Herberto Dhanis Pedro de Barros Camacho

Licenciado em Ciências da Engenharia Biomédica

Spatio-Temporal Brain Dynamics of the Feeling of a Presence

Dissertação para obtenção do Grau de Mestre em
Engenharia Biomédica

Orientador: Fosco Bernasconi, Doutor,
Laboratory of Cognitive Neurosciences,
Center of Neuroprosthetics,
École Polytechnique Fédérale de Lausanne

Co-Orientador: Professor Olaf Blanke, Doutor,
Laboratory of Cognitive Neurosciences,
Center of Neuroprosthetics,
École Polytechnique Fédérale de Lausanne

Júri:

Presidente: Doutora Célia Maria Reis Henriques

Arguente: Doutor Ricardo Nuno Pereira Verga e Afonso Vigário

Vogal: Doutora Carla Maria Quintão Pereira

FACULDADE DE CIÊNCIAS E TECNOLOGIA
UNIVERSIDADE NOVA DE LISBOA

Março 2017

Herberto Dhanis Pedro de Barros Camacho

Licenciado em Ciências da Engenharia Biomédica

Spatio-Temporal Brain Dynamics of the Feeling of a Presence

Dissertação para obtenção do Grau de Mestre em
Engenharia Biomédica

Orientador: Fosco Bernasconi, Doutor,
Laboratory of Cognitive Neurosciences,
Center of Neuroprosthetics,
École Polytechnique Fédérale de Lausanne

Co-Orientador: Professor Olaf Blanke, Doutor,
Laboratory of Cognitive Neurosciences,
Center of Neuroprosthetics,
École Polytechnique Fédérale de Lausanne

Júri:

Presidente: Doutora Célia Maria Reis Henriques

Arguente: Doutor Ricardo Nuno Pereira Verga e Afonso Vigário

Vogal: Doutora Carla Maria Quintão Pereira

FACULDADE DE CIÊNCIAS E TECNOLOGIA
UNIVERSIDADE NOVA DE LISBOA

Março 2017

Spatio-Temporal Brain Dynamics of the Feeling of a Presence

Acknowledgments

First off, I would like to express my sincere gratitude to my supervisor Fosco Bernasconi. This thesis would not have been possible without the skills and knowledge you have passed on to me, nor without the help and guidance you showed me throughout these eight months. I am very happy to have had you as my supervisor and I have no doubt you will be a reference in my life. Thank you so much!

I am also thankful to Professor Olaf Blanke, director of the LNCO and CNP, for having accepted me as a research intern and giving me the opportunity to work in one of the world's best neuroscience laboratory. I extend my gratitude to the École Polytechnique Fédérale de Lausanne which was my host university in Switzerland.

I would like to thank Professors André Klarsfeld and Pierre-Paul Vidal, coordinators of the BIN master from Paris-Descartes for having showed me the world of neuroscience.

To all the professors from the FCT-UNL, I express my honest gratitude for the scientific knowledge I learned from you, that certainly played a big part in the development of this thesis. In particular, I want to thank the professors directly linked to biomedical engineering, instrumentation and signal analysis.

To the people I have worked with, in the LNCO, thank you for receiving me so well and for making it an awesome place to work. Also to Nathan Faivre and Peter Grivaz for the opportunity to work in different projects.

À mes amis suisses, Angela Gianini, Camille Destors, David Burkhard, Enzo Poggio, Max Giro, Sara Verduci et tous les autres St. Bonifaciens, merci de m'avoir fait me sentir à la maison, et pas comme dans un pays étranger, lors de mon séjour à Genève. Vouz avez beaucoup compté pour moi.

Aos meus grandes amigos da faculdade que já são como família, Ana Pepe, Manuel Eliseu, Manuel Vicente, Mariana Ferreira, Miguel Carvalho e Susana Caixado, que tornaram este período de cinco anos na FCT um dos melhores da minha vida. Obrigado por todos os bons momentos que passámos.

Aos meus pais, Maria João e Kelso Herberto, e à minha avó Maria Alice, obrigado por me terem tornado na pessoa que sou hoje. Muito do que alcancei e espero alcançar é graças à educação e valores que me deram. Estou-vos profundamente agradecido por tudo o que fizeram por mim na vossa vida. Também agradeço aos meus padrinhos e à minha prima Carolina por estarem ao meu lado durante toda a minha vida. No fundo, um grande obrigado a vocês que são pessoas essenciais na minha vida!

Abstract

The Feeling of a Presence (FoP) is the strange sensation of perceiving someone close by, when no one is actually there. Although it is not perceived in any of the usual senses it is described as a strong feeling. The random nature and short duration of this psychotic hallucination, that mostly affects neurological patients, has made it quite difficult to study it in controlled conditions.

In 2014, a paper published by Olaf Blanke described the first experiment inducing the FoP in healthy individuals, achieved through sensorimotor mismatches generated by an illusory self-touch paradigm. Setting out to continue this investigation, we used the same robotic setup from 2014 that allows participants to stimulate themselves on the back, adding several protocols of synchronicity to study the temporal dynamics of the FoP. To address the neural correlates of the FoP, we used Electroencephalography (EEG) and a new strategy of data analysis, in the field of EEG, by applying a General Linear Model to our data.

Our results show that the subjective experience of the Feeling of a Presence, grows in a sigmoidal fashion with increasing delays, doubling its appearance from 100 msec to 400 msec of delay. The applied model, revealed significant effects of, the experimental conditions of synchronicity and from the interaction of these and the subjective experience of the FoP. When analyzing the brain sources, our data shows that both Secondary Somatosensory Cortex and Inferior Parietal Lobule are less activated when experiencing the FoP (compared when not experiencing the FoP), at respective latencies that match the components P100 and N140.

The presented data helps advance the knowledge of this psychotic trait. Studying the development of the FoP on healthy individuals, might lead to a better understanding of what happens in patients with positive symptoms of psychosis.

Keywords: Feeling of a Presence, Hallucinations, Self-Touch, General Linear Model, EEG, Psychosis, Psychotic-States, Positive Symptoms.

Resumo

A Sensação de Presença (SdP) pode ser descrita com a estranha sensação de que alguém está perto de nós, quando na verdade, ninguém se encontra por perto. Esta sensação, apesar de não ser experienciada pelos sentidos comuns, apresenta-se com grande certeza no indivíduo. A natureza aleatória e a curta duração desta alucinação psicótica que afeta principalmente pacientes neurológicos, torna muito difícil o seu estudo em ambientes controlados.

Em 2014, um artigo publicado por Olaf Blanke descreveu a primeira experiência capaz de induzir a SdP em indivíduos saudáveis, através de assíncronias em estímulos motoro-sensoriais, geradas por um paradigma que permite a ilusão de auto-toque. Com o objetivo de continuar esta investigação, utilizámos o mesmo sistema robótico de 2014 que permite aos participantes estimularem-se nas costas, adicionando vários protocolos de sincronia para estudar a dinâmica temporal da SdP. Para estudar as fontes cerebrais responsáveis pela SdP, utilizámos Eletroencefalografia (EEG) e uma nova estratégia de análise de dados de EEG que consiste na aplicação de um modelo geral lineal.

Os nosso resultados mostram que a experiência subjetiva da SdP, cresce de forma sigmoidal com o aumento da assíncronia temporal na estimulação, crescendo a sua percepção para o dobro ao passar de 100 milissegundos para 400 milissegundos. O modelo aplicado, revelou efeitos significativos para, o efeito das condições experimentais de assíncronia e para o efeito da interação entre os estas condições e a experiência subjetiva da SdP. Ao analisarmos as fontes cerebrais, percebemos que o Córtex Somatosensorial Secundário e o Lóbulo Inferior Parietal apresentam-se menos ativos na condição em que a SdP não é experienciada (comparando contra a situação em que há SdP). As regiões descritas aparecem temporalmente relacionadas com os componentes P100 e N140, respetivamente.

Os dados apresentados, ajudam a evoluir o conhecimento sobre este traço psicótico. Estudando em indivíduos saudáveis, o processo de evolução da SdP, esperamos melhorar a compreensão do que se passa em indivíduos com traços positivos de sintomas psicóticos.

Palavras-chave: Sensação de Presença, Alucinações, Auto-Toque, Modelo Geral Linear, EEG, Psicose, Estados Psicóticos, Traços Positivos de Psicose.

Table of Contents

Table of Figures

Table of Tables

Acronyms

FoP	Feeling of a Presence
BSC	Bodily Self-Consciousness
EEG	Electroencephalography
GLM	General Linear Model
RHI	Rubber Hand Illusion
SRHI	Somatic Rubber Hand Illusion
FBI	Full Body Illusion
TPJ	Temporo-Parietal Junction
SI	Primary Somatosensory Cortex
SII	Secondary Somatosensory Cortex
SEP	Sensorimotor Evoked Potentials
POI	Period of Interest
msec	Millisecond(s)
AP	Autoscopic Phenomena
OBE	Out-of-Body Experience
fMRI	functional Magnetic Resonance Imaging
ICA	Independent Component Analysis
MCP	Multiple Comparison Problem

1 Introduction

The Feeling of a Presence (FoP) is the strange sensation that someone is nearby, when actually no one is there. This sensed presence is an hallucination, which has been described in neurological and psychiatric patients, that as most likely made its way in the past, into stories or legends of divinity and obscure natures [1].

The FoP is considered a specific symptom of certain psychotic states. Despite its numerous descriptions both in neurological and psychiatric patients, little is known about this sensation which is the only kind of Autoscopic Phenomena to be part of psychotic states [2]. Mostly, this lack of knowledge, is due to the difficulty in reproducing this symptom in laboratories, as it is very unpredictable and usually of short duration.

