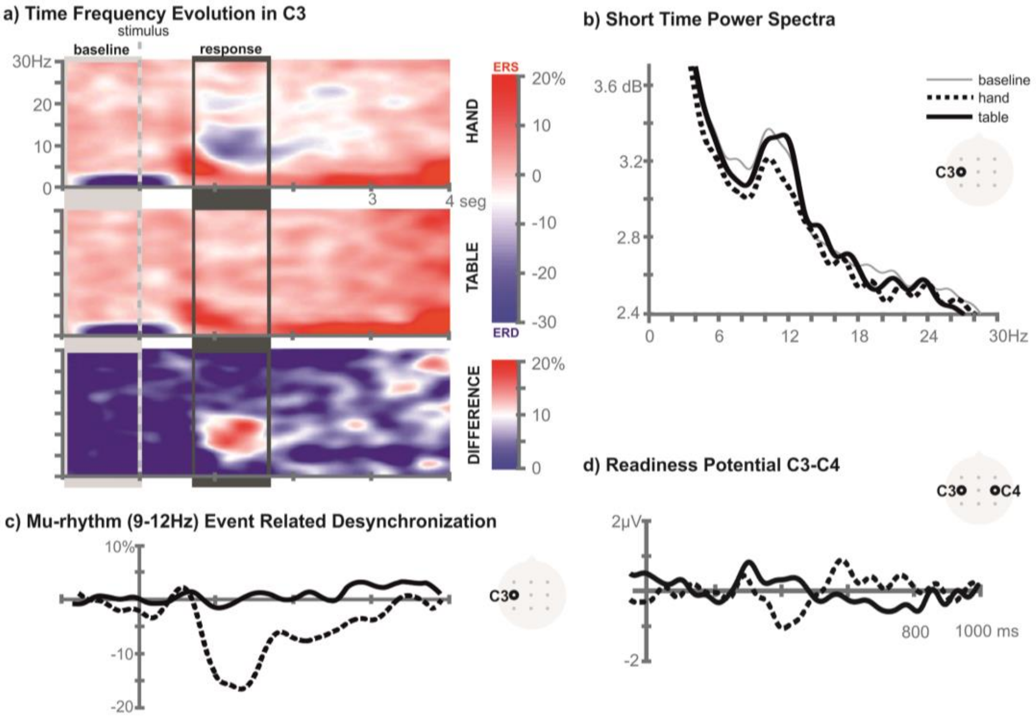

Figure 4-4 (A) Time frequency evolution of the two conditions and the difference in the spectral activity. (B) Grand averaged 1-s short-time power spectra calculated from EEG data (electrode C3) recorded. The baseline corresponds to the range −1 to 0 s before the stimuli and the activity period corresponds to the range 0.7–1.7 s after the stimuli. Both the baseline and TABLE frequency spectra show a peak in the mu-rhythm that is attenuated in the HAND condition. (C) Grand averaged mu-rhythm (9–12 Hz) event-related desynchronization for the C3 electrode. (D) Grand averaged RP (C3–C4) subtraction between the brain activity in the two hemispheres shows movement preparation effects. Low pass filter 8 Hz, half-amplitude cut-off.

In Figure 4-4a the Time Frequency evolution of the two conditions and the difference in the spectral activity can be observed; further representation of the Mu-rhythm evolution can be found in Figure 4-4c; and the 1-s power spectral differences between the reaction (0.7 to 1.7 seconds) and the baseline (-1to 0 seconds) can be found in

Figure 4-4b. The three visualizations show a clear attenuation in the mu-rhythm during the HAND condition.

The 1-s power spectrum of the mu-rhythm (9-12Hz) in both conditions (hand-baseline vs. table-baseline) was used for the statistical analysis. A repeated measures ANOVA with three factors [condition (HAND/TABLE) · electrode (Frontal/Central/Centro-parietal) · hemisphere (Left, Right)] was run to analyze the desynchronization. We found a significant main within-subject effect for the condition (F(1,18)=12.235, P=0.003). The distribution of this component was dependent on the electrode position as reflected by the significant interaction (condition · electrode F(2, 36)=8.751, P =0.001). Further post-hoc tests comparing the conditions in the parietal and central electrodes showed most prominent desynchronizations during the HAND condition in C3 (t(18)=-3.482, P=0.003) and CP3 (t(18)=-3.670, P=0.002). These results are similar to the mu-ERD effects induced when an imaginary hand movement is performed [Pfurtscheller and Lopes da Silva 1999; Neuper et al. 2005].

4.3.5. Readiness Potential

To detect which hemisphere was more activated, and thus if there was any movement preparation [Eimer 1998], we calculated the Readiness Potential as C3 - C4. An increase in negativity is expected if a movement is prepared with the contra lateral hemisphere.

Figure 4-4d depicts the response-locked Readiness Potential (C3-C4) activity that was analyzed via a paired-samples t-test for time-window 300 to 500 ms. A significant difference between conditions was found (t(19)=-2.237, p=0.038). This result shows negativity in the contralateral hemisphere (left, C3 electrode) during the HAND condition (Mean=-0.455 Std=1.183), which indicates right hand pre-movement activity versus a more positive response during the TABLE condition (Mean = 0.419 Std=1.221).

4.3.6. Relationship between Questionnaire Scores, P450 and mu

Here we examine the relationship between the EEG response variables (P450, mu), the *condition* (TABLE, HAND), and the subjective responses from the questionnaire. Table 4-1 shows strong positive correlations between Ownership and each of P450 and mu, and a positive correlation between Harm Hand and P450. There is a negative correlation between No Ownership and mu.

Table 4-2 Spearman Correlation Coefficients Between the Questionnaire Scores and EEG Variables

	Ownership	*Harm Hand*	*Harm Table*	*No Ownership*	*Body Threat*	*P450*	*mu*
p450	0.287	0.389	0.113	-0.021	0.289	1.0000	
	(0.0000)	(0.0000)	(0.089)	(0.751)	(0.0000)		
mu	0.266	0.093	-0.035	-0.169	0.040	0.029	1.0000
	(0.0000)	(0.160)	(0.601)	(0.011)	(0.545)	(0.658)	

n = 228. Overall $R^2 = 0.26$, $F(5,222) = 15.59$.
Shapiro-Wilk test for normality of residuals: $P = 0.10$. $P = 0.000$ means $P < 0.0005$

Correlations do not imply causality, but the fact that there are very strong correlations between variables obtained in totally different ways (questionnaire and electrical recordings from the scalp) suggests that there is something to be explained. It would be surprising indeed if these were just coincidental, especially given the underlying supposition of this Chapter that the level of ownership would be reflected in brain activity in just the way that these correlations suggest. In particular given the setup and based on previous results showing that body ownership is likely to be induced as a result of 1PP [Slater, Spanlang, Sanchez-Vives, et al. 2010], we would expect that the level of ownership would be positively associated with the feelings of threat to the hand and the body, which in turn would influence the P450 and mu values. These would also be influenced by the manipulated condition (i.e., whether the knife penetrated the hand or was close to it but did not penetrate).

Conventional approaches would have to treat the different relationships in separate linear models (for example, using regression) that cannot assess multiple simultaneous effects. For this purpose we turned to path analysis - for example [Kaplan 2009] - which can model multiple simultaneous stochastic equations. Although not conventional in this domain of research, it is a powerful method that we have used before in the context of body ownership studies [Kilteni et al. 2013; Llobera et al. 2013; Maselli and Slater 2013]. For the path analyses we used Maximum Likelihood estimation, with robust standard errors, available in Stata 13 (www.stata.com), and the questionnaire responses were modeled as ordinal logit variables.

We fitted the model as described above, with *Ownership* influencing *Harm Hand*, *Harm Table* and *Body Threat*. In turn these could influence P450 and mu, which were also influenced by condition. We fitted the path model and deleted paths with significance levels less than 0.05. The resulting path model is shown in Figure 4-5 and associated Table 4-3. It can be seen that *Ownership* is very strongly positively associated with the three harm variables. *Harm Hand* is very strongly positively associated with P450 and weakly with mu. *Harm Table* is weakly negatively associated with P450. *Condition* is strongly positively associated with P450 and negatively with mu. The overall fit of the model is good as shown by the last column of Table 4-3 which presents the correlations between values fitted by the model and the observed values of the response variables P450 and mu.

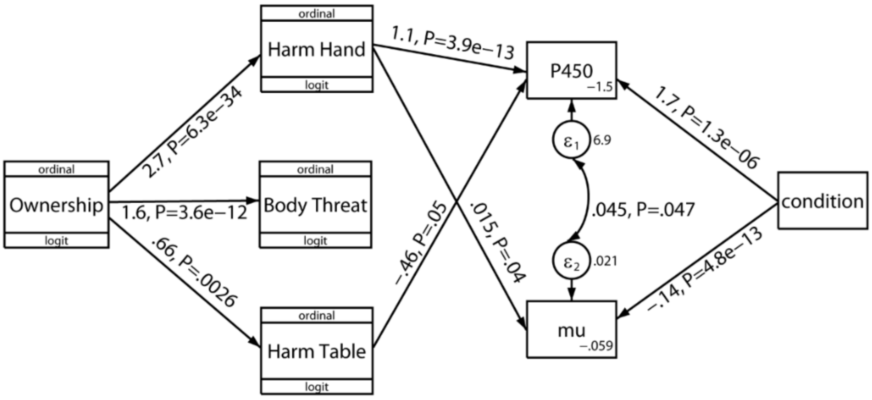

Figure 4-5 Path analysis for P450 and mu and in relation to questionnaire variables Harm Hand, Harm Table, Body Threat, Ownership and condition (TABLE = 0, HAND = 1). The values on the paths are the coefficients corresponding significance levels. The epsilon represent the random error term. The diagram can be interpreted as a set of simultaneous linear prediction equations. For example from Table 4-3 we can see that P450 = −1.50 + 1.69*condition + 1.08*(Harm Hand) − 0.46*(Harm Table) + epsilon. The circles are the random error terms and the epsilon circles are their variances. The curved path represents a covariance.

Table 4-3 Path Analysis for P450 and mu

	Coef.	Std. Err.	z	P	r, P (Pearson correlations)
P450					0.53, P = 0.0000
condition	1.69	0.35	4.84	0.000	
Harm Hand	1.08	0.15	7.26	0.000	
Harm Table	-0.46	0.23	-1.96	0.050	
Const.	-1.50	0.57	-2.63	0.009	
mu					0.45, P = 0.0000
condition	-0.14	0.02	-7.23	0.000	
Harm Hand	0.01	0.01	2.05	0.040	
Const.	-0.06	0.02	-2.42	0.015	
Harm Hand					
Ownership	2.71	0.22	12.14	0.000	
Harm Table					
Ownership	0.66	0.22	3.02	0.003	
Body Threat					
Ownership	1.56	0.22	6.95	0.000	

P = 0.00*0 means P < 0.00*05.

Now turning attention to the Readiness Potential (RP), this is based on a different set of data (n = 38) since RP is a bipolar difference of the activity between the C3 and C4 electrodes in the motor cortex so cannot be considered at the same time as P450 and mu. Applying path analysis to this data, only condition and *Harm Table* are significantly related to RP. Hence an ordinary regression can be used (although still we allow robust standard errors). The result is shown in Table 4-4, where condition (Knife in Hand) is negatively associated with RP but positively associated with *Harm Table*. This is consistent with a lateralization between hemispheres occurring during the preparation of a motor action, the RP (C3-C4) is more negative when there is preparation to move the right hand [Eimer 1998], which in the current experiment is the attacked hand. Therefore, a reduction in RP for higher scores in Harm Hand question indicates stronger preparation of movement.

Table 4-4 Regression for RP

	Coef.	Std. Err.	t	P>t
condition	-0.87	.38	-2.28	0.029
Harm Table	0.34	.16	2.18	0.036
Const.	-0.10	.41	-0.25	0.802

F(2,35) = 8.48, R2 = 0.17, P = 0.001, n = 38, Shapiro-Wilk (test for normality of residual errors) P = 0.24

4.4. Discussion

Our results suggest that participants instinctively avoided a virtual knife stab to their virtual body, thus activating the motor cortex and generating a mu-ERD, and a Readiness Potential, as would be expected if their real hand were threatened. Our study reproduced the results of [Fan and Han 2008; Li and Han 2010; Meng et al. 2012; Meng et al. 2013] in terms of ERP correlates, showing significant evidence that pain effects were found, with the means P450 showing greater amplitudes at the CP3 electrode location in the HAND compared to the TABLE condition.

Importantly, participants were instructed not to move their hand during the whole experiment – and this was verified by the EMG analysis. Although, only measuring the flexor carpi as in our setup could have not account for very subtle movements, any significant movements could be reliably recorded using this technique. Furthermore, if there were any instinctive mechanism to avoid the harm that was unconscious to the participants, this would as well enhance our theory that participants felt as if the harm was real and they responded accordingly. In fact, when doing the ERP study we found motor cortex activation in the HAND condition with a significantly greater negative Readiness Potential (C3-C4), associated with the intention of moving the right hand, this Readiness Potential was probably an instinctive reaction to the harm that could not be controlled consciously by the participants. Additionally, we found that when the virtual hand was attacked with the virtual knife, it elicited significant motor cortex activation. A significant mu-ERD was found when the knife attacked the hand - especially prominent in the C3 electrode - as if the participant were trying to avoid harm. This suppression of the mu-rhythm in the hand condition could be interpreted as being in agreement with previous observations about the involvement of this oscillatory desynchronization when a participant performs a hand motor action [Pfurtscheller and Lopes da Silva 1999]. Besides, this effect reproduces the results of [Yang et al. 2009; Perry et al. 2010; Whitmarsh et al. 2011], although we believe that the empathy level towards the virtual body was likely much higher than any previous pain observation experiment. Furthermore, illusory ownership over the virtual body provoked more prominent responses with greater similarity to those described by [Babiloni et al. 2008] in preparation for an electrical painful stimulation of the left index finger.

A recent paper by [Evans and Blanke 2013] showed that synchronous visuo-tactile feedback during the hand ownership illusion generates mu-ERD in the sensorimotor cortex similar to the one produced during motor imagery BCI. Although, in our experiment no tactile feedback was provided, we postulate that their results are compatible with our findings and suggest that the correlations found in the current experiment between the mu-ERD and P450 with the ownership illusion question may be related by a similar mechanism to the one they describe. Future research could assess whether tactile feedback would enhance the experience in the current scenario and inhibit any existing sensory mismatch. In this study tactile feedback was avoided to prevent overlaying activities in the sensorimotor cortex between the interpretation of tactile sensory information and the efferent motor reactions [Yetkin et al. 1995]. It would have been very difficult to dissociate between the effects of the tactile stimulation and the subconscious motor reaction to the harm. However, regarding the sensory mismatch, some participants reported a strange feeling in their finger at the end of the experiment that would indicate that they were having illusions of tactile stimulation through a top down mechanism.

According to [Pfurtscheller and Lopes da Silva 1999] an ERS in the beta-rhythm would typically be found in hand motor-imagery when the movement finishes. Nevertheless, in the current experiment we could not find significant beta rebound.