According to a study in the United Kingdom, surveying around 15.000 people, functional psychosis prevails on 0.45% of the population, however a much larger number of people (~7%) has experienced some sort of psychotic or psychotic-like state during their life [3]. There are no statistics showing how many people with psychosis are affected by the Feeling of a Presence, however, it is widely reported in conditions affecting sensory or motor systems [4].

1.1 Objectives and Motivation

Three years ago, in 2014, the Feeling of a Presence was induced for the first time in healthy people, in very controlled experimental conditions, without resorting to any drugs or brain stimulation [1]. Through means of a robotic master-slave system, the task at hand, put participants touching their own back, with specific protocols that introduced sensorimotor mismatches to achieve the FoP [1]. Arriving to this milestone opened the door to study the neural bases of the FoP. This master thesis is, consequently, part of a much larger study started by the Laboratory of Cognitive Neurosciences from the Center of Neuroprosthetics of the École Polytechnique Fedèrale de Lausanne, to understand the hallucination of the FoP in patients with psychosis or sensory/sensorimotor conditions.

The aim of this master thesis project is to study the temporal dynamics of the Feeling of a Presence and to identify brain regions associated with this hallucination in healthy individuals. Studying this phenomenon in healthy people and ideally comparing the sensation of presence, versus not sensing it, under the exact same experimental conditions will help to further understand the brain mechanisms that generate this sensation. Those findings, will be of great interest to understand and explain the neural mechanisms of hallucinations in patients with neurological or psychiatric disorders.

The approach chosen to study the FoP, is to target the bodily-self by inducing multisensory conflicts on the participants that take part on our experiments, in a similar way to what was done before [1].

1.2 Overview

The structure of this dissertation is presented here, for all the remainder chapters.

Background in Neuroscience

The concept of the Feeling of a Presence is presented. An effort is made to guide the reader through a logical path, starting with basic notions of the bodily-self and what manipulations can and have been made to study it. It is followed by a description of how the brain identifies self-touch and how sensorimotor integration is performed for self and other touch. Psychotic states are put in perspective, in order to present a possible mechanism for the FoP.

State of the Art

The article published in 2014 [1], where the FoP was induced for the first time in healthy participants is presented and its results are put into perspective with regards to the objectives of the present work.

Background in Electroencephalography

Concepts from electrophysiology, neurophysiology and technical details of imaging with electroencephalography are presented to the reader.

General Methods

This section describes all the steps of the data acquisition. Equipment that were used for every experiment is presented here, as well as the setup and paradigm of both experiments.

Temporal Dynamics of the FoP

In this section, we present all the methods, results and discussion regarding the behavior results of both experiments. Starting with methodology of analysis, we describe the methods used to analyze the behavior results. The results addressing this behavioral part on both experiments are then presented, followed by a discussion.

Neural Correlates of the FoP

All the specific methodology for EEG analysis is presented in the beginning. The imaging results are presented here, starting with SEP analysis and ending with the brain sources of the FoP. A discussion follows, linking our results to relevant literature.

General Conclusions

The present dissertation finishes with general conclusions linking both the behavior and imaging results with relevant literature. Achievements of this project are reaffirmed and followed by proposed future directions.

2 Background in Neuroscience

The Feeling of a Presence (FoP) is usually a bizarre concept to incognizant individuals. Here, we will clarify what this symptom is, by introducing the correct definition for the FoP and essential concepts believed to be underlining it. Normal functioning of the self, self-identifying mechanisms and psychotic states are put in perspective as to explain the proposed flow leading to the FoP.

2.1 The Feeling of a Presence

The Felling of a Presence can be defined as being aware of a presence nearby, when actually no one is there [1]. The first accurate description of the FoP [4] might be the one of psychologist William James in 1902, *"It often happens that an hallucination is imperfectly developed: the person affected will feel a 'presence' in the room, definitely localized, (…), and yet neither seen, heard, touched, nor cognized in any of the usual 'sensible' ways"* [5]. Psychiatrist and philosopher Karl Jaspers later described it in patients, *"There are patients who have a certain feeling (in the mental sense) or awareness that someone is close by, behind them or above them, someone that they can in no way perceive with the external senses, yet whose actual/concrete presence is clearly experienced"* [6].

This sensed presence is, indeed, mostly a specific symptom of a psychotic state happening to an individual suffering from a neurological disorder. However, as we can see from this extract, *"(…) that the party of explorers, at the extremity of their strength, had the constant delusion that there was one more member than could actually be counted"* [7], the FoP can also be experienced by healthy individuals facing extreme circumstances, ranging from situations with very poor stimuli, as darkness, isolation or even barren landscapes, to situations where an individual is pushed to the limit, like dehydration, extreme fatigue, sleep deprivation and injuries [7].

To clarify the phenomenology of the FoP we will address two case-studies, reporting this hallucination.

Case 1: A nun, aged 65 years-old, presented a hematoma at the left parieto-temporo-occipital junction, causing her to suffer from complex seizures and neurological disorders such as alexia (severe reading problems), visual agnosia (ignores certain visual stimuli) and right-sided hemianopia (blindness over the right-side). Aside from this, she also experienced several times a day the feeling of having a presence by her side. In her reports, she described it mostly as being "a shadow" composed by the lower half of a person. There were occasions however, where this half-shadow became a complete human figure (the appearance remained

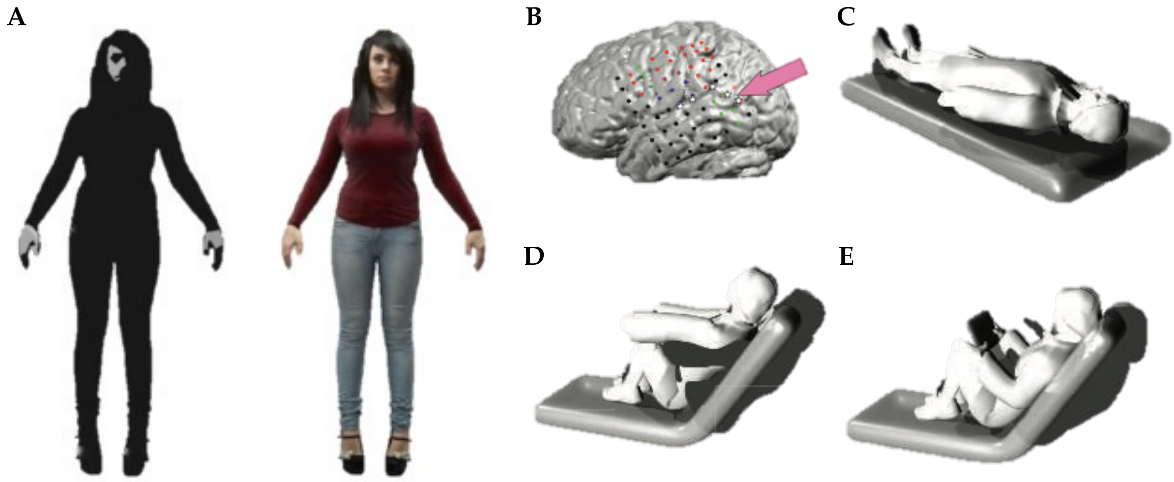


Figure 2.1 Feeling of a Presence
(A) Shadowy presence, as described by a 65 years old nun, with a hematoma affecting the left parieto-temporo-occipital junction. The presence is represented by the dark figure, while the nun is represented by the woman in color. **(B)** Adapted from Arzy et al., 2006 [9]. Site (temporal-parietal junction, TPJ), where the electrical stimulation was presented to a 22 years old woman, with the objective of inducing the FoP. The pink arrow points to the stimulated area **(C-E)** Adapted from Arzy et al., 2006 [9]. Scenarios in which the FoP manifested itself due to applied stimulation on the TPJ.

as the one of a shadow). In these situations of complete human figure, she could describe the shadow as a woman, always 20 to 30 cm to her right side, not touching her and with her exact same size (figure 2.1 A). She would only have this sensation while standing or walking and the presence would mimic her movements at the same pace. This was never accompanied by other hallucinations [8].

Case 2: A 22 years old woman, undergoing pre-surgical evaluation regarding epilepsy, demonstrated to have the FoP when focal electrical stimulation was applied over the temporo-parietal junction (TPJ, figure 2.1 B). Following these observations and before the surgery took place, she volunteered herself for electrical stimulation on this exact spot as part of an experiment to study the Feeling of a Presence. As reported by her, the induced presence was of undistinguishable gender and stood very close behind her, even in positions where it should not be physically possible for anyone to be there. For example, when she was laying down (figure 2.1 C-E). She knew 'it' was of young age. Describing this presence as "a shadow", she said it mimicked her positions and even seemed to try and interfere with her execution of required tasks, such as reading paragraphs [9]. This negative connotation given to the presence, goes in line with observations done in 52 Parkinsonian patients also suffering from the FoP, where almost 40% of the patients described the presence as "unpleasant" [4].

Similar descriptions of this presence, are frequently observed among patients with neurological or psychiatric disorders [1, 10, 11]. The phenomenology of the FoP in these patients has the common traces seen before, with a lateralization or posterior position of the presence and mostly an undistinguishable appearance [11]. A description of the FoP in a schizophrenic patient's autobiography shows how vivid and sometimes threatening this sensation can be: "*it was odd that he should push 'his' chair back every time I moved mine (…) I often* *felt as if someone were standing behind my chair. Then I would strike out backwards with my dagger, imagining that I was fighting an enemy"* [12].