We have shown that automatic neural mechanisms, such as pain responses, that occur in reality occurred in this case in response to events in the virtual reality scenario of this study. This is in line with previous findings that people do tend to have similar responses in IVR as they would to similar situations in reality [Sanchez-Vives and Slater 2005], except that we believe that this may be the first study to confirm this at the level of brain activity as measured by EEG.

Additionally the results are useful for understanding the neural and cognitive mechanisms of body perception. For the first time we have shown that neural responses (P450, mu and RP) are correlated with the subjective level of the ownership illusion and the subjective illusions of harm and threat to the body. It seems quite remarkable that these variables, being in principle totally unrelated to one another (electrical brain signals measured from the scalp compared with scores in a questionnaire) are nevertheless apparently strongly related. This correlation provides a cross validation that both the questionnaire responses and the electrical signals relate to the same underlying brain processes. This correlations are however hard to isolate from all the concurrent factors that may be modulating the current effects, as it can be seen in the path analysis. The path analysis, on the other hand that gives a wider perspective of how subjective responses may be related to the brain processes. More interestingly, the path analysis may discover relations that were previously hidden by some preexisting correlation. In our case, we observe how body ownership modulates all the rest of the subjective scoring, and we can observe how using the path analysis, the correlations between body threat disappear, as they were probably only modulated by body ownership in this case. The rest of the correlations remain explained through the path analysis without further variations.

A possible caveat in the interpretation of the present results is that we cannot easily dissociate some of the intrinsic factors that may be modulating the pattern of ERP responses observed as for example, self-location, empathy and ownership. However, based on previous empathy related related studies [Fan and Han 2008; Li and Han 2010; Meng et al. 2012; Meng et al. 2013] we can consider that the P450 component is mostly associated to empathy processing. Further studies have combined self-identification with empathy, studying how racial bias may influence these effects [Avenanti et al. 2010], indicating that the empathy increases when the self-identification is maximal. The new contribution in our experiment in the empathy processing is to enhance the self-identification by producing the illusion of body ownership. The relation between empathy and embodiment is certainly a major scientific question in the current experiment; we aimed at dissolving the boundaries between the two concepts. Even though empathy refers to the capacity to respond and understand experiences of another person [Decety and Jackson 2004], and the sense of embodiment has been described as a the experience of our self as being inside a body [Kilteni, Groten, et al. 2012], we do believe that they are related one to the other by the perspective effects. Embodiment is very dependent on perspective [Slater, Spanlang, Sanchez-Vives, et al. 2010], as well as perspective taking is a technique to induce empathy [Lamm et al. 2007]. Recent studies inside Virtual Reality have shown that Embodiment can itself be a technique to reduce racial bias [Peck et al. 2013], meaning that embodiment could modulate empathy. We suggest that a maximal level of empathy can be produced during embodiment, and that may be a reason why stronger reactions are found in the motor cortex in the present Chapter when compared to previous pain observation studies. Finally, we want to remark that this experiment emphasizes how much related embodiment may be of empathy, to the level of converging when the other person becomes one self.

Furthermore, in the current Chapter we observed new effects (mu-ERD and lateralization) that have not been reported before in previous empathy studies. We believe that these effects are observed for the first time due to the embodiment illusion induced in our experiment. Previous research has shown that embodiment can be modulated by different combinations of self-location and body ownership [Maselli and Slater 2013]. In our setup the control condition TABLE in which the knife did not appear where the hand was located, but 15cm away, did not trigger the brain activation, therefore indicating the possibility of harm to the own body is very relevant in the current study. Our results show that the exploitation of virtual body ownership illusions could be useful for further understanding the underlying neural mechanisms involved in cognitive processes of perception. Besides, the measurements of cognitive processes provide a promising tool to measure virtual embodiment.

This may also have implications not only for the measurement of virtual body ownership but also to discriminate strengths of this illusion, so that people reacting with a stronger EEG activation – greater P450 amplitude the virtual hand is attacked – may have a stronger illusion than people with weaker P450 amplitude.

The questionnaire responses indicated generally a very strong illusion of ownership over the virtual body. This could explain why the brain responses observed – P450, Readiness Potential and mu-ERD – were larger in comparison to previous experiments reported in the literature.

4.5. Conclusions

The present study suggests that when a person is in an immersive virtual reality and has a body ownership illusion towards a virtual body that apparently substitutes their own body, there are autonomic responses that correspond to what would be observed were the events to take place in reality. Overall automatic brain mechanisms—P450—were found in this variation of the classical pain observation experiment, which is consistent with what [Bufalari et al. 2007; Fan and Han 2008; Li and Han 2010; Meng et al. 2012; Meng et al. 2013] previously reported. However, our setup was not one concerned with participants experiencing empathy towards another person but rather experienced direct attacks to their own body, since both subjective and objective data point in that direction. The results support our initial hypothesis that a threat to a virtual hand, toward which the participant has an illusion of ownership, would significantly produce a harm prevention effect (measures using the RP (C3–C4) and oscillatory movement-related components, the mu-ERD) such as trying to move it away from the source of the harm. The questionnaire also confirmed high levels of ownership over the virtual body (see Figure 4-2). In addition, the correlation between the automatic brain mechanisms—P450—and the subjective illusion of ownership opens the door for a new promising measure of virtual embodiment.

5. DISRUPTING SENSE OF AGENCY OF THE VIRTUAL BODY ACTIONS

How do we recognize ourselves as the agents of our actions? In this Chapter, using time-sensitive neurophysiological signatures we identified in humans embodied in a virtual body two different error-monitoring loops involved in providing a coherent sense of the agency of our actions. While a very fast internal error-loop was observed for evaluating the correctness of our own actions, a slower external monitoring loop was triggered when participants were deceived regarding their own movements ("*avatar errors*").

This Chapter addresses the second hypothesis of this thesis. *When somebody is embodied in a virtual avatar and experiences agency of the body, any break in that agency (such as hijacking in the movements of the virtual body) would be clearly perceived as an external error.* The expectation is that a higher feeling of embodiment would lead to a stronger perception of the break in agency.

Here we present a second study showcasing a set of experiments to explore the implications at a neurological level of such an experience of control over our body and the agency of the actions performed. These experiments widen the current knowledge on agency schemas, showing evidences of the existence of both re-afferent and feedback error mechanisms that are concurrently working in the brain to detect agency disruptions.

At the neurophysiological level, the violation of the sense of agency of our action ("*this is not my error*") showed a strong similarity in topography and latency to other electrophysiological signatures related to semantic or conceptual violations. Distinct brain error detection mechanisms are in charge of distinguishing our own errors from those imposed by an external agent

Our work contributes to the growing field of body representation in the brain. We provide strong neural evidence in relation to understanding the integration of internal and sensory feedback information while being actors of our own actions.

The results of this Chapter have been shared with the community in form of presentations at the EU Project VERE Reviews. And in form of journal publication submitted [Padrao et al. 2016].

5.1. Background

We are usually not aware of the feeling of agency with respect to our actions or thoughts [Gallagher 2000]. As expected, in normal circumstances, when no conflicting information is experienced from the different re-afferent feedback sources no doubts are raised about the agency of the action. Indeed this is the normal experience of ourselves, where we typically feel that we are in control of our actions. This in itself might reflect the automaticity in the process that elicits this feeling about the correctness of the agency of our actions: *this action is mine*.

However, when an explicit judgment of agency is demanded or when an unexpected consequence of our actions is perceived, we can become aware of our body actions [Tsakiris et al. 2005]. A mismatch between the output and the perceived input results in a violation of this feeling of agency: *this action was not mine*. Interestingly, several studies have shown that this mechanism of agency attribution is probably affected not only in patients suffering the anarchic hand syndrome [Sala 1998] but also in patients with schizophrenia where it might explain the problems associated with delusions of control, hallucinatory experiences or thought insertion [Daprati et al. 1997; Frith 2005; Synofzik et al. 2010].

When executing most of our actions, an internal unconscious error-detection and prediction system constantly monitors and corrects our own behaviour. This incredible fast error-detection system is usually explained using internal forward models of motor control [Blakemore et al. 2002; Frith et al. 2000; Jeannerod 2006; Rodriguez-Fornells et al. 2002; Wolpert and Miall 1996]. According to such models, a feed-forward mechanism is used to generate constant predictions of the consequences of our own actions, using an efference copy [Holst and Mittelstaedt 1950]. The efference copy is used to compute error deviations from the expected goal of our on-going actions even before the action has been completed [Crapse and Sommer 2008]. If an internal error signal is triggered, the system might implement fast inhibitory commands, and error correction processes. Compensatory mechanisms will be triggered if an error is finally produced, e.g., post-error slowdown of the reaction time of the following trials after an error [Logan and Crump 2010; Marco-Pallarés et al. 2008; Rabbitt 1966]. Interestingly, these processes are independent and dissociable from the awareness of our own errors [Nieuwenhuis et al. 2001]; indeed conscious access to our own-errors is much slower than what we might actually think (at about, 500-750 ms [Rabbitt 2002]). Interestingly, using electroencephalographic (EEG) recordings, it has been found that the Error-related negativity (ERN) signal, provides an index of this fast internal error-monitoring loop [Rodriguez-Fornells et al. 2002; Gehring et al. 1993; Holroyd et al. 2005] most probably originating in the anterior cingulate cortex [Marco-Pallarés et al. 2008; Carter 1998; Holroyd et al. 2004; Ullsperger and von Cramon 2001].

The internal error-monitoring loop helps the organism to adapt to the ever-changing environment. However an external error-monitoring loop might also be important in order to further integrate new sensory incoming information about the real consequences of our current action (i.e. re-afferent feedback). If there is a coherent bodily perception we will attribute the agency of the action to ourselves. Usually our actions are accompanied by multimodal re-afferent feedback information, first from proprioceptive receptors, tactile information, and later visual or auditory feedback information (when available). When this multisensory information arrives at the visual, auditory and somatosensory regions of the brain with different neural transmission delays, a further evaluation during the multisensory integration might be conducted to inspect the agency of the actions: *was the expected outcome reached*?.

For example, when reaching for a cup of water, our internal forward model will help to provide the system with the exact parameters needed to adjust the grasping action and the corresponding movements needed. While this internal error-monitoring loop initially guides this action in an unconscious fashion, the external error loop might monitor, later in time, whether the final visuo-, tactile- and proprioceptive-feedback information was coherent with the initial goal of our action. Imagine that suddenly the expected information coming from grasping the cup of water and moving it to your mouth transmits the information that the object is made of rubber instead of a cup-ceramic or that it was not your hand that is moving but the hand of a different person! How is the system assessing whether these violations of the expected sensory consequences of your actions are incorrect? Is this external error-monitoring loop different from the internal error-monitoring described above and involved in fast-corrective actions? [Holroyd et al. 2005]

The objective of our research in this study has been to functionally dissociate both brain error-monitoring loops that provide a coherent sense of the agency of our actions and to evaluate the neural delays of both mechanisms. In order to study this we used ERP (multichannel EEG recording) in an IVE that allowed us to design an intriguing experimental setting (Figure 5-1a; Supplementary Movie [4]).

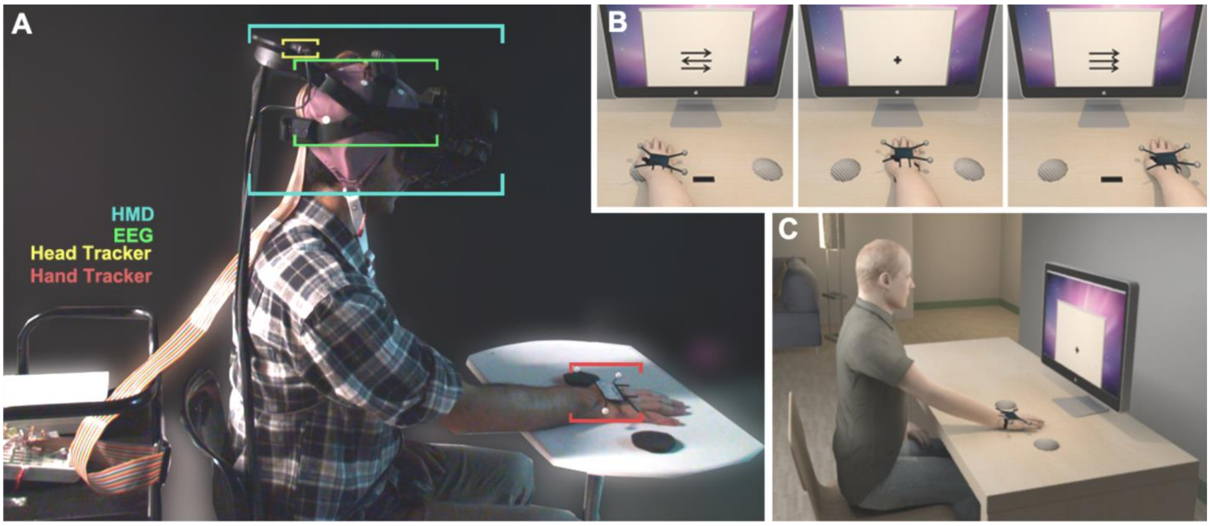

Figure 5-1 A. Participant in the laboratory with the HMD, EEG and the head and hand tracking systems. B. 1PP of the arrow flanker task. Participants performed fast movements with their right hand to the button in the direction of the central arrow and then go back to the starting position. In the InCM trials the virtual hand moved in the opposite direction to the participant real movements, thus generating an external-error. C. Virtual body of the participant in the IVE seen from a 3PP.

5.2. Materials and Methods

Most of the materials for these experiments are common with the rest of the experiments of this thesis, which have been previously introduced in Chapter 1. More precisely the Apparatus, Procedures and EEG recording of this experiment have been already described in Chapter 3. However some aspects of the experiments proposed to test this hypothesis are further described in this section.

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[4] See the supplementary movie http://youtu.be/lNjucylJxX8

5.2.1. Experiment 1

5.2.1.1. *Procedure*

While immersed in the virtual environment participants (n = 18 volunteers, 6 men; mean age, 26 years ± 7 SEM) were instructed to perform a standard error-prone attention reaction time task [Rodriguez-Fornells et al. 2002]. The Eriksen Flanker task consisted of three black arrows oriented horizontally, one central (target) and two flanker arrowheads above and below (Figure 5-1b). Participants were instructed to move their right hand towards the button in the direction of the central arrow showed in the screen and then return to the starting position. They were urged to respond both accurately and quickly. The buttons were both in the virtual table and in the real table, so the visuo-tactile contingencies were coherent (Figure 5-1).

Trials where compatible when the central arrow had the same direction of flankers (40% of the trials); on the contrary when target and flankers had opposite directions the trial was incompatible. Flanker incompatible condition was more frequently presented in order to increase the number of self-generated errors. Each stimuli presentation lasted 150 ms and the interval between two successive presentations was 1150 ms. A fixation cross was present during this interval, 1000 ms.

The movement of the virtual body had no noticeable delays when compared to the participant's real movement and this strong visuo-motor synchrony between the avatar and participant's movements was expected to create a strong feeling of ownership with the virtual body [Banakou et al. 2013; Peck et al. 2013; Slater et al. 2009]. During the task participants had to give only one response per trial and avoid correcting movements, after touching the corresponding button their hand should return to the initial position (0,0,0), equidistant to the two buttons.