Looking at the subjective reports of this presence, from both case studies and from the psychiatric patient's autobiography, we can try to understand the origin of this sensation by analyzing specific traits. This presence is near the individual, in his/her extra-personal space and mimics the person's movements. If we consider that the TPJ, which is the area affected in both case studies, has been associated with self-other distinction and multisensory integration at different levels [9], such phenomenology could suggest that the person affected by it, is in fact experiencing a disturbance of the experienced self [9], that leads to a paroxysmal disorder of body image.

To continue to possible mechanisms of the FoP and to link it with psychosis, it is necessary to present the reader with essential concepts that most likely underline this hallucinative process.

2.2 Bodily Self-Consciousness

In the previous chapter, we claimed that the Feeling of a Presence might be caused, due to a poor representation of the experienced self. Here, we will explain what we refer to as 'self', some of its characteristics and how researchers have been manipulating it.

Self-consciousness is an impressive phenomenon that allows us to identify with an 'I', different from the outside world, distinct from the community, that bounds the subjective experiences one lives to a unitary self [13]. The mechanisms of self-consciousness are of extreme complexity, comprising both multisensory integration at different levels and higher cognitive processes, such as understanding one's identity over time [14]. As a clarification note, we refer to multisensory integration as the confluency of information from different sensory systems that leads to an understanding that would not be possible by just relying on one of the systems [13]. Pressing a button and hearing a sound is a simple example where the integration of signals from two different sensory systems leads to the understanding that the button and the sound are most likely associated.

A successful approach to study self-consciousness that has been employed by several researchers, is to focus on simpler mechanisms that lie in the heart of this process [13, 15-22]. One possible path is to look directly at the subject of experience, or in other words to a more bodily form of self-consciousness. This form of consciousness is referred to as, Bodily Self-Consciousness (BSC) and it targets the brain mechanisms that represent the body [13, 14, 22, 23]. Such body representations exist in the primary somatosensory cortex (SI) [24] and are most likely the result of a conjugation between an innate structural representation of the body and the acquisition of structural representations through non-visual sensorimotor experiences throughout our lives [25]. One of the arguments for this approach is that the bases of the self, should rely essentially on representations of the body [23], as indeed, most of our objective or subjective experiences have our body as an active part of that task even if we don't think about it: "*When I decide to write, I do not need to look for my hand in the same way that I have to look for a pen or a piece of paper, for the simple reason that my hand is always there*" [26].

In general, BSC should be considered as a process that allows global identification with one's own body, generating a singular body 'entity' and is crucial in distinguish the body from the outside world [13, 23].

Even if considered a simpler approach, BSC is still dependent on a complex multisensory integration process. This integration of information relies essentially on proprioceptive, vestibular and body related visual inputs [22]. At the same time, BSC is constrained by the same proprioceptive system in which it depends, body-related visual stimuli, time and space. The proprioceptive system in the sense of one's body position for example, body-related visual stimuli such as the visual observation of being touched on the right hand (visuo-tactile stimuli). Space and time produce the same constraint, generating a stronger integration, the closer different stimuli are, in space and/or time [22]. More complex constraints exist, especially regarding space, however, addressing them would greatly exceed the purpose of this introduction.

With a broader view on BSC we can focus on some of its essential aspects. Three main characteristics have been identified and associated with the normal functioning of this process [13, 15, 16]:

- **Self-Identification -** knowing that this body belongs to "me" and identifying "myself" with it;
- **Self-Location -** knowing where "I" am;
- **First-Person Perspective -** being aware of the perspective from where "I" perceive the world.

It is noteworthy that self-location and first-person perspective are usually entangled. Nevertheless, there are extremely specific situations where they can be separated [15].

Other characteristics might be essential to BSC, such as agency (the sense of being the cause of your own actions [27]), but the three aforementioned components are identified as the main components of this process [13]. One of the reasons for this has to do with independency. At least, regarding the first two components, it has been demonstrated experimentally that it is possible to manipulate one of the aspects without influencing the other [17, 14, 28]. Regarding First-Person Perspective, there is an open debate on its dependency from Self-Location and in addition they have never been dissociated experimentally. Nonetheless, there are known situations where the former changes without affecting the latter such as Out-of-Body Experiences [2, 14].

It's mainly by manipulating one of these three aspects that researchers investigate BSC [13, 14, 22, 23]. These easily understood definitions are difficult to take a hold of in terms of experimentation [13]. When these topics started to be investigated, most of the early experiments showed curious results, even if limited by what they could manipulate at the time. Participants seemed to present changes in some aspects of BSC such as self-location, in simple experiments that used mirrors to change the visual feedback of arm movements [13, 29]. Recent technological developments came as an enormous aid to these studies, especially, computational developments that allow the precise delivery of stimuli, and Virtual Reality [13]. Curiously one of the experiments that gave a good contribution to understanding BSC did not need any kind of technology. The Rubber Hand Illusion (RHI), although operating in a smaller scale, gave researchers a window through which they could gaze into some of the fundamental aspects of whole body consciousness [23]. Eventually, more complex illusions appeared to study whole-body manipulations of the self, such as the Full Body Illusion (FBI) [13, 23]. These two illusions will be introduced with more detail in the following sub-chapters.

For the specific case of the Feeling of a Presence we will only focus on Self-Identification, as its dysfunctions seem to be more pertinent for this symptom.

2.2.1 Self-Identification

Self-Identification is having a sense of ownership over your own body and its individual parts, even in situations, such as amputation, where the perception of one or more limbs is altered [13]. It remains quite unclear how the brain goes from individual body parts ownership to the feeling of having a human body. For now, it is believed that the mechanism through which the brain does this, is by transitioning from multiple attribution of single limbs to a concept of a whole body [17].

Researchers can study the bodily-self by manipulating the multisensory integration in which BSC relies [13, 16, 30]. For example, by manipulating visual and tactile stimuli it is possible to induce illusory states of BSC. It is said that a person is in an illusory state of bodily self-consciousness if one or more of the three aspects mentioned before, changes to something that is not true (e.g. for self-location, believing you are in a physical position that is not your actual position) [13]. This does not necessarily have to include whole body changes, it can be specific to smaller parts of the body, such as a hand [21, 30].

2.2.1.1 Rubber Hand Illusion

The Rubber Hand Illusion (RHI) is an example of how illusory states of BSC can be induced in a lower scale. It consists on having the participant's hand placed on a table in front of him/her, occluding said hand and respective arm from the participant's view, and then

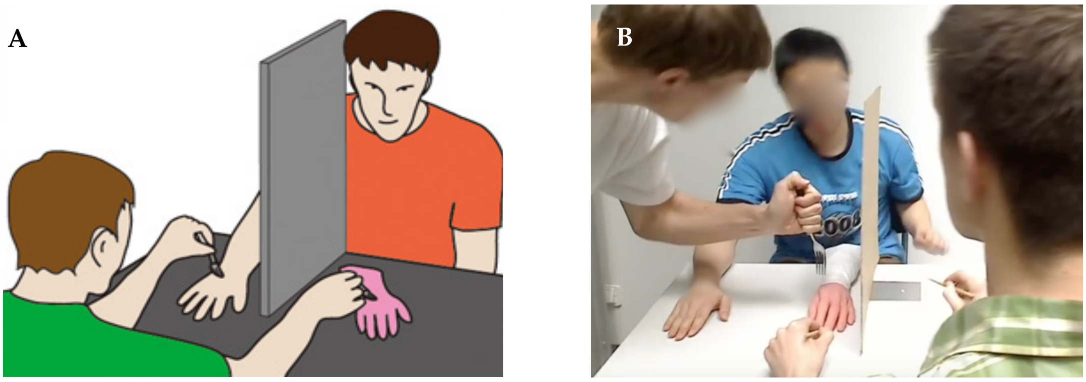


Figure 2.2 Depictions of the Rubber Hand Illusion
(A) A participant sees a rubber hand being brushed at the same time as his real right hand is being brushed by an experimenter. His real hand his however occluded from his view due to a barrier. The synchronicity of the visual stimuli on the rubber hand and the tactile stimuli on his hand, trick him into believing that the rubber hand is his real hand. **(B)** Adapted from [32]. A frame extracted from a video where the RHI is being performed, shows how strong this effect is. The participant (blue shirt) retracts his left hand about a quarter of a second after perceiving that the rubber hand, that by now he 'thinks' is his own, is being attacked by a fork.

placing a rubber hand in a location consistent with the position of the real limb (figure 2.2 A) [13, 18, 30]. With this experimental setup researchers were able to demonstrate that applying visuotactile stimuli to the rubber hand with synchronous tactile stimuli applied to the occluded real hand, can induce the belief of ownership of the rubber hand mainly because it tricks the participant into thinking that he/she is indeed feeling the stimuli applied to the fake hand [13, 30]. This is true, as long as the fake limb, is presented in a position that is congruent with the anatomy of the arm, is in fact something resembling a human hand and the stimuli is applied to both hands (rubber and real) in a synchronous way [13]. The RHI is in fact so strong, that participants react very quickly and in a defensive manner when the rubber hand is threatened by an external attacker (figure 2.2 B), considering a previous exposure to this illusion of at least a few minutes [31].

Experiments with this paradigm have given great contributions for the study of BSC. Even if they operate in a limb scale, they are an open door to understand important features of BSC such has body ownership [13, 18, 23]. Moreover, the results of illusory self-attribution of the fake hand and mislocalization have been compared to the illusory perceptions that some neurological patients have regarding their whole body [18].

2.2.1.2 Full Body Illusion

In a Full Body Illusion (FBI), researchers put participants in conditions where the harmony of specific visuotactile stimuli is capable of changing aspects of the participant's BSC, making him identify his body as something else (should be similar to a human figure), rather than his actual body [13, 14, 17, 19, 20, 22]. In contrast with our previous example (RHI), this illusion is capable of inducing whole-body changes.

Early studies with the FBI tried to acquire knowledge about BSC but lacked the controlled experimental conditions that new technologies can provide. An example of these older studies [29] used mirrors to make the participant see himself/herself in a different position than the one in which he/she was (figure 2.3 A). By making movements, the participant would see his/her reflection moving as well, but in a completely different position. After a few minutes, he/she started to report identification with the reflection and its different position. Nowadays, a common setup to generate this type of self-identification illusion, makes use of a head mounted display (HMD), conveniently placed on the participant's head, showing in real time the footage of a camera placed behind him/her, in such a way that the participant is seeing himself/herself from behind. Stroking movements are then applied to the participants back with a stick (figure 2.3 B). The HMD is displaying in such a way that either the participant sees everything in synchrony or in asynchrony if a small delay (typically 500 msec) is added to the camera's transmission. In the synchronous condition, participants report self-identification with the body they see in front of them, which after all is just an image of their body, not their real body (or even a real body for that matter) [13, 19]. The reason why this distinction is important lies with the difference between self-awareness and self-identification. For example, when an individual observes himself/herself in a mirror, he/she is engaging in the activity of self-recognition (through self-observation), which is an essential part of self-awareness. However, this individual would not report self-identification with this mirrored image in the sense of the described characteristic of self-identification (knowing that 'this' body belongs to 'me') as he/she knows it is just a mirrored image and not his/her real body [33].

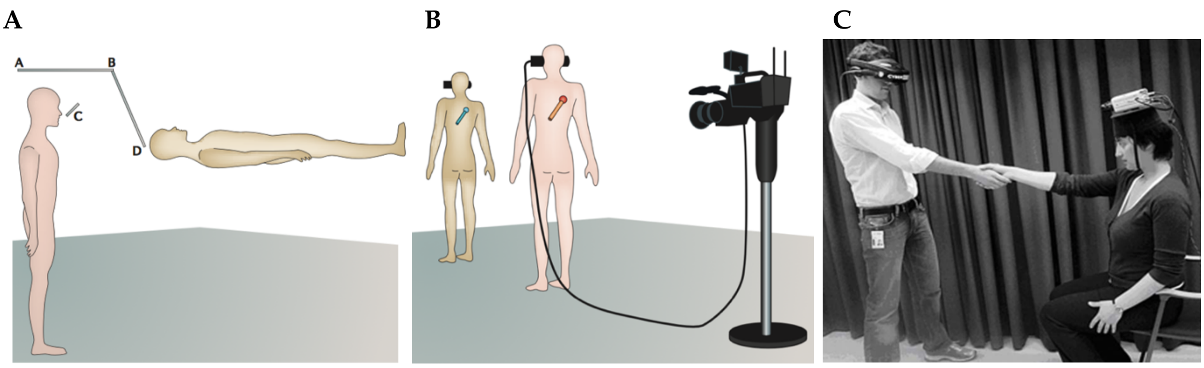


Figure 2.3 Depictions of the Full-Body Illusion
(A) Adapted from Blanke, O., 2012 [13]. Example of an old setup used to induce the FBI. Mirrors are placed in such a way that the participant (pink body) sees himself in a supine position in front of him (brown body). **(B)** Adapted from Blanke, O., 2012 [13]. A participant (pink body) sees himself from behind through a HMD that is connected to a camera filming his own back. At the same time, a researcher strokes the participant's back with a stick. In case the HMD is live, the participant sees a virtual body in front of him (brown body) being stroked at the same time he feels the strokes on his back, generating the FBI. This is not the case if the transmission is delayed. **(C)** Adapted from Petkova & Ehrsson, 2008 [34]. A different approach to the FBI, induces in participants the vivid experience of swapping bodies with someone else. A participant wearing a HMD stand in front of a seated experimenter which has two CCTV cameras on her head, showing her point of view. The CCTVs are connected to the HMD. Squeezing hands synchronously for two minutes results in the self-identification of the arm of the experimenter as being the arm of the participant.

A different approach to the FBI is capable of making participants 'believe' they have swapped bodies with someone else (figure 2.3 C). The setup for this illusion puts the participant in front of the experimenter, with the former wearing a HMD and the latter equipped with two CCTV cameras presenting the experimenter's point of view. This disposition allows the participant to see his/her physical body from the knees to the shoulders. Participant and experimenter would then squeeze each other's hand repeatedly for two minutes in a synchronous manner and then for another two minutes but with the experimenter being random in her squeezes. Participants reported a vivid sensation of owning the arm of the experimenter and the sensation of feeling their body behind it. Moreover, they reported to feel as if the sensations from the squeezes were clearly originating from the experimenter's hand. Researchers also performed skin conductance analysis during random threating attacks to both hands in the two conditions, which revealed that in the synchronous condition, threaths to the experimenter's hand would enlicit stronger skin conductance responses, which indicates a change in the participant's arousal, confirming that ownership of the experimenter's hand was achieved [34].

The FBI has been used for a multitude of purposes related to the study of BSC [13], existing multiple setups and paradigms to do it, including one to partially simulate an Out-of-Boby Experience [20]. Coupled with imaging techniques it has given a direct insight on the brain regions that might be responsible for processes of self-identification and body ownership [13, 17, 28].

2.2.1.3 Putting Body-Limb Ownership Together

The contributions of both the RHI and the FBI studies have been immense towards the understanding of the essential aspects of BSC. How the body goes from having a sense of ownership of different body parts to the whole-body is an interesting question that appeared after observing the results of the RHI and similar setups. Having seen how both limb and body ownership can be manipulated, we will give a brief overview on the mentioned subject.

Trunk-related multisensory processing as become the focus of recent research, as seen with the FBI. Such focus allows the exploration of a system that potentially represents more the body than an individual body-part [13]. Trunk-related processing has been showed to also be involved in important aspects of BSC that regard ownership of other body-parts, something that does not happen the other way around [22]. Corroborating this effect, a study with the FBI performed with an artificial human shaped body showed that besides integration of the body parts affected by the touches in the FBI, a secondary process unifies the parts into the percept of a whole body, thus propagating the local effect to regions of the body that were not directly subjected to the FBI [17, 22].

Naturally, there is still the need for individual multisensory processing of body parts leading to ownership of said body part. Two studies with the RHI paradigm coupled with fMRI have pointed out that the premotor cortex and the cerebellum play important roles in the matter of body ownership, more specifically in the self-attribution of the involved body-parts [18, 21]. Furthermore, for the consciousness of a whole body, one would also expect an area responsible for joining together the inputs from different sensory modalities from single mobile body parts, such as hands or the head, to the torso-centered reference frame. The brain region responsible for this has been pointed out as the Post Parietal Cortex [22].

The role of vision in the multisensory integration of BSC has been suggested to be more peripheral, mostly by studies performing variations of the RHI where participants are blindfolded. Serino et al. 2015 [22], debates a role for visual stimuli that goes in line with the constraints to BSC presented in the beginning of this chapter. He purposes that the role of vision should be such of top-down processing, conscious affecting unconscious processes, for example, helping to distinguish "*between objects that can and cannot be attributed to one's body as a function of their visual appearance and anatomical coherence with the physical body*" [22].

With the conclusion of this chapter, three essential messages should be kept in mind. First, the three essential characteristics of BSC, self-identification, self-location and first-person perspective. Second, the proprioceptive system and tactile stimuli holding a major role in the construction of the bodily-self (and consequently, a major role in manipulating it). Finally, the existence of constraints to BSC, mainly proximity in time. From this, we move on to introduce the mechanisms of a process that also contributes to the bodily-self and is essential for our project.

2.3 Sensorimotor Integration and Self-Touch

In the previous chapter, essential concepts on the bodily-self were presented alongside with common experimental paradigms to manipulate bodily self-consciousness and study the bodily-self. However, we did not enter in detail on how the mechanisms behind the bases of self-identification work. In the present chapter, we will present one mechanism believed to influence self-identification and therefore able to alter the state of BSC [25, 35, 36]. This mechanism relies on self-touch and its comprehension is essential to understand the experiments designed in this master thesis project.

Self-touch is the specific situation in which someone generates both an action and a sensation on himself/herself [25, 37]. It is believed to contribute to fundamental aspects of BSC [24, 25, 36], such as body representations [36] and self-identification [35], mainly due to the role it plays in agency (being the main agent of an action or the active cause of certain sensations [27]). Earlier in this introduction, we presented the rubber hand illusion, in which misattributed ownership of the hand, for a rubber hand, is induced through synchronous

Figure 2.4 Depiction of the Somatic Rubber Hand Illusion Adapted from Ehrsson, 2005 [18]. In a more recent setup of the RHI, a blindfolded participant receives tactile stimuli from a researcher on her right hand, while he guides her left index finger to touch a rubber hand. When done synchronously the somatic rubber hand illusion can be considered self-induced and produces the same effects as the classical RHI.

tactile and visuotactile stimuli, to the real and fake hands respectively. However, Ehrsson demonstrated that this illusion can be induced without the component of vision being involved [18]. In 2005 they managed to induce the RHI in blindfolded individuals, through a paradigm that relies on self-touch, or better said, illusory self-touch [18]. In this setup called the Somatic Rubber Hand Illusion (SRHI, figure 2.4), the blindfolded participant has his/her right index finger being guided by the experimenter, so that he/she touches the rubber hand, at the same time as the researcher touches the participant's real left hand. This experiment not only showed that the RHI can be self-induced, but it also demonstrated that changes in self-identification and self-location towards the fake limb can be aroused just by tactile stimuli, if both the action of touching and the feeling of being touched, fulfill the necessary requirements to identify self-touch, or in other words, as long as these two sensations are in synchrony [18].