The experiment started with a Congruent Movement (CM) condition when the movements of the virtual body were in all cases synchronous to those executed by the participant. During this condition participants became familiar with the flanker task dynamics. Participants performed 160 trials in total (96 incompatible, 64 compatible trials). If the number of errors in this phase was less than 8-10%, participants had to repeat the training and were requested to be faster. Importantly, in CM condition the movements of the virtual body were matched to those executed by the participant inducing a strong illusion of ownership and agency, the extents of the illusions were assessed through a questionnaire (see below).

After a short break participants continued with the InCongruent Movement (InCM) condition when in some infrequent trials the virtual hand movements incongruent with the intended movement of the participant. In these trials participants' correct movements were replaced by a movement of the virtual embodied arm in the opposite (incorrect) direction thus violating their internal intentions and causing an external-error. During the external-errors participants did not notice anything until they started moving. To accomplish this effect we calculated the symmetrical position of the hand respect the yz plane, and the real movement of the participant was flipped towards the opposite direction. This means that correct responses, self-generated and external-errors were all performed exactly at almost the same speed and timing (without noticeable delay). The InCM condition was divided in two blocks of 640 trials in each block (approximately 15 minutes each). The total amount of external-errors matched approximately the percentage of natural self-generated errors in compatible trials (approx. 5-6% of trials).

We then compared the ERP responses for the correct responses; for the external-errors; and for situations in which the participant really performed an error (self-generated errors).

5.2.1.2. Movement Onset

The hand tracker movements were later analysed offline to calculate participants' reaction times and response accuracy. The onset of the movement was vital to this study since the ERP needed to be response-locked. Participants' hand position was projected over the x axis – which represented the Euclidean distance between the two buttons. Using the first derivative of the position the initiation of the movement was calculated. Each trial was then classified into one of four different types: correct, error, correction and not responded (Figure 5-2).

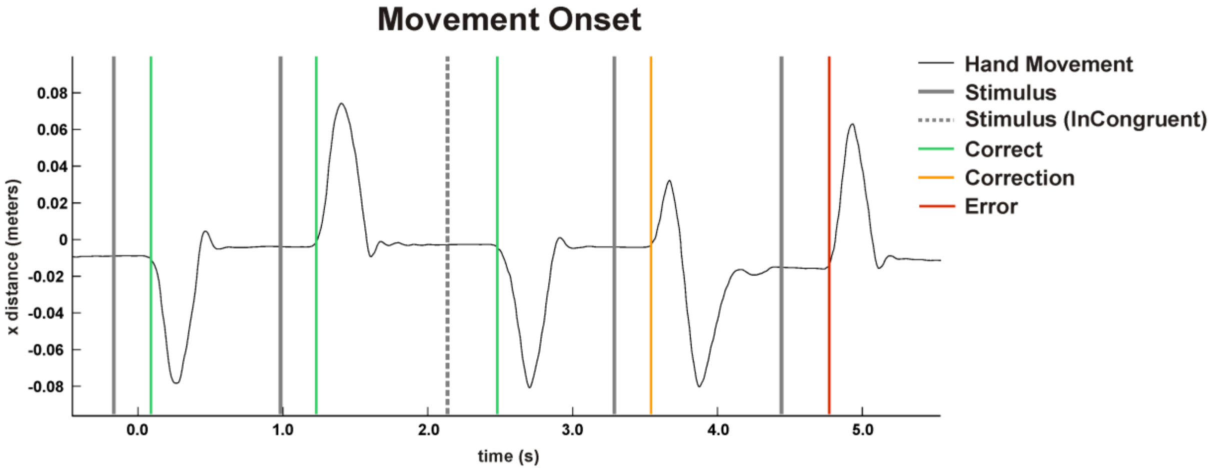

Figure 5-2 Six seconds of hand movement of a participant showing 5 trials; the first three are correct responses, the next one is a correction and the last one is a real error. Notice that the last of the correct trials is an InCM trial: the virtual hand went in the opposite direction, which resulted in an external-error.

5.2.1.3. EEG Analysis

ERPs were averaged for epochs of -300 to 600 ms with baseline set from -50 to 0 ms locked to the onset of the response. Mean ERP voltages were analysed by a three-way repeated measures ANOVA with factors *Correctness* (correct responses, self-generated errors, external-errors) x *anterior-posterior location* (Frontal, Central, Parietal) x *lateral location* (left, midline, right). Voltages of ERPs for the statistical analysis were calculated for selected time windows: at about 80-120 ms after self-generated errors and about 310-360 ms after external-errors. These epochs were selected based on visual inspection. The Greenhouse-Geisser epsilon correction was applied when necessary. A low pass filter (10 Hz, half-amplitude cut-off) was applied in all ERP computations.

5.2.2. Experiment 2

5.2.2.1. Procedure

Nine participants (6 women; mean age, 25 years ± 8 SEM) that had previously taken part in Experiment 1 returned to the laboratory two weeks after to participate in this control experiment where participants observed of their own pre-recorded performance while remaining immobile. Prior to this observation the recorded movements were cleaned off-line from corrected movements by substituting them for complete movements of the same participant. I.e. participants either visualized errors or correct trials. In order to avoid errors of the observer, only the middle arrow remained in the screen and the flanker arrows were removed [van Schie et al. 2004]. Participants were asked to count the number of times the virtual body movement was an error, so they would remain attentive during the task.

5.2.2.2. EEG Analysis

Time-locked ERPs were averaged for epochs of -300 to 600 ms, with baseline set from -100 to 0 ms. Since participants were not moving in this experiment, the ERPs were locked to the onset of the observed movement. The differences related with observed internal vs external error responses were first studied, however participants were unable to distinguish self-generated errors and external-errors. Therefore a bin of *Observed Errors* contained both type of errors for the analysis presented in the Results section. Mean ERP voltages were statistically analysed by a three-way repeated measures ANOVA with factors *Correctness* (Observed Correct, Observed Error) x *Anterior-posterior location* (Frontal, Central, Parietal) x *Lateral location* (left, midline, right). A low pass filter (10 Hz, half-amplitude cut-off) was applied in all computations.

5.2.3. Questionnaire

The subjective illusion of body ownership, localization and agency towards the virtual body in both experiments was evaluated through a questionnaire at the end of each of the condition. The questionnaire was adapted from previous studies [Botvinick and Cohen 1998; Longo et al. 2008] and contained a set of statements that had to be scored with a 7-point Likert scale ranging from “strongly disagree” (-3) to “strongly agree” (+3). The questions were:

- Related to the sense of body ownership:

Q1. It felt as if the virtual body was my body (*my Body*)

Q3. It seemed as if I might have had more than one body (*more Than One Body*).

An increase in body ownership should be related to high scores in Q1 and low scores in Q3.

- Related to the sense of proprioception:

Q2. I felt as if my hand was located where I saw the virtual hand to be (*collocated Hand*)

Q4. It seemed as if the position of the hand I was feeling came from somewhere between my own hand and the virtual hand (*dislocated Hand*).

- Related to the sense of agency:

Q5. Most of the time, the movements of the virtual hand seemed to be my movements (*my Movements*).

Q7. Sometimes, the virtual hand seemed to be moving by itself (*not My Movements*).

Q5 and Q7 were related with visuo-motor integration processes, important for the evaluation of the effectiveness of our experimental manipulation. Higher scores were expected in Q5 and lower scores in Q7 in the CM condition when compared to the InCM condition.

Q6. Sometimes, I felt that the movements of the virtual hand were influencing my own .movements (*Influence*).

- Exploratory and consistency check:

Q8. It sometimes felt as if my real hand was turning 'virtual' (*my Hand Virtual).*

Q9. It seems sometimes that the errors were not caused by myself (*not My Errors*).

Q9 was evaluating if participants were able to differentiate their own errors from the external errors expected to be higher in the InCM than the CM condition.

5.3. Results

5.3.1. Experiment 1

5.3.1.1. Questionnaire

The results of the questionnaire accounting for the experiences of body ownership, agency and during the conditions CM and InCM can be observed in Figure 5-3. Non-parametric Wilcoxon matched-pairs signed-rank tests were used to statistically analyse the questionnaire scores.

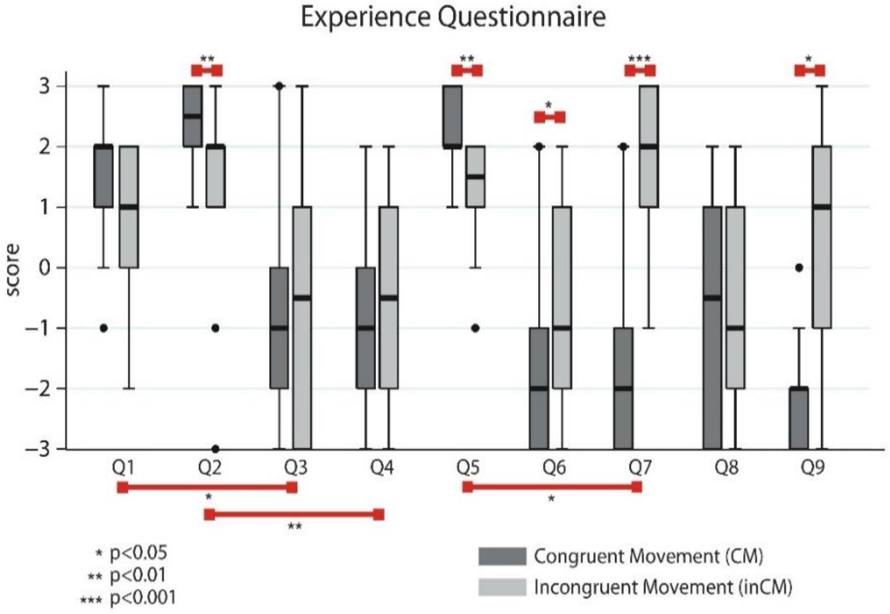

Figure 5-3 Results (medians and interquartile ranges) of the questionnaire assessing the feeling of ownership and agency during CM and InCM conditions [7-point Likert scale: "strongly disagree"(-3) to "strongly agree"(+3)]. Global illusory ownership and violation of the sense of agency of the virtual body were corroborated by the scores on relevant questionnaire items for ownership (Q1 and Q2) and agency (Q5, Q6 and Q9). Significant differences were tested with non-parametric Wilcoxon signed-rank tests.

In both CM and InCM conditions a similarly strong feeling of ownership was induced (Q1, Z = 1.519, p = 0.13). Additionally, the control question for body ownership Q3 had significantly lower scores than Q1 in both CM and InCM conditions (Z = 3.682, p = 0.0002; Z = 2.489, p = 0.013, respectively). These results are consistent with previous findings [Banakou et al. 2013; Kalckert and Ehrsson 2012; Peck et al. 2013; Sanchez-Vives et al. 2010; Slater, Spanlang, Sanchez-Vives, et al. 2010].

However, the external-errors that occasionally diverged between real and virtual hand locations in the InCM condition, produced a significant proprioceptive drift between the two locations (Q2 significant differences CM vs InCM, Z = 2.902, p = 0.004).

This another effect of the external-errors was the break on agency in the InCM condition. Participant's sense of agency was reported significantly lower in the InCM condition, see questions Q5, Q6, Q7 and Q9 (Figure 5-3). Participants showed a greater sense of agency in CM when compared to InCM (Q5, Z = -3.266, p = 0.0012). In contrast the control question for agency had higher scores in the InCM condition (Q7, Z = 3.648, p = 0.0003) indicating an impaired sense of agency due to the external-errors produced during the InCM condition

In fact, the external-errors also influenced significantly more the participants' feeling about their movements (Q6, Z=1.978, p = 0.048). Even though, participants were aware that the external-errors introduced by the virtual body were not their own errors (Q9, Z=3.543, p = 0.0004).

5.3.1.2. Behavioural performance

Participants were faster and more accurate when responding to compatible trials compared to the incompatible ones: accuracy (compatible trials: mean + SD, 91.5 ± 6.9%; incompatible trials: 77.1 ± 10.5%, t (17) = 11.302 $p < 0.001$), this is consistent with findings in previous Erikson flanker tasks [Rodriguez-Fornells et al. 2002]. A consistent reaction time was also found for correct responses (compatible: 259 ± 36 ms; incompatible trials: 273 ± 44 ms, t (17) = -4.48, $p < 0.001$).

The percentages of self-generated errors produced by the participants were equivalent both in the CM (17 ± 9%) and in the InCM conditions (17 ± 8%) ($t(17) < 1$); thus the inclusion of external-errors did not have a major impact on overall performance.

The compensatory cognitive control mechanisms involved on the *post-error slowing* [Logan and Crump 2010; Marco-Pallarés et al. 2008; Rabbitt 2002] were triggered both after self-generated and external-errors (270 ± 46 ms; 292 ± 51 ms, respectively). Whereas the normal timing between correct trials was of 262 ± 42 ms (compared to self-generated errors: t (17) = 2.7, P = 0.027; compared to external-errors t (17) = 7.1, P < 0.001).

Interestingly, larger post-error slowing effects were found after external-errors (~30 ms) than after self-generated errors (8 ms). This is a surprising effect considering that during external-errors participants were actually performing a correct movement. In sum, external-errors had a great impact in participant's performance. The expected (correct) output of their motor command and the observed (incorrect) movement performed by their virtual body self-representation induced large compensatory cognitive control mechanisms.

5.3.1.3. ERP Stimulus-locked activity

ERP responses for correct, self-generated errors and external-errors were compared through a repeated measures ANOVA.

A Error-related negativity (ERN) component at frontocentral locations [Gehring et al. 1993; Rodriguez-Fornells et al. 2002] was found about 100 ms after the onset of the movement in the self-generated errors (see *blue line* in Figure 5-4). The ERN is a neural signature of the internal error-monitoring system taking place in the medial-frontal cortex, which uses internal forward models of the motor plan (efference copy) to detect errors in on-going actions [Coles et al. 2001; Holroyd et al. 2005; Rodriguez-Fornells et al. 2002].

The repeated measures ANOVA on the ERN epoch voltage (80-120 ms) for the three types of responses (correct, self-generated error, external-error) showed a main effect of *Correctness* ($F(2,34) = 12.9$, $P < 0.001$) as well as a significant interaction between *Correctness* x *Antero-posterior location* ($F(4,68) = 6.6$, $P < 0.001$) indicating a maximal effect of the ERN signal at frontal electrodes of the scalp for self-generated errors.

Surprisingly and in contrast to real errors, when external-errors were compared to correct responses in the CM condition, no clear traces of the ERN component were registered at frontocentral locations. Instead, we observed the development of a large negative ERP component, a N400 (see *green line*, Figure 5-4), which peaked later at about 350-400 ms, with maximum at parietal electrode locations (ANOVA: Correctness, ($F(2,34) = 14.4$, $P < 0.001$; Correctness x Electrode (midline), $F(4,68) = 11.8$, $P < 0.001$; maximum effect at the parietal electrode).