Compelling evidence on how self-touch affects BSC has also been gathered with neurological patients. A woman aged 60 years-old suffered a large hemorrhagic stroke which damaged her right parietal and frontal lobes. Thus, she ended up suffering from recursive somatoparaphrenia (denying that a limb is part of your body) of her left arm, misoplegia of the left arm (negative feelings and/or physical violence, towards the affected limb) and hemianaesthesia on the left side (loss of sensation on one side of the body). The latter, made it impossible for her to perceive any somatosensory input acting on the left side of her body. However, when she was the one touching her contralesional hand (with her right hand), she would have a sense of touch. Interestingly, shortly after the stroke episode she reported that 'stroking' the affected limb improved her feeling that the arm was after all, a part of herself.

This lead to a series of experiments showing that self-touch would, not only generate self-identification/ownership towards the affected limb but even work if a rubber arm was used instead. Plus, researchers reported striking changes in attitude towards the arm being touched, going from feelings as strong as disgust in the beginning, to gentle and warm caresses in the end. In this case study, not only does self-touch appear as a strong mediator of BSC but it is also seen reinforcing body representations [35].

Knowing that self-touch can modulate BSC we must further investigate the mechanisms underlining self-touch and address important brain features of these specific mechanisms, such as predictions.

2.3.1 Considerations on Self-Touch

Even if most of us are ticklish, we cannot tickle ourselves. This is a fact that most of us have noticed at some point of our lives, even if we haven't exactly thought about it. An experiment carried out in 1971 [38] tried to better understand why this happens. For this purpose, researchers designed three tickling conditions - one where the experimenter tickles the participant, a second one performed by the participant on himself/herself and a third where the participant's arm is controlled by the experimenter and used to tickle the participant passively. As expected, researchers observed that the most ticklish condition was the one where the tickling had an external source (performed by the experimenter) and that it was impossible to arise a tickling sensation in the second condition, where the tickles were self-administered. For researchers, this difference in experienced sensation had to be explained by the extra knowledge participants have in self-administered tickling. In this condition, participants are aware of both the motor command used to produce the tickling and the sensory feedback coming from the arm producing the tickles. None of this knowledge is present in an externally produced tickle, and only one, the sensory feedback from the arm, is present in a passively produced tickle, like in the third condition [38]. These observations start to show us the path to the distinction between self and other touch.

Looking also at this distinction between self and other touch from a different perspective, another experiment was carried out, having participants asked to match a produced force. This force is applied to their left index fingers with a lever attached to a torque motor. One must then match the force under two different conditions. In one of them, the force is matched by pressing with the right hand the exact same lever that puts pressure on the left index finger (figure 2.5 A), whereas on the other one a joystick is used to move the lever against the left index finger with different ratios of force depending on how you manipulate the joystick (figure 2.5 B). What stands out from this study is that participants consistently overestimated the force applied to their left index fingers when they tried to match it directly (first condition, versus a condition where an intermediator, the joystick, with unknown parameters to the user is used; figure 2.5 C) [39]. The presented explanation for this

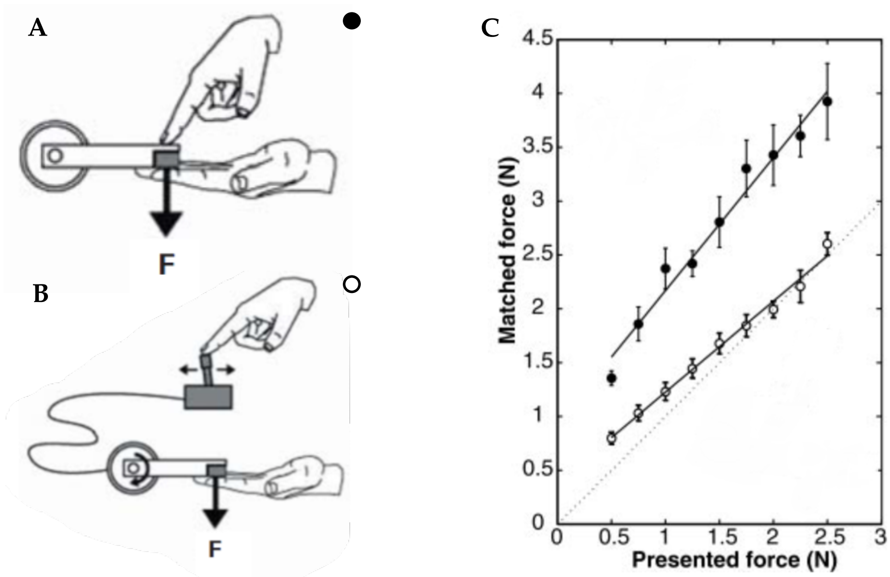


Figure 2.5 Depictions of the Matching Force Task
Adapted from Shergill et al., 2003 [39]. **(A)** After an external force is applied by the lever to the participant's left index finger, the participant has to match that force by directly pressing on the lever with is right index finger (left index finger is still under the lever). **(B)** After an external force is applied by the lever to the participant's left index finger, the participant uses his right index finger to move a joystick that is controlling the force applied to his left index finger by the lever. Again he should match the force that was previously presented. The participant is unaware of the parameters that link movement of the joystick and applied force. **(C)** Results from comparing the forces the participants judged to be matching the presented forces and the actual presented forces. Dashed grey line represents a perfect match. Participants consistently applied a greater force when they were matching the presented force directly with their right index on the lever, whilst when using the joystick, the external force was almost perfectly matched.

is that self-generated forces are perceived as weaker than externally produced ones, suggesting a possible sensory attenuation for self-touch: *"This could arise from a predictive process in which the sensory consequences of a movement are anticipated and used to attenuate the percepts related to these sensations"* [39].

For now, the conclusion we should retain from these experiments is that some sort prediction mechanism is being activated for every movement we make. The objective of such predictions is likely to be the one of attenuating the sensory sensations that will be aroused by the movement. Other purposes might underline this mechanism. However, these are the only conclusions we can take for now, based on these studies.

2.3.2 The Predictive Brain

The concept of a 'predictive brain' has been growing in cognitive neurosciences as one of the most important features of the brain. It mainly refers to the importance of anticipation and expectation in cognitive processes. As we have just seen in the preceding chapter, there is evidence supporting that the brain tries to predict the outcome of its actions. If we try to think about the reasons for why the brain would do this, we should consider that every action we take starts with a more or less concrete goal and that online predictions during such actions are a good way to control how the desired action is evolving [40]. In fact, it goes even further, as it can be used for distinguishing self-other actions [40].

The sensorimotor integration system provides a mechanism to address the prediction aspects of self-touch discussed in the previous chapter. According to Wolpert, the sensorimotor system should be viewed as an observer that constantly has the objective of estimating both its state and the state of the environment surrounding it [41].

Daniel Wolpert has in fact given several contributions to a possible internal model for sensorimotor integration [37, 41- 43]. He hypothesizes that this model should mimic the casual flow of a process, therefore, like a forward model. This model would consider the two knowledges described in the previous chapter, the motor command and the feedback information coming from the proprioceptive system [37]. As example, lets imagine an arm movement. Given a certain motor command and an initial state, the brain runs a copy of the motor command (efference copy) through a forward model of the arm's dynamics as a way to assess the next state of the arm. Following this process, the next state of the arm is used to determine the expected sensory feedback of this new arm position, thanks to a sensory output model. When both the sensory prediction and the real sensory feedback are available, they are compared and a difference between the sensations is obtained (figure 2.6) [37, 41, 42]. It is believed that this assessment has various purposes, alongside with the self-monitoring (through online predictions) mentioned before. When only small differences are detected, these sensory predictions are used to attenuate the incoming sensory feedback, as it is considered irrelevant (after all it came for the person's own actions) [42, 44, 45]. In the same

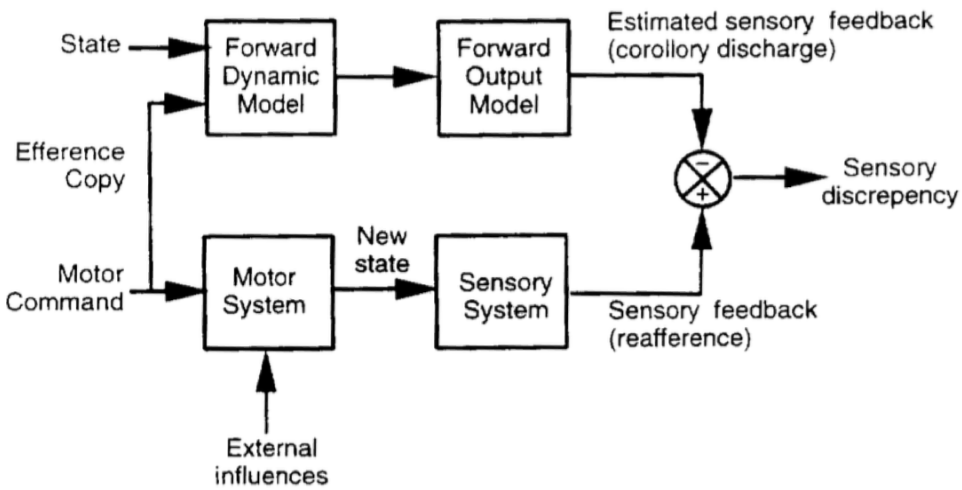


Figure 2.6 Internal Model for Motor Control
Adapted from Wolpert et al., 1996 [42]. The most accepted model for sensorimotor integration consists of a process that simulates real activity generated by a motor command. When a motor command arises, a copy goes through a forward model of the dynamics of the affected limb, taken into consideration the current state. The output, which is the resulting state due to the motor command is then used to predict the sensory consequences of such action. At the mean time, real sensory feedback has become available and the brain follows with a comparison of the real and predicted feedbacks. A sensory discrepancy is the final result of this process, being used for both state correction, model improvement and responsibility assessments.

situation, such small differences can also be used to improve the forward dynamic model [37]. Larger differences, mean that the predictions did not match the sensory input. In this scenario, no attenuation occurs and the stimuli is considered salient and possibly externally generated [40].

By constantly making predictions, the brain tries to continuously assess how its actions are performing and more importantly it is deciding which stimuli will be processed more extensively by analyzing the difference between the input and the prediction. It has been shown that expectations shorten perception time, speed recognition, interpretation of events, and allow the brain to prepare adequate reactions [40]. Moreover, in the case of a match between sensory feedback and sensory prediction, the brain does not need to devote time to an input if it is considered a non-salient stimulus. Mismatches on the other hand, require more focus from the brain to understand what went wrong or if an external action as acted upon one of the sensory systems. Furthermore, depending on the size of the discrepancy, it can be communicated to a higher level, making the person aware of something being 'wrong' [40]. In the specific case of self-touch, differences should always be of a very small order.

Finally, according to the present model, we hypothesize that timing is one of the most important considerations. These processes are constantly running for every simple movement a person does. They do not 'wait' for sensory feedback to be available beyond a reasonable time window, therefore, being delayed or the absence of incoming sensory feedback would be considered a mismatch [46, 47] and as consequence a salient stimulus to which the individual would become aware of [35, 40]. It is noteworthy that looking at illusions presented in previous chapters, both the RHI and the FBI work when the stimuli involved are presented in synchronous conditions.

From this chapter, we understand the basis of the mechanism that underlies how the brain identifies self-touch and by extension, a mechanism that contributes to BSC states, specifically to the self-identification aspect, mentioned earlier. Similarly to what was done by Frith in 2008, who linked relevant phenomenology of psychotic states with positive symptoms of psychosis and some of its mechanisms [53], we can create hypothesis on how relevant phenomenology of psychotic states can be related to the FoP. Also, by knowing how this predictive mechanism works we can use it to generate further illusions.

2.4 Psychosis and Psychotic States

In the preceding chapters, we have made several mentions to psychotic states and even stated that the FoP is related to psychosis. Studying the mechanisms of psychotic states, can therefore be helpful to understand the process that underlines the FoP.

Psychotic states are the main consequence of conditions that distort both thinking and perception [48]. Two known examples of such conditions are schizophrenia and bipolar disorder. A psychotic-like state, is the occurrence of a symptom associated with a psychotic state, on an otherwise healthy individual. This can happen for a multitude of reasons ranging from substance abuse to conditions where the body is pushed to the limit (such as minimal survival conditions) [49].

Psychotic symptoms are divided in positive symptoms and negative symptoms. The prior refers to psychopathologies of delusions, hallucinations, thought disorders, paranoia, among others that are the result of a diminished self-affection creating an exaggeration of otherwise normal human characteristics (e.g. inner speech perceived as external voices) [49, 50]. The latter refers to apathy, catatonic withdrawal, lack of communication and such other symptoms that can also be associated to depression [49]. Negative symptoms should not be associated with diminishment on affect or thinking, but rather with perplexity (hyper-reflexivity, de-automatization of movement) making patients always conscious of every tiny aspect of the actions they do (e.g. movements), which a normal person would naturally fail to report [50].

Going back to the Feeling of a Presence, why do we claim that its mechanisms are related to psychotic states and not to other types of phenomena? Body reduplications are the main core of Autoscopic Phenomena (AP) for example, which comprise a small group of mostly non-psychotic events. However, in all the main illusions of AP the individual is always conscious that what he/she is experiencing is not real [2]. Moreover, such reduplication is primarily visual [2]. This is not the case for the FoP. When this sensed presence appears, even if it mimics all the individual's movements he/she will not identify it as being a reduplication of their bodies [8, 9], but rather attribute it to an external agent [4]. We have seen this in chapter '*2.1 – The Feeling of a Presence*', with examples from case-studies and autobiographies where even though the sensed presence mimics the individual's body structure and movements, it is never attributed as the individual's own body. On situations of AP, individuals see a person identical to them mimicking them, but they clearly understand that they are seeing an abnormal reduplication of themselves. In the popularized scenario of OBEs, individuals usually see their body, from above, laying on the bed. In such conditions, self-location and first-person perspective are attributed to this new higher position but incredibly, self-identification remains with the seen physical body on the bed [2].

Attributing one's own actions to an external agent is also the case for several hallucinations in schizophrenic patients. Blakemore, proposes that hallucinations of alien control are in fact a consequence coming from poor timing of the brain's predictions, which ultimately result in perceiving the consequences of a movement before being aware of initiating it [10]. "*My fingers pick up the pen, but I don't control them. What they do has nothing to do with me*" [51].

Another reason to why we associate the FoP with psychotic states can be viewed in the light of the previously seen model for sensorimotor integration, presented in psychotic patients, as we will see in the next sub-chapter.

2.4.1 Prediction Deficits in Schizophrenia

The experiment discussed in chapter '2.*3.1 – Considerations on Self-Touch*', regarding matching an externally applied force had several follow-up studies. A Brief Report shed light in the functioning of sensorimotor integration processes in patients with Schizophrenia [52]. The matching force experiment was repeated in the same way, but this time healthy participants and patients with schizophrenia were recruited. Again, participants were presented with an external force applied by the lever sitting on top of their left index finger. They had to match this force in one of two ways, over several trials. Either they pressed directly the lever with their right index finger, making pressure on their left index finger, or they controlled with the right index finger, a joystick that moved the lever and therefore applied force on their left index finger.

The results of this experiment (figure 2.7), revealed that both groups of participants had a worse performance when trying to match the external force, by pressing directly on the lever that sits on top of their left index finger. This was expected and believed to be due to the sensory attenuation that was discussed in previous chapters. What is striking in this experiment, is that schizophrenic patients have a better and more accurate performance in the self-touch condition when compared to healthy subjects. Such performance is indicative that schizophrenic patients have less sensory attenuation when performing self-touch, which most likely is the result of impaired sensory predictions [52]. Not having the same level of sensory attenuation as healthy people, allows them to better judge the force they are imposing on their own finger. Unfortunately, as we have seen on chapter '2*.3 - Sensorimotor Integration and Self-Touch*', these sensory predictions can be used to attenuate incoming sensory input from self-generated actions [42] and as a result ignore these non-salient stimuli [40]. By having low sensory attenuation, we can construct a strong hypothesis saying that in schizophrenic patients, some poorly-attenuated self-generated stimuli is considered salient or external by the brain, contributing to a bad performance in judging one's actions as their own, leading to a diminished self-affection, which in its turn can be responsible for psychiatric symptoms [10, 50, 53].

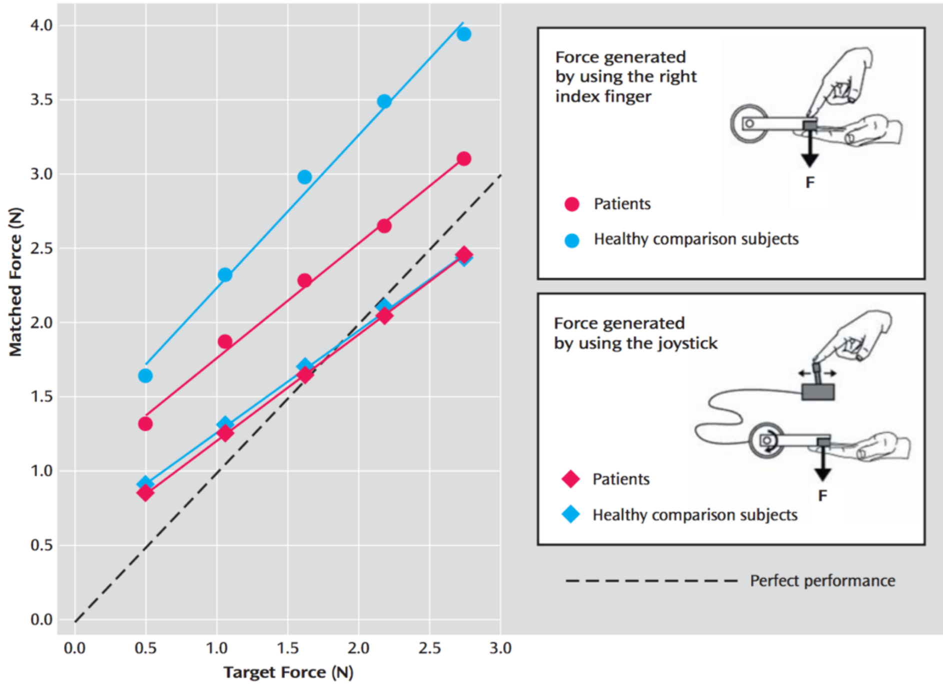


Figure 2.7 Matching Force Task with Healthy Participants and Schizophrenic Patients
Adapted from Shergill et al., 2005 [52]. Healthy participants and schizophrenic patients were required to match an external force to their left index fingers, by either pressing the lever on top of the left index finger or by controlling a joystick that made the lever move. Healthy participants were worse in this task when compared to the patients. This data seems to suggest that schizophrenic patients have a weaker sensory attenuation when performing a condition of self-touch.