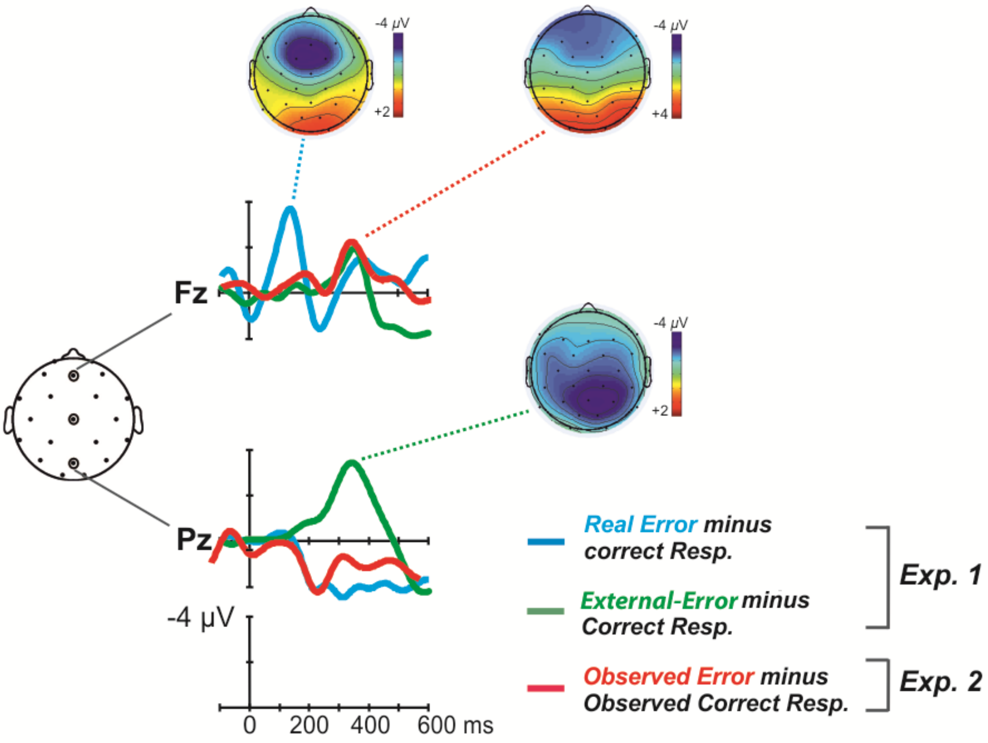

Figure 5-4 Response-locked grand average ERPs for the difference waveforms computed subtracting the correct responses from the self-generated errors (blue line) or the external-errors (green line). For Experiment 2 results, the observed correct trials were subtracted from the observed errors (red line). The self-generated errors (blue line) show the standard ERN that appeared at frontocentral sites immediately after the erroneous response (at about 100 ms). In contrast, to external-errors (green line) show a larger negative activity at 400 ms (N400). During Experiment 2, the observed errors (red line) show a delayed ERN-like component at frontal electrodes.

This result is important as it clearly suggests a neurophysiological dissociation between the internal error-monitoring loop and the external one, which is involved in evaluation of the sense of agency of our own actions in conflicting contexts (contrasting the internal proprioceptive and efference copy representations of the current action executed with the incorrect visual feedback of the avatar performing a different action). In ERP analysis, different topographical distributions and latencies of two ERP components provide direct evidence of the necessary involvement of at least different neurophysiological mechanisms [Picton et al. 1995].

In order to test more accurately whether the scalp distribution of both components differed, we carried out an additional statistical analysis considering all the 27 electrode locations registered and testing for the interaction between Condition [ERN (real Error minus Correct difference) - N400 (false Error – Correct difference)] x Electrodes at 27 locations. A significant interaction was obtained ($F(1,17)=5.3$, $P < 0.001$) demonstrating the implication of distinct neural sources in the generation of both ERP components associated respectively to the internal-error loop (ERN) and the external-error monitoring loop (N400).

5.3.2. Experiment 2

5.3.2.1. *ERP Stimulus-locked activity*

In order to rule out the possibility that the observed N400 effects could be due to the mere observation of an avatar performing a wrong action instead of the output of the external-error monitoring loop, we carried out a **control ERP experiment (Experiment 2)**. Participants were invited back to the laboratory but on this occasion they were only asked to observe the avatar movements. We were particularly interested on the ERP response to trials with an erroneous action.

The ERP analysis on the observation of erroneous actions did not show the parietal N400 component observed during the external-errors in Experiment 1. Instead a delayed frontal ERN-like component was elicited about 300 ms after occurrence of the avatar's erroneous action, at the frontal electrode (see *red line* Fz electrode Figure 5-4). The present results are in agreement with previous experiments showing error-related brain activity when participants have been exposed to errors performed by other agents (i.e. observational errors), where no parietal N400 was reported [van Schie et al. 2004]. This result rules out the possibility that the parietal N400 component elicited under violations on agency could be due to mere observational effects.

5.3.2.2. Questionnaire

During the Experiment 2 participants were instructed to observe how the avatar performed the movements in direction to the target, while resting their two hands on the table. At the end of the Experiment 2 participants answered the same questionnaire as in Experiment 1 (Figure 5-5).

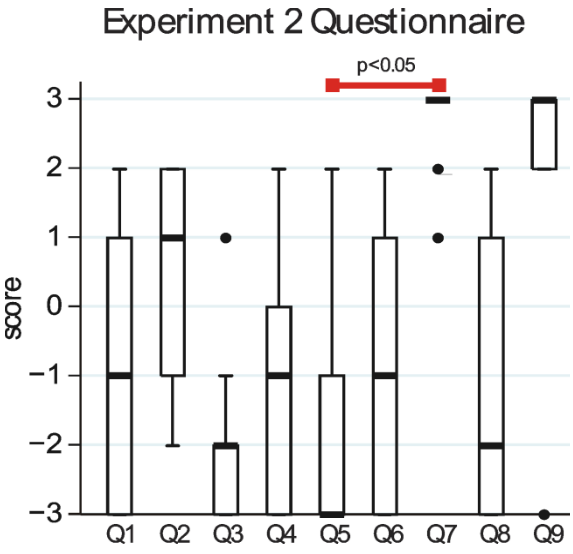

Figure 5-5 Score of the questionnaire after the observation task (Experiment 2). The embodiment illusion was decreased during the observation task: Q1, Q2 and Q5 compared with control questions Q3, Q4 and Q7 respectively (all P values > 0.05). The Boxplot shows the medians and interquartile ranges.

The questionnaire scores were statistically tested with non-parametric Wilcoxon signed-rank tests. When comparing the scores to the ones in the Experiment 1 CM condition, participants showed a decreased experience of body ownership (Q1, Z= -2.032, p = 0.042), suggesting that the experience of body ownership had been disrupted by the visuo-motor asynchrony.

The proprioceptive sense was also significantly diminished in Experiment 2 when compared to Experiment 1 (Q2, Z= -2.687, p < 0. 007). Scores were also divergent when comparing the scores between the real and the virtual hand localizations as if the participant was having illusions of a dislocated limb (Q2 vs. Q4, Z= 1.807, p < 0. 071).

Additionally, the sense of agency was also lost (comparison Exp 2 vs. Exp 1, Q5, Z= -2.536, p < 0. 011), participants noticed that they could not control the virtual movements (Q5 vs. Q7, Z= -2.570, p = 0.012).

Overall, these results show a decreased level of embodiment in the Experiment 2 since the three most commonly described aspects of embodiment -body ownership, localization and agency [Kilteni et al. 2012]- had lower scores than in Experiment 1.

5.3.3. Relationships between the ownership illusion and the agency breaks

In order to further explore the implication of the agency breaks in the embodiment illusion, the external-error monitoring loop (N400) amplitude was further explored.

A negative correlation of the N400 voltage with the subjective strength of virtual body ownership (computed as the difference Q1-Q3) was found (r(18) = -0.6, P < 0.009) (Figure 5-6). This correlation indicated that stronger subjective feelings of body ownership derived on stronger the amplitude of the N400 following agency violations.

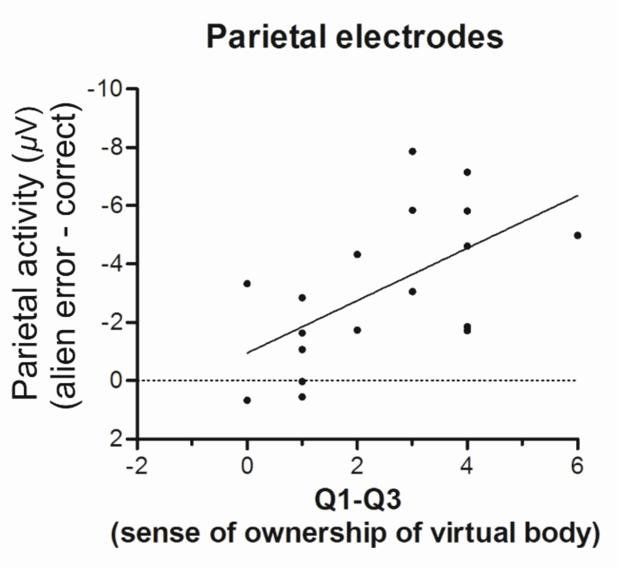

Figure 5-6 The body ownership towards the virtual body was negatively correlated with the N400 parietal activity ($r(18) = -0.6$, $P < 0.009$). The amplitude of this ERP signal was computed subtracting the correct responses voltage from the external-errors one in parietal electrodes (Pz, P3, P4 electrodes). The subjective strength of virtual body ownership was computed as the difference Q1-Q3.

5.4. Discussion

Overall, the present study shows the comparison between real performance errors in which the internal error-monitoring loop operated at very fast velocity against those situations in which a violation of their own actions was perceived (an avatar or external error). This experimental condition impaired the feeling of agency and also disrupted the feeling of ownership induced by the 1PP in IVE.

As shown in the post-error slowing phenomena, the impact of external-errors was larger o than the slowing effect elicited after the self-generated errors, suggesting that compensatory cognitive control mechanisms were activated as well, even when no real errors were produced. Two different neurophysiological signatures appeared associated to internal and external error monitoring, the ERN and the N400 component, respectively.

While the appearance of the first component (ERN) was predicted considering previous literature on internal error monitoring [Gehring et al. 1993; Holroyd et al. 2005; Rodriguez-Fornells et al. 2002], the appearance of the N400 during the false avatar errors was unpredicted. As mentioned earlier, our ability to recognize ourselves as agents of our own behaviour depends on constantly monitoring the sensory consequences of our actions. In normal everyday circumstances and running in the background of our consciousness, we experience an implicit and diffuse sense of coherence regarding the feeling of agency, mostly because there is a perfect congruence between the internal representations of our actions (e.g., efference copy), the expected effects of the actions executed and the flow of resulting sensory events (multimodal reafferent feedback) [Pacherie 2001]. When a mismatch is detected between any of these internal and re-afferent signals a violation of the sense of agency might be triggered. Thus the N400 could be reflecting the output of this comparison process, which might lie at the core of the external-error-monitoring loop.

Interestingly and in agreement with the previous statement, a significant association was observed between the amplitude of the N400 component (*external-error* minus *correct responses*) and the subjective feeling of body ownership (Figure 5-6). The larger the subjective feeling of body ownership the strongest the N400 amplitude or the electrophysiological signature of agency violation.

Furthermore, the timing of this comparison process (with approx. 350-400 ms delay after the error) is slower than that needed for the internal-error monitoring loop (in between 60-150 ms) which depends exclusively on the efference copy information. As the external error-monitoring loop requires the processing of different feedback information arriving at the somatosensory, visual and auditory regions with different neural delays, this comparison process might not finished until the degree of coherence is computed and a coherent multimodal representation is built. More importantly, the parietal distribution of the N400 component converges with the results of functional neuroimaging and studies in lesions with a diminished feeling of agency in which the importance of the inferior parietal cortex has been highlighted [Farrer et al. 2008] to be responsible for the comparison processes between intentions and action consequences [Desmurget et al. 2009].

An intriguing question to be explored is the exact computational nature of this comparison process. The N400 component discovered in the present study associated to the external error monitoring resembles, in terms of scalp distribution and latency, to the well-known N400 component associated to semantic and conceptual violations. This component has been classically attributed to the violation of semantic or conceptual information [Kutas and Federmeier 2011] (e.g., when listening to the sentence "*I am going to eat a house*") and it has also been found to occur as a result of observing incorrect motor plans (e.g., inserting screwdriver versus key into a keyhole) [Bach et al. 2009]. Thus an interesting question is the extent to which the clash in the feeling of agency (*this is not my action*) reflects a violation in the process of understanding our own actions (or our own body movement semantics). In this sense, the comparison process underlying linguistic inputs or conceptual representations might not be too different from that carried out when comparing the ability to recognize ourselves as agents of our actions, as it might rely as well on the congruence of our own actions and their external consequences.

In sum, using ERPs, we dissociated both internal and external error-monitoring controllers and we unravelled the timing of both monitoring processes associated to the violation of the feeling of agency. We believe the present results might provide crucial evidence about how to distinguish at the neurophysiological level own- vs. alien-mistakes in non-humans agents governed by remotely and distantly located minds, e.g. in scenarios where humans are embodied in robots[5].

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[5] For an example of this see http://www.bbc.co.uk/news/technology-18017745

6. SELF-RECOGNITION IN COMPUTER GENERATED FACES

Within virtual reality through multisensory integration we can make participants believe that their body has been substituted by a virtual body that they control. Indeed, avatars are a growing basis for research in different fields, including Psychology, Social Sciences and even Neuroscience. Recently with the look-alike avatar pipelines we can create virtual characters that look like the participants in a matter of minutes. But will that have a real impact into the participant identification with the virtual body?

This Chapter addresses the third hypothesis of this thesis. *Given a virtual body we can potentially measure different levels of self-identification: an avatar that looks like the participant is interiorized unconsciously to a different level than an avatar that doesn't look-alike*. It is well known that during the embodiment illusion avatars are accepted as the self-body through multisensory stimulation [Banakou et al. 2013; Llobera et al. 2013; Kilteni et al. 2012]. This illusion can be induced to avatars of different races and genders that share more or less similarities with the participant [Peck et al. 2013; Slater et al. 2010]. However, other research has shown that the more the avatar looks like the participant the stronger the identification is [Bailenson and Segovia 2010; Blom et al. 2014].

Here we present the last study of this thesis that explores the neural basis of self-recognition. We assess the implications of the subconscious mechanisms that may be processing self-identification with avatars by investigating the temporal dynamics of the brain activity during observation of computer generated faces compared to real faces in an ERPs study.

Our work contributes to the field of self-recognition. We provide strong neural evidence that avatar faces may be integrated as real faces and that look-alike avatars can be recognised as the self to a greater extent than other avatars.

The results of this Chapter have been shared with the community in form of presentations at the 2nd VERE PhD Symposium [Gonzalez-Franco et al. 2014]. And in form of journal publication submitted [Gonzalez-Franco et al. n.d.].

6.1. Background

Computer generated characters, or avatars, are becoming increasingly important in society and are also a growing basis for research in different fields ranging from gaming to neuroscience. In the field of neuroscience avatars can be used to substitute the bodies of people, thus being a convenient technology for research purposes as they can be manipulated in a controlled manner and made to take on characteristics even beyond human limits [Normand et al. 2011; Kilteni et al. 2012]. Such technologies can also be used to explore the neural traces of the body representation in the brain [González-Franco et al. 2014; Padrão et al. n.d.]. Furthermore, evidence suggests that avatars, at least under certain conditions, evoke reactions in people who treat them as if they were real [Pan et al. 2012; Rovira et al. 2009; Llobera et al. 2010; Slater et al. 2006]. Moreover when avatars are used to substitute the bodies of people behavioural and attitude changes have been reported [Banakou et al. 2013; Peck et al. 2013].

Even though avatars are obviously not real, they tend to elicit similar responses as if they were real [Sanchez-Vives and Slater 2005]. In fact, physically similar avatars influence people's behaviour inducing changes in their task performance [Bailenson and Segovia 2010]: participants increased their physical activity after being exposed to a fatter doppelganger [Fox and Bailenson 2009]. A strong identification with look-alike avatars, that is avatars that have a facial appearance that is similar to the actual person, has also been described to induce changes to participants' physiological responses [Fox et al. 2012]. Other research has focused on the participant's perceived resemblance between themselves and a set of virtual avatars finding that there is a significant tolerance for self-recognition in computer generated faces [Blom, Bellido Rivas, et al. 2014]. Here we exploit EEG to find neurophysiological evidence of this visual perception processing in the context of such look-alike avatars. In particular we consider whether a virtual face that is looks alike to the real face might generate electrical brain activity that is similar to what occurs when seeing the real face. In other words are we unconsciously able to distinguish whether an avatar looks like us?

It has been shown that processing of faces differs from that of other objects in terms of brain activity through the use of EEG [Bentin et al. 1996; Allison et al. 1999; Eimer 2000; Caldara et al. 2003], MEG [Liu et al. 2002], and fMRI [Vuilleumier et al. 2001]. Furthermore, TMS studies have also demonstrated that the Occipital Face Area (OFA) is necessary for some face computations [Rossion, Caldara, et al. 2003], where healthy participants experienced an impairment in a face discrimination task during TMS similar to the deficiencies showed by patients with prosopagnosia who cannot recognize faces [Pitcher et al. 2008; Pitcher et al. 2011]. Largely the observer expertise over the presented object affects the brain potentials: after a period of observational training of nonface objects the responses of N170 significantly decreased (20%) when compared to subjects that were untrained for those objects [Gauthier et al. 2003; Rossion et al. 2004]. A similar training effect is found for faces, younger children that do not have the expertise of an adult show different brain potentials during face observation tasks [Taylor et al. 2004].

In fact, these brain mechanisms seem to play an important role not only in the distinction between faces and other objects, but also with respect to the evaluation of the emotional state of the face [Eimer and Holmes 2007; Vuilleumier et al. 2001], and in the classification of faces with different degrees of familiarity (self, familiar, unfamiliar) [Bentin and Deouell 2000; Sui et al. 2006; Platek and Kemp 2009; Keyes et al. 2010; Ramasubbu et al. 2011]. Therefore, these mechanisms are sensitive to the owner of the face such that images of our own face are processed differently than the faces of others, i.e. familiarity of the face impacts its processing (see [Devue and Brédart 2011] for a recent review in self-recognition mechanisms). Results have shown that the visual processing of faces induces specific Event Related Potentials (ERPs) modulations on early visual components (just 200ms after the stimuli is presented): the appearance of a occipito-parietal negative N170 component followed by a positive P200, which is accompanied with a frontal Vertex Positive Potential (VPP) followed by a negative N200 [Rossion, Joyce, et al. 2003; Keyes et al. 2010; Sui et al. 2006; Bentin and Deouell 2000].

Based on this research, we aim to find out the extent to which computer generated faces are processed as real faces in the brain, and also whether self-recognition of a physically similar avatar may elicit measurable neurophysiological effects. In this context previous research with ERPs has found that caricaturing familiar and unfamiliar faces with distortions of up to 30% did not affect the processing of the familiar faces whereas the unfamiliar faces elicited significant effects of the caricaturing [Kaufmann and Schweinberger 2008]. Furthermore, in that research the familiarity differences (familiar vs. unfamiliar) remained prominent and similar in both veridical and caricature faces [Kaufmann and Schweinberger 2008].

We exploit previous research on self, familiar and unfamiliar faces to compare the temporal dynamics of the processing of computer generated (virtual) and real faces. To do so an ERP study was prepared with three different levels of familiarity: self, familiar and unfamiliar other, similar to previous research on real faces [Keyes et al. 2010; Sui et al. 2006]. The comparison is two-fold: we inspect the differences when processing virtual avatar faces and their real counterparts, in addition to the three familiarity levels. The aim is both to study the time course of the computer generated faces' visual processing as well as the possible adaptation mechanisms after longer exposure. With ERPs not only can we study the effects of look-alike computer generated avatars, but also track on-line adaptive changes without requesting participants to provide constantly behavioral judgments. In this way, beyond the insights of the present study, the methodology presented may provide a new objective measure to evaluate the appearance effects across time as well as to determine the likeness of an avatar to its real counterpart.

6.2. Materials and Methods:

6.2.1. Participants

Seventeen neurologically healthy male subjects between the ages of 25 and 41 (M=33.05, SD=4.83), with normal or corrected vision participated in the experiment. They were recruited by email from the laboratory mailing list. Subjects gave informed consent according to the declaration of Helsinki, and the experiment was approved by the ethics committee of Universitat de Barcelona.

6.2.2. Look-alike avatars

We took three photographs (front, left and right profile) of each participant in order to create their look-alike avatars. In all cases participants were requested to hold a neutral face to avoid emotion processing during the observation, as it has been shown emotions on faces generate different brain traces and even activate the mirror neuron system [Likowski et al. 2012]. Avatars were generated using the fast creation of look-a-like avatars pipeline described in [Blom, Bellido Rivas, et al. 2014]. The resultant virtual avatars were tweaked manually to make minor improvements to the visual likeness, and the avatars were bald due to limitations of the pipeline. We used the original frontal picture and a frontal capture of the resulting avatar for the observation task (Figure 6-1).

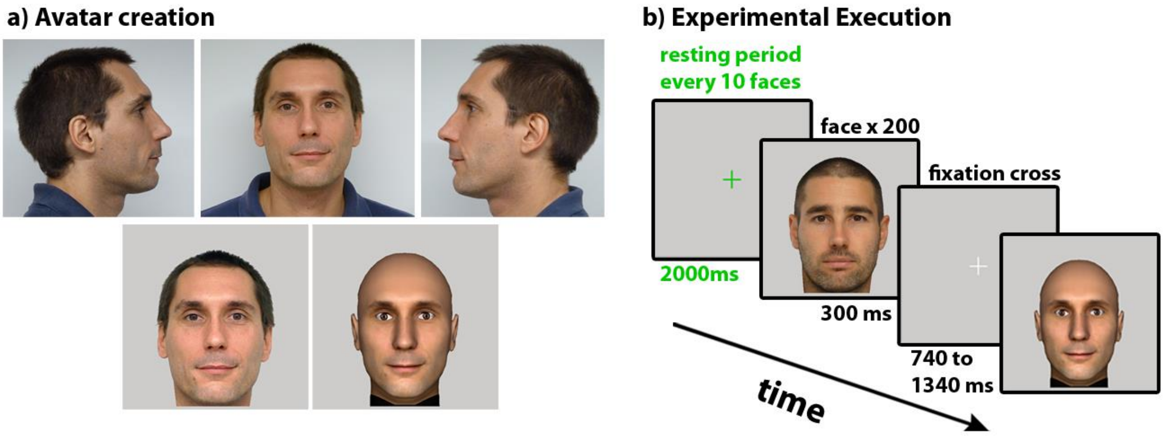

Figure 6-1 a) Creation of the look-alike avatar, the three pictures used for the avatar generation on the top. The final pictures used for the experiment as real and virtual. b) Experimental execution. The six faces (S, SV, F, FV, U, UV) were randomly ordered in blocks of 10. Each face was displayed for 300 ms, followed by a variable time of 740 - 1340 ms in which a fixation cross appeared. After each block there was a short resting period of 2 seconds for blinking.

Both images (the real and the computer generated one) were processed to equalize pupil-pupil distance across all images and to ensure that the vertical midline of the image bisected the face; this involved a minor scaling of the entire image, and left the normal proportions of the face invariant. The images were saved at 520 x 520 pixels, in colour and with averaged luminance to avoid effects of uncontrolled interstimulus perceptual variance that have been found to influence the N170 component [Thierry et al. 2007]. Controlling this particular variance corrects the N170 face sensitivity [Bentin et al. 2007]. All the faces were in a neutral emotional state.

6.2.3. Stimuli

The experimental design included two factors: *Virtuality* and *Familiarity*. The *Virtuality* factor consisted of either a photographic image of the real person (R) or an image of the look-alike virtual avatar (V). The *Familiarity* factor consisted of the three levels: self (S), familiar (F) or unfamiliar other (U). The unfamiliar person (U) had no previous relation to any of the participants, and he consented to use his real and virtual pictures for the purposes of this experiment. Since we wanted to study the effects of self-specific processing rather than habituation to the face – e.g. participants see themselves in mirrors very frequently – the familiar faces (F) were extracted from work mates seen every day by the participants.

In total subjects were exposed to the six images 200 times in a classical ERP setup summing to a total of 1200 faces to be observed by each participant during the experiment that lasted approximately 30 minutes. The *Familiarity* factor was based on the existing literature on ERPs and self-face processing.

The visual stimuli were displayed using XVR [Tecchia et al. 2010] on an Intel Core i7 at screen resolution 1920x1080 pixels. The six faces (SR, SV, FR, FV, UR, UV) were randomly ordered in blocks of 10. Each face was displayed for 300 ms, followed by a variable time of 740 - 1340 ms in which a fixation cross appeared (Figure 6-1b). After each block of 10 pictures there was a short resting period of 2 seconds for blinking.

Participants were instructed to maintain the focus on the fixation point and to minimize blinks and eye movements.

6.2.4. Questionnaire

Before mounting the EEG cap and starting the experiment we administered a short questionnaire in which each of the participants had to rate the **realism** of both the real and avatar pictures from 1 (not alike at all) to 5 (totally looks like the real person). Specifically they were asked to answer whether: "*The picture looks like the real person*". The realism of the faces when compared to the real person were not available for the unfamiliar case as participants did not know the real person. Instead they were asked to compare the similarity of the avatar face to the picture face (from 1 to 5): "*The computer generated face looks like the real face*". This **similarity** rating was performed for all familiarity pairs of real-avatar pictures.

In order to detect changes in the scoring that were due to the experimental exposure or adaptation effects, participants were asked to rate again all the faces and avatars after the experiment.

6.2.5. EEG Recording

Continuous EEG was acquired from 64 active electrodes located at standard 10-20 positions with a g.HIamp multichannel amplifier manufactured by g.Tec Medical Engineering. Active ring electrodes (g.LADYbird) were used in a standardized cap (g.GAMMAcap), both from g.tec. The activity was referenced to the earlobe and the ground electrode was located in the frontal area of the head. Signals where digitalized at 256 Hz frequency rate, a notch Butterworth filter 4th order from 48-52Hz was used to eliminate the AC. Ocular movements were detected from FP1, FP2, AF7 and AF8.

The EEG was segmented offline into 1200 ms epochs starting 200 ms before the stimulus onset. Trials where the faces were consecutively repeated were rejected off-line. There was a repetition rate of 2.99%. Trials in which ocular movements were found (EOG greater than 50μV) or the absolute amplitude of the signal at any electrode was greater than 150μV were rejected. The average acceptance rate was of 74% trials per participant.

ERPs time-locked to the onset of the stimuli for each condition and participant were averaged for epochs of -200 to 900 ms with the baseline set from -200 to 0 ms. Mean amplitudes were calculated where there were discernible peaks in the average ERP waveform for each of the 17 participants; these included the epochs N170 (170-210ms) and P200 (250-300ms) of the right and left occipito-parietal cortex. Which are consistent with those proposed in previous experiments [Sui et al. 2006; Keyes et al. 2010] .

The original ERPs for each subject were transformed into reference-free Current Source Density (CSD) estimates (μV/cm2 units) using a spherical spline surface Laplacian Matlab-based CSD toolbox [Kayser and Tenke 2006] to better explore the topographical maps.

6.3. Results

6.3.1. Faces Evaluation

Participant rated of the **realism** of the faces by answering the question "the face looks like the real person"; and the **similarity** between the computer generated face and the photograph by answering the question "the computer generated face looks like the face in the photograph" (Figure 6-2). After the experiment, participants were asked to rate again all the faces, in order to detect changes in the scoring due to the experimental exposure. There were no significant differences between any of the real or virtual faces in the pre-post scoring for the **realism** question (Wilcoxon signed-rank tests, all p>.45), nor for the **similarity** pre-post (Wilcoxon signed-rank tests, all p>.55). The real images scores served as a consistency control, none of the real pictures scored less than a four. Furthermore, there were not significant differences among the scores for all the computer generated faces, which indicates that all of them were perceived similarly realistic (Friedman, p>.368).

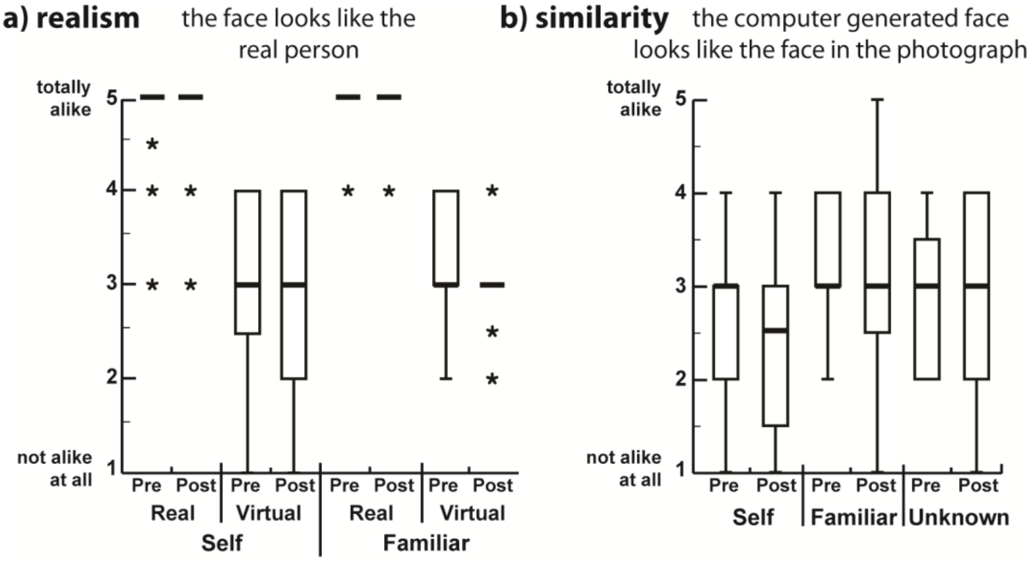

Figure 6-2 Scores for the different faces, at the pre and post questionnaires. From 1 (not alike at all) to 5 (totally looks alike), participants rated the faces through two questions: realism, similarity. a)

Realism: compared the pictures to the real person that they knew. b) Similarity: compared the real picture to the virtual picture independently if they knew or not the person on the picture.