2.4.2 Proposed Mechanism for the FoP

The mechanisms of bodily self-consciousness do not work as they are supposed to for everyone. Malfunctions at the level of sensorimotor integration are likely to generate problems such as a poor sense of self, poor agency and due to that, some of the positive symptoms seen in psychotic states [52-54].

The causes for the FoP are still quite debated, however, if we consider, that the phenomenology of the FoP points to bodily-self disturbances [4, 9, 32], the sensorimotor integration problems associated with psychosis in schizophrenia [52, 54] and the fact that the FoP has been induced with sensorimotor mismatches [1] (chapter 3 'State of the Art'), it seems feasible to say that the FoP is mostly a problem of misattributing one's own bodily signals, considering them as external ones coming from current daily life, i.e. self-touch from external touches. With this in mind, we advance the hypothesis that the FoP might be derived from a misinterpretation of one's own actions, with a cause that might be similar to the impairment of the sensory predictions of the sensorimotor integration model in schizophrenic patients [1, 9]. We also purpose in advance a general and hypothetical flow of events that leads to the FoP, in accordance to the literature on psychotic symptoms and the observed phenomenology.

We suppose that the FoP starts with deficits in sensory predictions of self-generated actions, which then leads to the misinterpretation of one's own actions. This misinterpretation causes a poor sense of self, which is in general responsible for the attribution of one's action to external parties, thus generating the FoP.

Please note that this is one of the proposed hypothesis for a FoP mechanism based on its phenomenology, analysis of similar bodily-self disturbances and psychotics symptoms related to the body, currently being investigated by the Laboratory of Cognitive Neurosciences.

3 State of the Art

The Feeling of a Presence is a quite new topic to be addressed by Neuroscience in such an experimental way. Although its descriptions date from more than one century ago, it has never been experimentally self-induced in a controlled environment, mainly due to its unpredictable nature and short duration. This was achieved for the first time in healthy subjects, two years ago here in the Laboratory of Cognitive Neurosciences from the Center of Neuroprosthetics of the EPFL, with resort to a robotic system. The idea for the experiment we are about to address came after five spontaneous reports from different participants saying they had a feeling of a strange presence close to them when performing a variant of the Full-Body Illusion that was supposed to be self-induced.

Considering this is quite recent and that several articles are currently in preparation, the state of the art on the induction of the Feeling of a Presence on healthy subjects is quite limited.

3.1 Robotically-Induced Psychotic-Like State

A recent study from Olaf Blanke [1] managed to induce for the first time in healthy individuals, a specific symptom of some psychotic-states, the Feeling of a Presence. This was achieved through sensorimotor mismatches.

This study made use of a master-slave robotic system, controlled by the participants, in order to induce the FoP. Participants (blindfolded and noise isolated) had to perform tapping

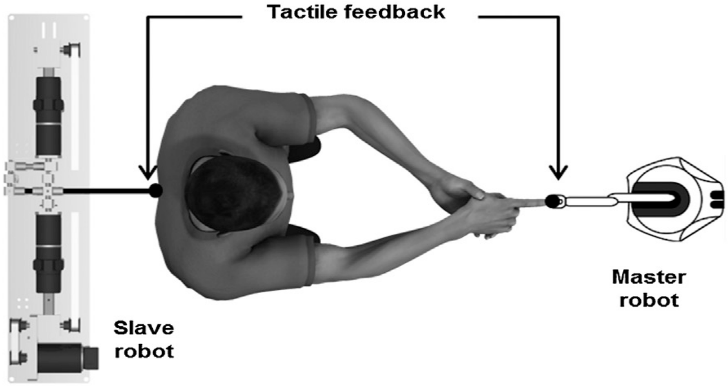


Figure 3.1 Setup Design for the FoP
Adapted from Blanke et al. 2014 [1]. A participant manipulates the master robot that stands in front of him, attached to his finger. Movements in any of the three axis (x, y, z) are transmitted to the slave robot behind exactly at the same time, or with a delay of 500 msec. The participant will feel a force feedback on his finger, from the touch on the back performed by the slave robot, depending on the protocol.

movements in the space in front of them with the master robot attached to their index finger. By doing so, the slave robot reproduced each movement behind the participant, touching their back (figure 3.1).

This was performed with different protocols: synchrony vs. asynchrony, where asynchrony comprehends a 500 millisecond temporal mismatch between the participant's movement and the touch on the back, combined with presence of force feedback on the index finger when a touch on the back happened versus the absence of such feedback. The FoP occurred clearly in the scenario that generated more sensorimotor conflicts, which was asynchronous stimulation without force feedback (figure 3.2 A).

Researchers also performed a numerosity judgment task, to assess if it was possible that the Feeling of a Presence was an effect of suggestion due to the questionnaires. When entering the room participants (new participants) would see four other people and be informed that at any given time during the experiment one or more of these people could approach the area of the experiment. During the sessions, researchers would ask the blindfolded and noise isolated participants to report how many people they felt were close to them. Participants significantly judge that more people were close, when experiencing the asynchronous condition (figure 3.2 B). No one actually approached the participants at any time, which assures that the only difference between conditions was truly the synchrony protocol being used.

It is also a conclusion from this study, that the FoP in psychotic patients is most likely caused by sensory impairment due to lesion or misinterpretation of the biological input signals [1] (in healthy people could be caused for example by extreme conditions [7]), meaning that by misinterpreting your own actions (in this case poking yourself on the back) you attribute them to something or someone else in the environment. It is evident for example in cases of schizophrenia that some stimuli (eg. proprioceptive stimuli) are not correctly assessed

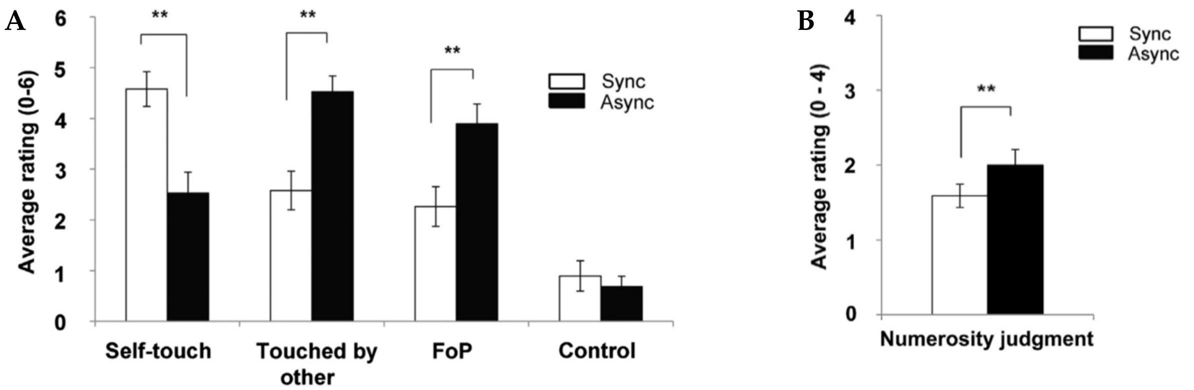


Figure 3.2 Questionnaire Results from Blanke et al. 2014
Adapted from Blanke et al., 2014 [1] **(A)** Results from the questionnaire applied to assess Self-touch and FoP during part of the study from Blanke et al. 2014. Participants rated the FoP significantly higher in asynchronous condition (as well as touched by other). Self-touch followed the opposite trend. **(B)** Numerosity task (regarding the question: *How many people do you feel close to you?*), reveals that subjects significantly report more people being close to them under the asynchronous condition. Note that, there was never anyone close to the participants.

(**) Significant differences between synchronous and asynchronous conditions, with $p < 0.01$.

by the brain as belonging to the person. As they are still inputs coming to the brain they need to be interpreted even if wrongly, which eventually might lead to the attribution of certain self-produced stimuli to an external agent [1, 7, 52, 54]. In the case of the Feeling of a Presence this is mostly associated with lesions occurring on the insular, frontoparietal and temporoparietal cortexes [1] (figure 3.3).

All of these brain regions have important roles in Bodily-Self Consciousness aspects. The Insula has for a long time been suspected of being related to the awareness of one's own body inputs and therefore directly connected to Bodily Self-Consciousness [55]. It is also connected to some addictive behaviours and sudden realizations of logical realities [56]. Regarding the Frontoparietal cortex it is essential for somatosensory associations and it's debated its importance in controlling essential aspects of spatial attention [57]. In its turn the Temporoparietal Junction is related to the interpretation of human thoughts and cognition, especially as in the presence of another person [58]. The study we are addressing also compared psychotic FoP-patients against control psychotic patients. By performing lesion analysis and crossing the two groups, the study points out the main responsible for the Feeling of a Presence seems to be more specifically the frontoparietal brain regions [1].