There were significant differences when comparing the **realism** scores between the virtual and the real faces (Wilcoxon signed rank tests, all p<.001). This indicates that even though all the participants did recognize themselves and their confederates in the avatar faces, the avatars were not perceived as overly realistic as the real faces (Figure 6-2a). To the **similarity** question all avatars were rated equally similar to their real counterparts (Figure 6-2b).

6.3.2. EEG Analysis

In order to explore how the faces were processed in the brain we proceeded to study well-defined visual processing-related ERP components in occipito-parietal cortex, such as the N170 and the P200 components (see, [Sui et al. 2006; Keyes et al. 2010]). Visual inspection of Figure 6-3 shows a clear negative voltage during the N170 and a positive voltage during the P200 in both hemispheres.

The amplitude of each component was extracted for each participant in the specified time-windows (N170: 170-210ms; P200: 250-300ms) and analysed via a repeated measures ANOVA with three within-subject factors: *Hemisphere* (left, right; please specify which electrodes did you use here) x *Familiarity* (self, familiar, other) x *Virtuality* (real, virtual). Importantly, only the first 100 trials of each condition are taken into account for this section to avoid the effects of adaptation (see below for the analysis of fast adaptation). Mauchly test was run to account for significant differences on the variances. In cases where the test was positive (<0.05) we applied and noted the corresponding correction for sphericity.

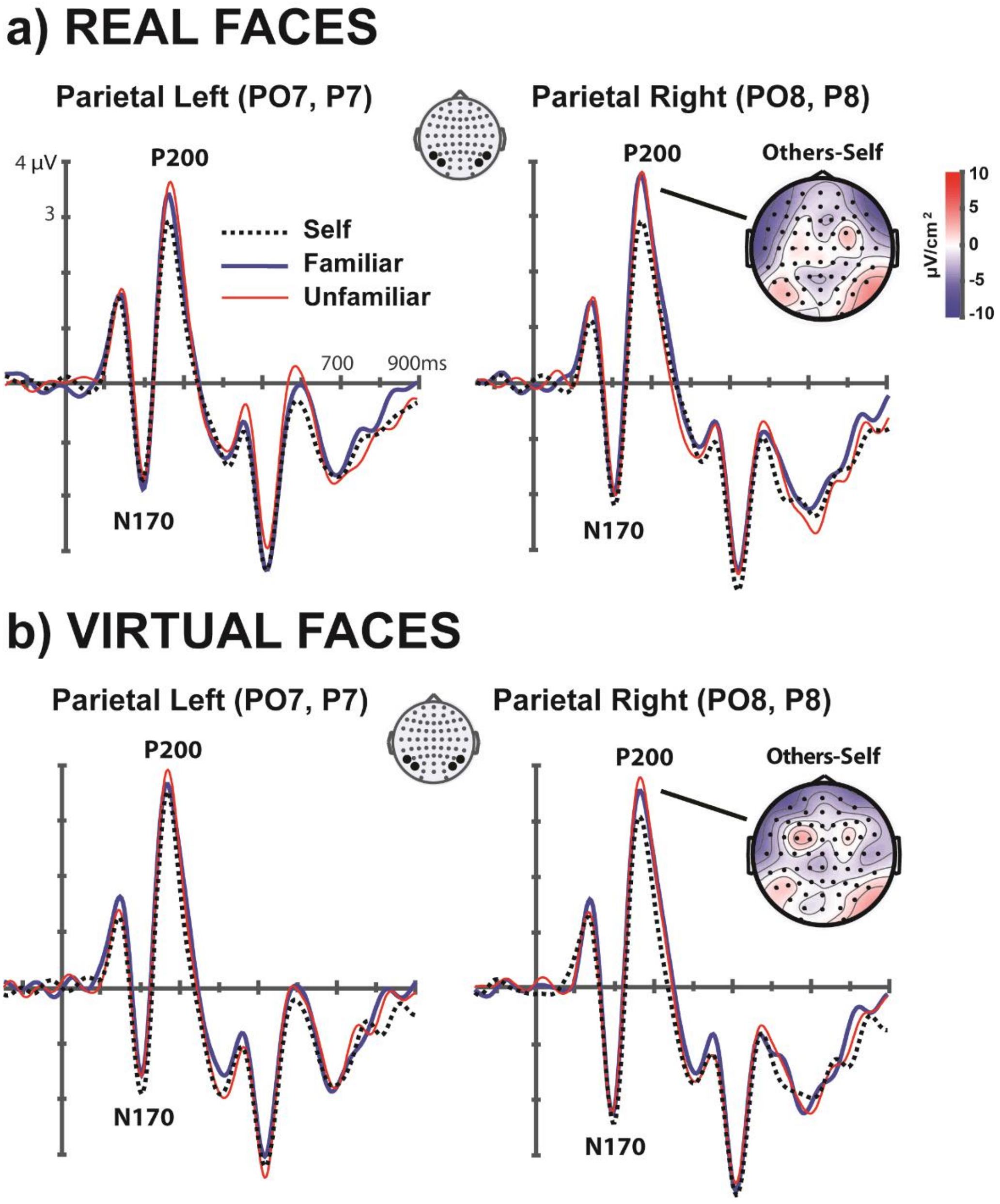

Figure 6-3 Grand average ERPs for the 17 subjects of the parietal electrodes (PO7, P7) and (PO8, P8) elicited during the first 100 trials by a) Real faces: self, familiar, and other. b) Virtual faces: self, familiar, and other. The CSD topographical plots show how the difference between others-self for the P200 component is mainly located in the occipito-parietal cortex. A low pass filter (15 Hz, half-amplitude cut-off) was applied in these grand averaged graphs.

The same repeated measures ANOVA was run on the P200 component. This analysis showed a significant main effect of *Familiarity* (F(2,32)=7.253, p<0.003) (Figure 6-3). Post-hoc pairwise comparisons with the Bonferroni adjustment (pooling together the amplitude in all electrode locations for both hemispheres) showed significant differences between *self* (2.681 ± 0.319 μv) vs. *familiar* (3.147 ± 0.298 μv) (t=5.618, p=0.046) and *self* vs. *unfamiliar* (3.277 ± 0.298 μv) (t=5.618, p=0.011) but not between *familiar* vs. *unfamiliar* (t=5.618, p=1), indicating the existence of a self-oriented processing (Figure 6-3).

A visual exploration of the grand average ERP (Figure 6-3) shows stronger voltage differences in the right hemisphere locations both for the real and virtual faces. More precisely the *virtual-self* (2.768 ± 0.291 μv) was processed in a significantly different voltage than the *virtual-familiar* (3.186 ± 0.260 μv) or the *virtual-unfamiliar* (3.357 ± 0.338 μv) (t=3.757, p<0.25). However, when comparing the *virtual-self* (2.767 ± 0.291 μv) to the *real-self* (2.522 ± 0.353 μv) voltage no significant differences were found (t=1.180, p=0.255). Indicating that the self-avatar was classified differently than the others, in the same way than the self-real face was classified differently from the other faces. In contrast, the pairwise comparison *familiar* vs. *unfamiliar* was not significant for all cases (t<0.8, p>0.3), indicating that the neural mechanisms related to the P200 component are oriented mainly towards self-recognition and not so much towards others' faces recognition (Figure 6-4).

Interestingly, regarding the nature of the face presented, we can see a significant main effect of *Virtuality* (F(1,16)=7, 946, p=0.012); and an interaction was also found between *Hemisphere* x *Virtuality* (F(1,16)=4.335, p=0.05). Virtual faces (3.212 ± 0.249) elicited larger amplitudes when compared to real faces (2.816 ± 0.360) in the *left hemisphere* (t=4.430, p<0.001). The same effect was not found in the *right hemisphere* locations (t=0.722, p=0.480). This clear difference between virtual and real faces in the P200 component is depicted in Figure 6-4.

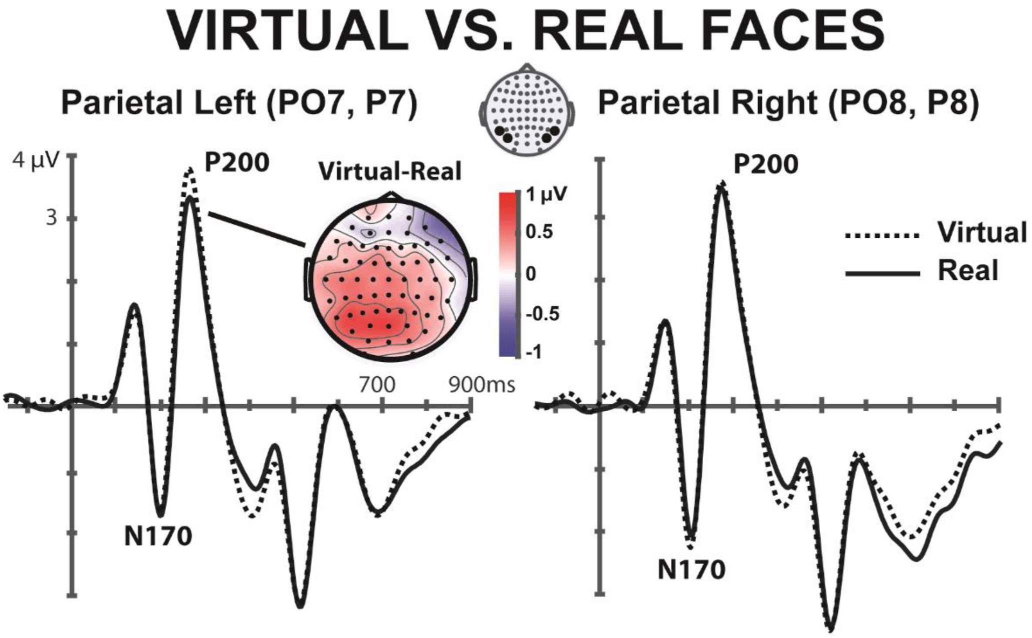

Figure 6-4 Grand average ERPs of the 17 subjects in the parietal electrodes (PO7,P7) and (PO8,P8) elicited by the real and the computer generated faces for the first 100 trials. There is a significant difference in the P200, mainly in the parietal left electrodes. A low pass filter (15 Hz, half-amplitude cut-off) was applied in these grand averaged graphs.

Overall these results suggest that the amplitude of the P200 component is sensitive to the nature of the face, whether it is a computer generated or a real face, as well as the *familiarity* level of the face. It as though the P200 is clearly oriented to self-recognition in faces as the neural processing seems to distinguish self from other faces. This particular effect of self-identification and familiarity works for both the *virtual* and the *real* faces, indicating that avatars that look alike the self are recognized as the self to a higher extent than other avatars.

6.3.3. Rapid Adaptation Effects

In the previous section, we have seen how the P200 component was sensitive to both *Virtuality* and *Familiarity*, whereas in this section we want to investigate the modulation of these effects over time. In Figure 6-5 we can see the evolution of the amplitude of the

P200 component for the *Virtuality* parameter across the whole experiment. The amplitude of the P200 component was computed in bins of 30 trials for both *virtual* and *real* faces (pooling together all the conditions) in the left hemisphere, where the effect of *Virtuality* was stronger. An important observation in this Figure 6-5 (top panel) is the clear tendency of the amplitude of the P200 component to be progressively reduced in the virtual condition, tending to merge with the real face condition. In Figure 6-5 (lower panel) we show also the grand average ERP for the first 50 and last 50 trials of each condition showing a clear reduction of the P200 amplitude differences in the last trials.

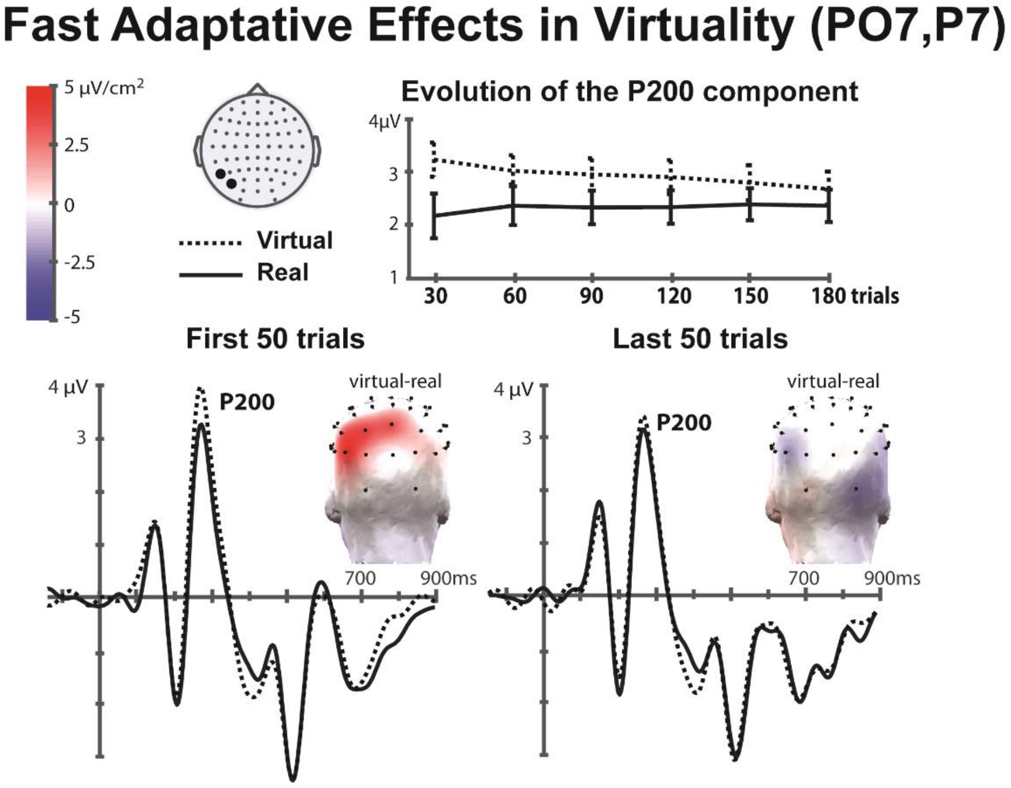

Figure 6-5 The top panel shows the time evolution of the P200 amplitude in the left tempo-parietal cortex (P07, P7); presenting the cumulative voltage over blocks of 30 trials (the error bars show the standard error of the different participants ERPs). We observe how in the first trials the virtual and the real faces are processed as different objects; however, this effect is reduced after the overexposure. In the panel below we observe the grand averaged ERPs of the first and last 50 trials, and a clear reduction of the P200 component is also observed. The topographical plots show

the CSD of the P200 component difference (virtual-real) in the scalp, we can see how the difference decreases over the last trials. A low pass filter (15 Hz, half-amplitude cut-off) was applied to these grand averaged graphs.

In order to analyse these effects statistically, we conducted a repeated measures ANOVA with factors *Time* (bins, 1 to 6) x *Virtuality* (real, virtual) focused on left-hemisphere electrodes (PO7, P7) where the effect was observed to be larger (Figure 6-4).

The analysis showed a significant main effect on *Virtuality* (F(1,16)=18.407, p=0.001). Importantly and coherent with our expectations of the results presented in Figure 6-5 (top), a clear significant interaction effect was found (*Time* x *Virtuality* (F(5,80)=2.865, p=0.02), indicating a significant decay of the P200 amplitude over time. Further pairwise comparisons showed that while a significant *Virtuality* effect was present in the first 50 trials (t=4.037 p=0.001), no significant effects were observed in the last 50 trials (t=1.169 p=0.26).

These findings suggest that the virtual faces are initially processed as different from the real faces, as if they were not faces but another kind of objects, which is analogous to what happens with exposure to faces vs. flowers or other objects [Keyes et al. 2010; Bentin et al. 1996; Allison et al. 1999]. Nevertheless, this effect is reduced overtime, and both real and virtual faces finally converge to be classified as the same class of objects: faces.

A similar analysis was run to study *Familiarity* effects over time at the P200 component. For that purpose bins of 30 trials were used for a repeated measures ANOVA with factors *Time* (bins, 1 to 6) x *Familiarity* (self, familiar, other). A significant main effect was found for *Familiarity* (F(2,32)=5.308, p=0.010); however, no interaction effects were observed for *Time* x *Familiarity* on the P200 component (F(10,160) < 1). These results suggest that the effect of *familiarity* did not significantly decay over time in the present design. The analysis was also done with the virtual faces alone and there was no interaction of *Time.* This indicated that the self-recognition mechanisms are still functioning after longer exposures and both the look-alike avatar and the real face are processed as belonging to different familiarity levels when compared to the other faces.

6.3.4. Self-identification subjective scores match the unconscious responses

In the previous sections we have shown that the P200 amplitude was dependent on the *Familiarity* factor, and in this section we wanted to explore whether that voltage could be related to the subjective self-identification score.

Since different participants may have different amplitudes in their components we normalized the amplitude by calculating the voltage difference from the self-virtual avatar to the self-real face for each participant (SV-SR) pooling together all the occipito-parietal electrodes in both hemispheres (PO7, PO8, P7,P8). Closer to zero values would indicate a greater self-identification, while more positive values would mean a lesser self-identification with the avatars, since in general a more reduced voltage in the P200 is associated with self-identification [Keyes et al. 2010; Sui et al. 2006].

The resulting voltage difference was then contrasted to the initial reported score of **realism** for the self-virtual face. In that question participants rated whether the avatar looked like themselves. A significant Spearman Correlation was found between the resulting voltage (SV-SR) and the subjective score (r(17)=0.49, p=0.045), Figure 6-6.

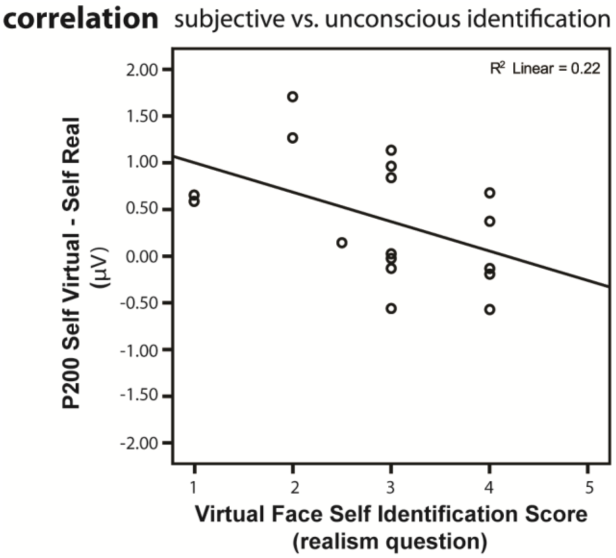

Figure 6-6 Correlation between the virtual self-face identification scores in the realism question and the P200 voltage difference between the virtual-self - real-self (SV-SR). The closer the voltage difference is to zero the greater the identification.

6.4. Discussion

Novel effects related to computer generated virtual faces have been presented in form of early neural processes able to dissociate levels of *Familiarity* not only for the real faces but also for the virtual faces. The P200 component showed traces of self-recognition aligned with previous research on real faces [Keyes et al. 2010]. The novelty in this case is that the self-recognition brain mechanisms seem to work also for computer generated faces that look alike the self, which could be interpreted as if the self-avatar was recognized as the self to a higher extent than others' avatars. This interpretation is also in agreement with previous studies that found how a caricatured distortion of up to a 30% on a familiar face did not affect the OFA recognition mechanisms [Kaufmann and Schweinberger 2008] (granting that Kaufmann et al. did not include self-images as familiar faces). Our results support Keyes et al. (2010) findings in terms of differences in P200 for *Familiarity*. In the current experiment we found that the P200 component was differentiated for self vs. others in both the computer generated and real faces. Even though Keyes et al. also found differences by face owner in N170 components, we did not find significant effects in that early component. This is not a major caveat to our interpretations since other studies have found the N170 component to be strongly influenced by perceptual variances [Thierry et al. 2007], and there has been some controversy on the correct use of the N170 for face sensitivity [Bentin et al. 2007; Thierry et al. 2007]. Overall, our findings are consistent with previous results showing a rapid identification of faces in early stages involving the OFA visual cortex (occipito-parietal electrodes). All these effects can be observed well in the real voltage and current source density maps (Figure 6-3).

Additionally our results showed that the amplitude of the P200 component is also sensitive to the nature of the face, whether it is computer generated or a real face. We found evidence in the left parietal electrodes that the *Virtuality* of the faces affected the voltage of the P200 component only in the first trials of the experiment, but not in later trials (Figure 6-5). In contrast with previous research that found faces to be distinctly processed from other objects (flowers, cars etc.) during observation tasks [Keyes et al. 2010; Bentin et al. 1996; Allison et al. 1999; Caldara et al. 2003; Rossion et al. 2004], our results seem to indicate that both computer generated and real faces elicited equivalent ERP components after a fast adaptation process. In the current experiment virtual faces were processed as a different category than the real faces only at the beginning of the exposition, with a rapid adaptation effect: in later trials the P200 categorizing effect disappears and both virtual and real faces are processed as the same class of objects. This effect of modulation by visual expertise has also been described before in unknown objects observation where after a greater familiarity with the objects the components are modulated accordingly [Gauthier et al. 2003; Rossion et al. 2004]. Furthermore, studies with children of different ages also showed how expertise influences face processing [Taylor et al. 2004]. We suggest that in a similar way since participants were not previously exposed to the computer generated faces they required a small number of trials to gain visual expertise. The results of our experiment provides evidence that virtual faces were internally processed in a similar way to real faces after such adaptation. The initial *Virtuality* effect in P200 diminished and was not significant after a longer exposure indicating a rapid adaptation effect. This result is also in accordance with the findings on caricatured distortions on faces [Kaufmann and Schweinberger 2008], in which the brain also indistinctly processed caricatured and veridical faces as equivalent.

Overall, our results suggest that the brain is not only capable of accepting a computer generated look-alike face as his/her own but also of distinguishing it from others' virtual faces. Thus, virtual faces seemed to have been processed at a low level (ERPs) in congruence with higher-level functions (subjective questionnaire): a significant correlation was found between the subjective score of self-identification and the occipito-parietal voltage in P200. A correlation between the subjective scoring and the self-identification mechanism of P200 suggests that conscious self-reporting is somehow influenced by the underlying unconscious visual processing of the faces. This correlation can be interpreted also as a validation that P200 to be indeed related to self-recognition, as it has been previously suggested by other authors [Keyes et al. 2010].

6.5. Conclusions

Avatars have been used successfully as feasible substitutes of the body to study issues in neuroscience and psychology [Banakou et al. 2013; Maselli and Slater 2013; Kilteni, Normand, et al. 2012; González-Franco et al. 2014]. Some studies have found that behavioural responses may be modulated when such avatars look like the participants indicating that there are some self-identification effects [Bailenson and Segovia 2010; Fox and Bailenson 2009]. The current research found neural traces of such self-identification in avatars at an unconscious level: differences in ERPs were prominent for the *Familiarity* levels in the P200 component, showing that the look alike avatars were indeed self-recognized. Furthermore, a significant correlation was found between the self-identification scoring and the P200 component presumably related with self-recognition mechanisms [Keyes et al. 2010].

The current findings have implications both for the field of embodiment as well as for the field of neuroscience and self-recognition. For the field of embodiment we provide objective evidence that avatars may be regarded as real people and that look-alike avatars can be recognized as the self and processed very similarly to self-images. In general, this finding has important implications for future and existing research as it validates previous studies that have shown a change in the participant's behaviour when avatars have similarities to the participant [Bailenson and Segovia 2010; Fox and Bailenson 2009].

Regarding the field of neuroscience, the present study contributes towards expanding the frontiers of self-recognition and face processing. More precisely, we provide evidence of the link between higher level functions and the internal low level processing of faces. Furthermore, these EEG results open new avenues in the area of self-reporting as they be used as a new method for self-recognition of computer generated faces, especially when dealing with complex scenarios such as the exploration of the uncanny valley [Seyama and Nagayama 2007], where very realistic computer generated faces may produce a drastic rejection of the face. Or also for the reporting of subtle differences among faces that are not consciously perceived by the participants while their brain may be able to discriminate more detailed self-identification levels [Blom, Bellido Rivas, et al. 2014].

7. CONCLUSIONS

In this thesis we carried out a series of studies where the representation of the human body and activity in which it was engaged was externally manipulated in various ways while the corresponding electroencephalography (EEG) responses were measured. A series of hypotheses and experiments have been presented and the conclusions extracted from these can be summarized into two main blocs:

- On one hand, this work endorses the capabilities of body substitution technologies (i.e. virtual embodiment) for the empirical study of neuroscience theories related to agency, body ownership and other bodily experiences (Chapters 4 and 5). It does so by providing neurophysiological insights that validate the use of virtual reality for producing full body ownership illusions in virtual bodies. Besides, this thesis also widens the understanding of identification mechanisms over the surrogate virtual bodies (in Chapter 6).
- On the other hand, this research provides new objective evidence of response-as-if-real to virtual stimuli under the grounds that humans behave realistically when they experience presence illusions in virtual reality [Sanchez-Vives and Slater 2005]. Significant brain activation was registered when certain experimental conditions were reproduced in virtual reality (Chapters 4, 5 and 6).

Overall, this thesis provides new neurophysiological evidence of the body representation in the brain by exploring the traces of the bodily perception using virtual reality. More detailed conclusions per experimental Chapter follow.

7.1. A threat to the virtual body

In line with Hypothesis 1 – *A stimulus directed to the embodied virtual body will result in a brain response equivalent to what we would expect if the stimulus happened to the* *participant's real body* – we found automatic brain traces in participants who underwent direct attacks to their embodied virtual bodies similar to the ones that would be found if the events were to take place in a real scenario.

During the experimentation participants were instructed to refrain from moving, however the attacking to the substitute body resulted on an automatic harm prevention effect in the motor cortex (significant Readiness Potential and mu-rhythm desynchronization). Furthermore, the brain mechanisms associated with pain perception – P450 component in the CP3 electrode location – were correlated with the subjective illusion of body ownership, indicating that stronger illusions derived in stronger pain perception.

Overall, this study has provided a measure of response-as-if-real indicating that participants accepted their given virtual bodies as their own also at unconscious levels – *this is me* –, thus seconding existing and future experimentation on the self-body perception that use mannequins and virtual bodies [Ehrsson 2007; Slater et al. 2009]. Furthermore, the methodology presented has opened new avenues for novel measures of virtual embodiment based on objective neurophysiological data, thus being an important contribution to the field of virtual embodiment.

7.2. Disrupting sense of agency of the virtual body actions

In line with Hypothesis 2 – *When somebody is embodied in a virtual avatar and experiences agency of that body, any break in that agency (such as hijacking in the movements of the virtual body) would be clearly perceived as an externally generated error* – results showed that disruptions in the agency while controlling the virtual body were rapidly interpreted in the brain as a violation in the body semantics.

While self-produced errors showed a classical error-related negativity (ERN), externally-generated errors elicited a stronger and delayed negativity (at about 400 ms, N400) with a parietal distribution. Interestingly, the N400 component elicited by the external-errors showed a very similar scalp topography to the classical N400 related to language semantic-conceptual violations (e.g., "*this chair is drinking*") [Kutas and Hillyard 1980]. Thus, these brain-related signatures are a clear evidence of the violation or disruption in the sense of agency ("*this was not my planned action*").

Furthermore, these results reflect an internal clash between the *efference copy* (sensory predictions) and the unexpected visual feedback of the embodied avatar performing an incorrect action. In this sense, prior representations of the virtual body (sensory predictions) have to be coherent with the resulting body action, which in normal circumstances provides us with the sensation of being in control of our actions. In agreement with this idea we observed that the amplitude of the N400 following external-errors was correlated with the subjective feeling of body ownership with the avatar.

In sum, the findings revealed an electrophysiological signature associated with body agency disruptions. These results shed new light on the timing required by the human brain to differentiate self-generated and external-errors, providing new neural evidences regarding the integration of internal and sensory feedback information in the build-up of a coherent sense of agency.

These findings have implications for the current perspectives on agency schemas, proposing and demonstrating the existing theory of re-afferent and feedback error mechanisms that are concurrently functioning in the brain to detect agency disruptions – *I was the one controlling the action* [Gallagher 2000]. Additionally, these results endorse virtual reality technologies for empirical research in neuroscience as we provide objective evidence that avatars can be used as a platform to study theories in agency and body ownership.

7.3. Self-recognition in computer generated faces

In line with Hypothesis 3 – *Given a virtual body we can potentially measure different levels of self-identification: an avatar that looks like the participant is interiorized unconsciously to a different level than an avatar that does not look alike* – results showed shared underlying mechanisms for self-identification in real and virtual faces in the visual cortex.

Strong evidence that virtual faces are internally processed in a similar way to real faces are provided. A rapid adaptation effect was found: even though virtual faces were initially classified as different from the real faces – P200 component [Keyes et al. 2010] – the *Virtuality* effect diminished and was not significant anymore after a longer exposure.

Besides, neural signatures suggest that the brain is capable of accepting a computer generated look-alike face as the self and distinguish it from other virtual faces. Additionally, we provide evidences of the link between higher level functions (top-down driven subjective questionnaire) and the internal low level processing of faces – P200 component. A significant correlation was found between the subjective score of self-identification and the occipito-parietal voltage in P200, linking the automatic mechanisms to the higher cognitive functions used for self-reporting.

The current findings have implications both for the field of embodiment as well as for the field of neuroscience and self-recognition. For the field of embodiment we provide objective evidence that avatars may be regarded as actual people and that look-alike avatars' faces can be recognized as selves and processed very similarly to self-images. In general, these results have important implications as they validate previous studies that have shown changes in people's behaviour when avatars bear similarities to the participant [Bailenson and Segovia 2010; Fox and Bailenson 2009].

Regarding the field of neuroscience, the present study contributes to expand the frontiers of self-recognition and face processing. Furthermore, the EEG results may be used as a new method to replace self-reporting in the context of self-identification, especially when dealing with complex scenarios, where subtle differences among faces may not be consciously perceived by the participants, while their brain may be able to discriminate more detailed self-identification levels.

7.4. Future Work

Each of the studies conducted in this Thesis suggests areas for future investigation, which are detailed in the following paragraphs.

In "a threat to the virtual body" a very strong illusion of ownership over the virtual body was postulated to be an explanatory factor of the larger brain responses observed – P450, Readiness Potential and mu-ERD– in comparison to previous experiments in empathy triggered by pain observation in others [Bufalari et al. 2007; Meng et al. 2012]. A future experiment could explicitly account for this comparison by reducing the level of ownership through a third person perspective and comparing it to the results obtained in the 1PP condition. This would involve observing the brain reactions to seeing somebody else being attacked in an IVE.

The current results could also be further studied by focusing on the effects of self-location with respect to the threat-stimuli to test the importance of the visuo-proprioceptive congruency in the current setup. This could be done by varying the location of the real hand from respect to the virtual one and searching for the threshold where the virtual hand is no longer perceived as the participants own.

The experimental setting offered by "violating agency of the virtual body" also raises new questions. This setup not only provides a unique opportunity to study the experience of agency while being embodied in a virtual body controlling, but also opens new avenues to current research focused on the mental processes underlying agency attribution in both healthy and clinical populations. In fact the results found in this study could be further compared with the neurophysiological responses of patients suffering of the anarchic hand syndrome [Sala 1998] or delusions of control [Frith et al. 2000] in future experiments.

Furthermore, the neural responses could be used as a non-subjective measure of embodiment, therefore future studies may explore the extent in which EEG may be exploited as an objective measure of embodiment.

There is also future work to be explored in the context of the results of the "Self-recognition in computer generated faces". For example, future studies could exploit these EEG results for the exploration of the uncanny valley [Seyama and Nagayama 2007], where a very realistic yet not perfect human avatar observation results on the rejection of the characters by the observers – i.e. some people experienced this effect in movies when observing characters such as the Benjamin Button or Gollum. There are several neuroscience theories about the cause such rejection, and using a similar approach to the present one researchers could explore this curious effect, whether it depends on the external appearance or more on the behavioural part and the animations applied to them.

In conclusion, this thesis has contributed in a complementary way to fields as diverse as neuroscience and real-time computer graphics, grounded on the ideal of multidisciplinary approaches to address and demonstrate prevailing hypothesis and theories in science. Therefore, the findings and collection of studies in this thesis contribute to future investigations in fields going from virtual substitution technologies to neuroscience. In effect, this thesis particularly advances research in neuroscience by converging the use of electrophysiological recording and body substitution technologies in Virtual Reality for exploring the body perception and representation in the brain.

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APPENDIX

List of Abbreviations

DoF	Degrees of Freedom
EEG	Electroencephalography
EMG	Electromyography
ERD	Event Related Desynchronization
ERN	Error Related Negativity
ERP	Event Related Potential
ERS	Event Related Synchronization
fMRI	Functional Magnetic Resonance Imaging
FoV	Field of View
FPS	Frequency Power Spectra
HMD	Head Mounted Display
IRB	Institutional Review Board
IVE	Immersive Virtual Environment
IVR	Immersive Virtual Reality
MEG	Magnetoencephalography
MEP	Motor Evoked Potentials
PET	Positron Emission Tomography
RP	Readiness Potential
SEP	Somatosensory Evoked Potentials
TMS	Transcranial Magnetic Stimulation
VR	Virtual Reality
1PP	First Person Perspective
3PP	Third Person Perspective

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Materials for the experiments

Participant Informed Consent

To be completed by volunteers. We would like you to read the following questions carefully.

Have you read the information sheet about this study? YES/NO

Have you had an opportunity to ask questions and discuss this study? YES/NO

Have you received satisfactory answers to all your questions? YES/NO

Have you received enough information about this study? YES/NO

Which investigator have you spoken to about this study? *Mar González Franco*
Do you understand that you are free to withdraw from this study?

- ***At any time*** ***YES/NO***
- Without giving a reason for withdrawing YES/NO

Do you understand and accept the risks associated with the use of virtual reality equipment? YES/NO

Do you agree to take part in this study? YES/NO

Do you agree to be video taped? YES/NO

Do you agree to be audio taped? YES/NO

Do you agree to wear the EEG cap and have gel put in your hair? YES/NO

Do you agree to be contacted in two weeks to answer some questions about your experience? YES/NO

I certify that I do not have epilepsy. I certify that I will not be driving a car, motorcycle, bicycle, or use other types of complex machinery that could be a danger to myself or others, within 3 hours after the termination of the study.

Signed…………………………………...………… **Date**……………………………...

Name in block letters……………………………..…………………………………...

In case you have any enquiries regarding this study in the future, please contact:

Mel Slater

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Information that we collect will never be reported in a way that individuals can be identified. Information will be reported in aggregate, and any verbal comments that you make, if written about in subsequent papers, will be presented anonymously.

Demographic information

Your Given ID Number	
Your Age	
Your Gender	○ Male ○ Female
Handedness	○ Right ○ Left
How fluent is your English?	Basic ○ Proficient ○ Fluent ○
Occupational status	Undergraduate Student ○ Master Student ○ PhD Student ○ Research Assistant/Fellow ○ Staff –system, technical ○ Faculty ○ Administrative Staff ○ Other ○
Are you taking any medication?	○ Yes ○ No If yes, please specify:
Did you consume more than 2 units of alcohol within the last 6 hours? *(2 units of alcohol = 1 pint of beer or 2 glasses of wine)*	○ Yes ○ No
Please state your level of computer literacy on a scale of (1...7) (novice) 1○ 2○ 3○ 4○ 5○ 6○ 7○ (expert)	
Please rate your level of experience with computer *programming*: (novice) 1○ 2○ 3○ 4○ 5○ 6○ 7○ (expert)	
Have you ever experienced 'virtual reality' before? (no experience) 1○ 2○ 3○ 4○ 5○ 6○ 7○ (extensive experience)	
How many times did you play video games (at home, work, school, or arcades) in the last year?	Never ○ 1 - 5 ○ 6 - 10 ○ 11 - 15 ○ 16 - 20 ○ 21 - 25 ○ > 25 ○
How many *hours per week* do you spend playing video games?	0 ○ < 1 ○ 1 - 3 ○ 3 - 5 ○ 5 - 7 ○ 7 - 9 ○ > 9 ○

Experiment information

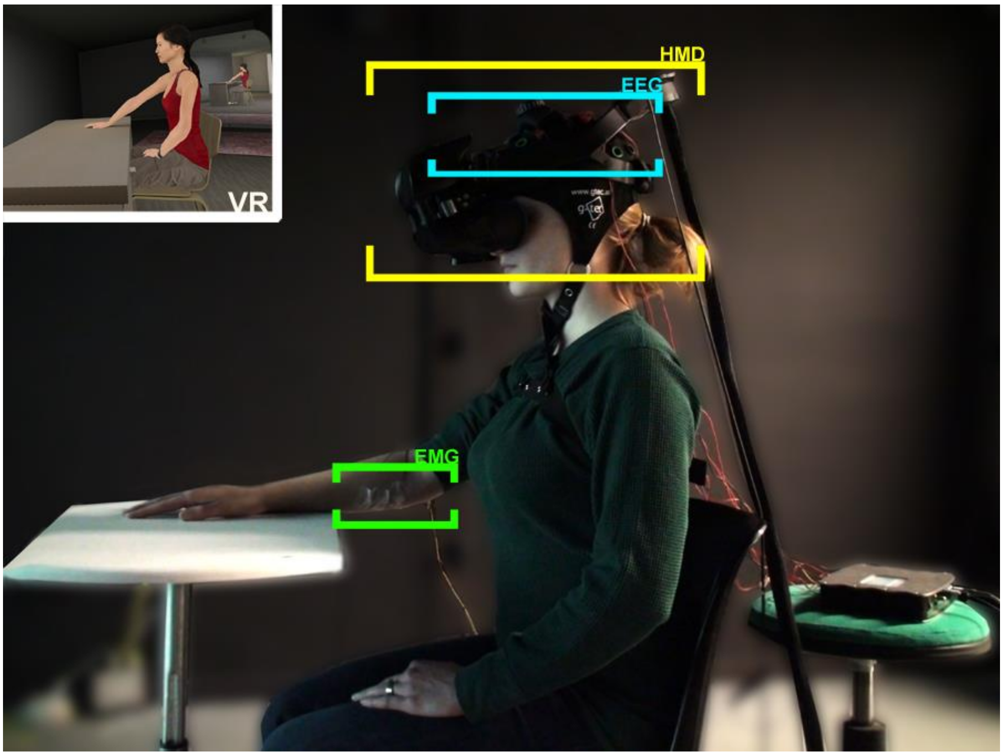
"A threat to the virtual hand"

This experiment is part of a series where we are attempting to learn about people's responses to virtual reality experiences.

In this experiment you will wear EEG cap to read your EEG brain activity. The cap has electrodes that require gel to be put in your hair. EMG will also be recorded to measure your muscle activation during the experiment. Additionally you will wear a head-mounted display (HMD) that will show you a virtual world.

For the duration of the experiment you will sit in front of a table and put your right hand on the table. The left hand will remain on your lap. It's crucial that you look at your hand during the whole experiment, and that you don't move your hand at any moment.

Below, you can see a person wearing all the equipment. On the upper-left corner a view of the avatar in the Virtual Reality.



The experiment consists of approximately 15 minutes preparing the EEG and EMG and 30 minutes in a virtual world. Then you will be asked to fill out a questionnaire. The whole experiment should take approximately half an hour. We will pay you for your participation.

If you have any questions now, please ask.

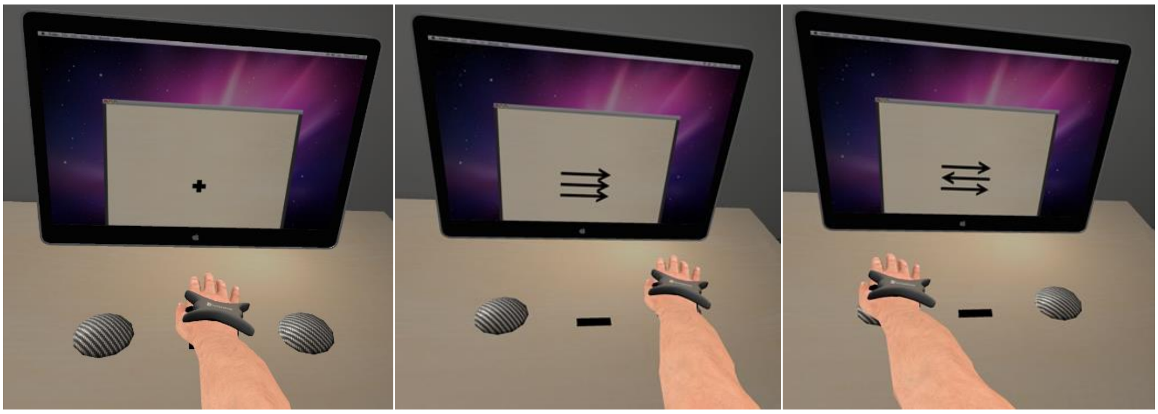
Remember that you are free to leave the experiment at any time without giving reasons.

"Violating agency of the virtual body"

This experiment is part of a series where we are attempting to learn about people's responses to virtual reality experiences.

In this experiment you will wear EEG cap to read your EEG brain activity. The cap has electrodes that require gel to be put in your hair. Additionally you will wear a head-mounted display (HMD) that will show you a virtual world.

For the duration of the experiment you will sit in front of a table and put your right hand on the table. The left hand will remain on your lap. You will complete a task with your right hand as it is explained in the image below.



The task consists on moving the hand from an initial point towards the direction that the middle arrow indicates. Try to do your best at the maximum velocity. You should try to avoid corrections once you'd chosen a direction. The arrows appear every 1.5 seconds. You have to go back to the initial point after each trial.

The experiment consists of a training phase before starting, followed by two blocks of tasks of approximately 15 minutes each. You will be asked to fill out a questionnaire. The whole experiment should take approximately half an hour.

If you have any questions now, please ask.

Remember that you are free to leave the experiment at any time without giving reasons.

"Self-recognition in computer generated faces"

This experiment is part of a series where we are attempting to learn about people's responses to virtual reality experiences.

In this experiment you will wear EEG cap to read your EEG brain activity. The cap has electrodes that require gel to be put in your hair.

We will first take 3 pictures of you to generate a virtual avatar. Then for the duration of the experiment you will sit in front of a table and observe a total of 200 faces that will appear in the screen in intervals of 1 to 2 seconds.

Please try your best to only blink only when indicated.

The whole experiment should take approximately half an hour.

If you have any questions now, please ask.

Remember that you are free to leave the experiment at any time without giving reasons.

Virtual Reality Experience Questionnaire

“A threat to the virtual hand”

The following questions will be given to the participant at the end of the experience.

How much do you agree with the following statements about your experience?

1. On a scale from 1 to 10 assuming that 10 is that the hand was yours, I felt as if the hand I saw in the virtual world might be my hand.

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2. On a scale from 1 to 10 assuming that 10 is the feeling that the knife would definitely harm you, I had the feeling that I might be harmed when I saw the knife inside the hand.

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3. On a scale from 1 to 10 assuming that 10 is the feeling that the knife would definitely harm you, I had the feeling that I might be harmed when I saw the knife outside the hand.

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4. On a scale from 1 to 10 assuming that 10 is that the hand was of another person, The hand I saw was the hand of another person.

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5. On a scale from 1 to 10 assuming that 10 is the feeling that the knife would definitely harm you, I saw the knife as a threat to my body.

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7. What do you think about the experience? How did you feel during the experiment?

“Violating agency of the virtual body”

Now please answer few questions about your experience in the virtual environment and the task you performed.

How much do you agree with the following statements about your experience? Each statement should be answered with:

Be honest with your responses.

-3: totally in disagreement ------------------ 3: totally in agreement

1. **It felt as if the virtual body was my body.**
   -3 -2 -1 0 1 2 3

2. **I felt as if my hand was located where I saw the virtual hand to be**
   -3 -2 -1 0 1 2 3

3. **It seemed as if I might have had more than one body**
   -3 -2 -1 0 1 2 3

4. **It seemed as if the position of the hand I was feeling came from somewhere between my own hand and the virtual hand**
   -3 -2 -1 0 1 2 3

5. **Most of the times, the movements of the virtual hand seemed to be my movements**
   -3 -2 -1 0 1 2 3

6. **Sometimes, I felt that the movements of the virtual hand were influencing my own movements.**
   -3 -2 -1 0 1 2 3

7. **Sometimes, the virtual hand seemed to be moving by itself**
   -3 -2 -1 0 1 2 3

8. **It sometimes felt as if my real hand was turning ‘virtual’**
   -3 -2 -1 0 1 2 3

9. **It seems sometimes that the errors were not caused by myself**
   -3 -2 -1 0 1 2 3

"Self-recognition in computer generated faces"

Now you will rate the faces that the experimenter will show you in a scale from 1 to 5 to two different questions:

The picture looks like a real person: 1 (not alike at all) to 5 (totally looks like a real person)

The computer generated face looks like the real face: 1 (not alike at all) to 5 (totally looks like the real person)