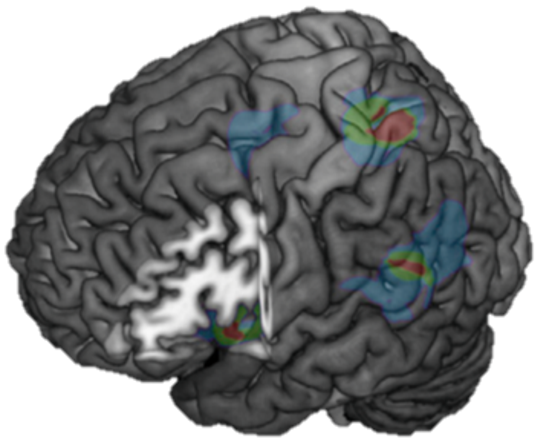


Figure 3.3 Lesion Overlap Analysis for FoP Patients
Adapted from Blanke et al., 2014 [1]. The analysis of the lesions which overlapped in the case of FoP patients revealed three regions, being them, the temporoparietal cortex (Brodmann area 22), the frontoparietal cortex (Brodmann area 7) and the insula (Brodmann area 48). Blue: Three patients; Green: Four patients; Red: Five patients. The regions previously described correspond to the maximum number patients in the overlap analysis (5).

4 Background in Electroencephalography

Electroencephalography (EEG) is a technique used to record the electrical fields of the brain. To do so, it makes use of electrodes placed on a person's head, alongside with one or two electrodes that serve as references for the rest (figure 4.1 A-B) [59]. Its applications are mostly related to academic research in the field of cognitive neurosciences, such as the topic being approached on this thesis. However, EEG is also used by clinicians in specific situations ranging from epilepsy diagnosis to the identification of sleep disorders [60]. More recently, EEG has become an essential part of brain computer interfaces, allowing people to control computer programs or some pieces of hardware by performing certain mental tasks [61].

The reason why EEG is vastly used in cognitive neuroscience lies with the anatomy of behaviour and cognitive processes, and with the time resolution it provides. Starting with the former, these processes are not specific to small groups of neurons but rather to brain regions and to the interaction between different brain areas. Considering the size of the brain regions involved, an assessment at a larger scale, such as the one EEG provides, is fortunate. A modern EEG equipment can be specific enough to record 10 million neurons at a 1 cm scale. Even if the tendency in EEG is to reduce this number, as to improve spatial resolution, it is definitely considered a large-scale measurement when comparing with microarrays and intracranial recordings. This type of scale allows researchers to run analysis for activity, coherence, interconnectivity between regions, or other types of analysis [60]. A more simple analysis of an electroencephalogram could even be performed by a naïve user. When seeing the EEG of a person with eyes open or closed one can clearly notice the increased activity of alpha waves

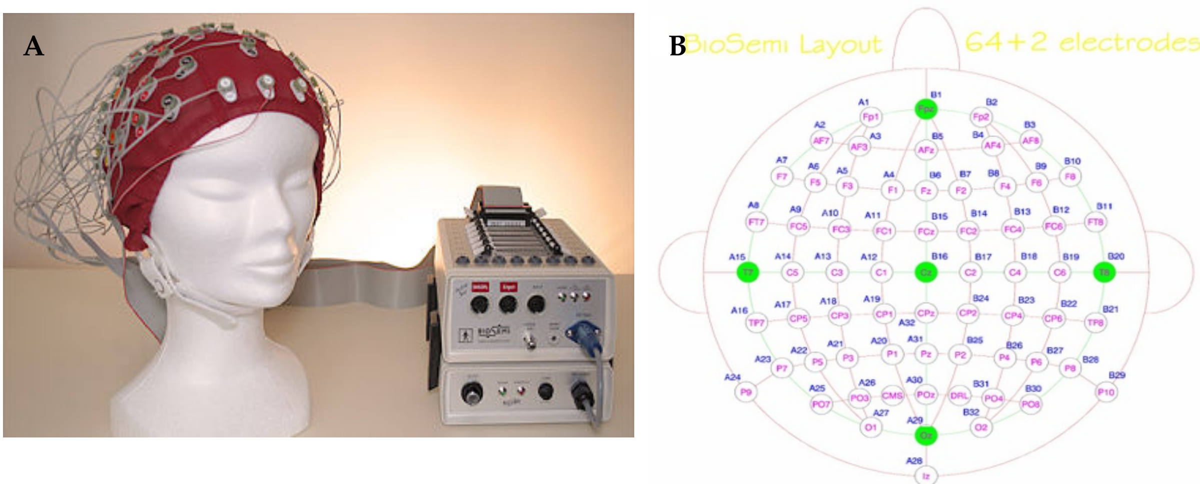


Figure 4.1 Electroencephalography Apparatus
(A) Head Model using a 64-biosemi EEG. On the right side the battery and amplifier are in view. **(B)** 10/20 Layout for the 64 channels EEG depicted on (A), with the references identified as CMS and DRL.

in the latter case. Finally, considering timing, EEG provides a millisecond resolution appropriate for accompanying the development of most cognitive processes.

4.1 EEG and Neurophysics

The EEG is not sensible to a single neuron's activity nor to action potentials. As we have seen before, a reasonable goal for an EEG detects around 10 million neurons in the 1 cm scale. In fact, a single electrode placed on the head would report feedback from around half a billion neurons [60].

The electrical fields detected by the EEG are generated by large groups of neurons located on the human brain cortex, the pyramidal neurons [62]. These neurons are arranged in palisade-like structures, resulting in aligned main dendritic trees all perpendicular to the cortical surface (figure 4.2 A). When activated synchronously by post-synaptic activity, the resulting electrical field can be detected at a distance from the source [63]. Interestingly the EEG is not sensitive to this post-synaptic occurrences, at least directly. What the EEG detects are the extracellular currents generated by post-synaptic activity [60, 63].

Synaptic activity is most of the times the main source of extracellular current flow. Both dendrites and soma of a neuron form a tree-like structure where thousands of synaptic-sites are located. Excitatory currents for example are responsible for the influx of cations to the intracellular mean, while a return current balances the extracellular medium with a flux of the opposite charge (negative). A dipole (or higher order) is now formed (figure 4.2 B) and can be picked up by an electrode up to a certain distance [64]. On the contrary, action potentials on a neuron's axon are a very small contributor to the extracellular medium in a global perspective, mainly due to the lack of synchrony between neurons when such events occur and to their small duration (< 2 msec) [64].

A B

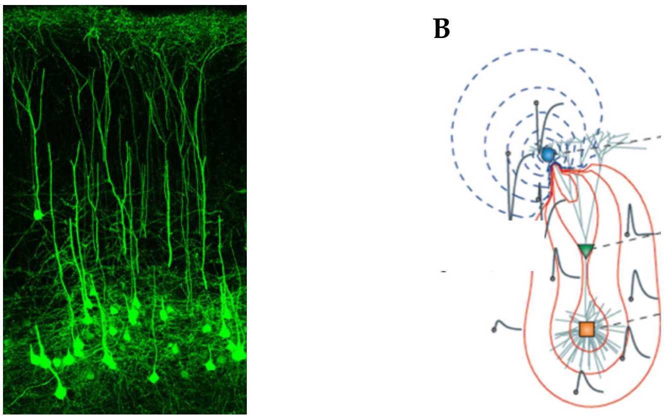


Figure 4.2 Depictions of Pyramidal Neurons
(A) Retrieved from University of Tennessee Health Science Center, Neuroscience Institute. Somatosensory cortical area pyramidal neurons and their apical dendrites labeled with yellow fluorescent protein. Image was taken with a 40X oil objective. **(B)** Adapted from Nunez et al., 2006 [61]. Depiction of the effects on the extracellular medium when an excitatory current input is presented to the apical dendrite in the blue circle. The blue dotted line represents the negative equipotential lines while the red line is the positive equipotential.

5 General Methods

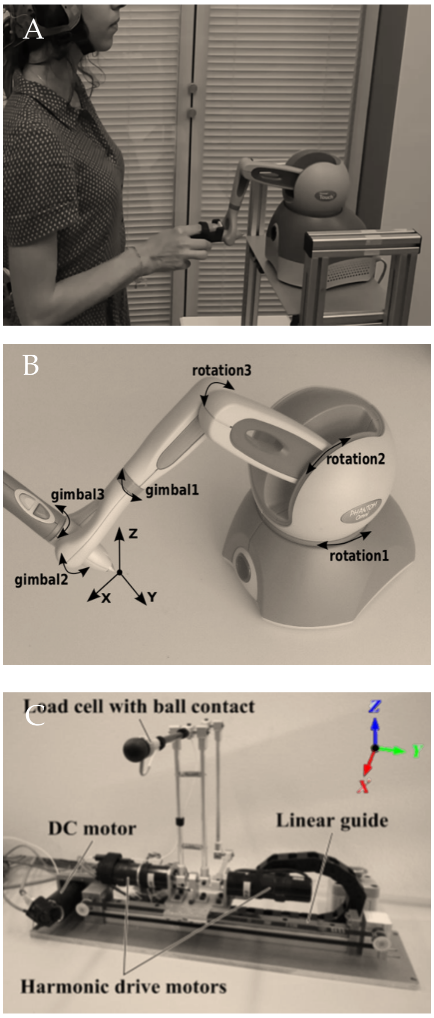
To induce the Feeling of a Presence as described previously in the state of the art and within the bases of self-induction, our paradigm follows a similar approach to the one used in Blanke et al., 2014 [1]. In this study, healthy participants manipulated a robotic system that allows them to stimulate their own back. Such manipulation was previously done either synchronously or asynchronously, with only one protocol of temporal mismatch. As there is compelling evidence pointing in the direction that the temporal mismatch between the manipulation performed by the participant and the actual touch on the back is one of the main factor making this sensation arise [1, 37], we wanted to investigate the temporal dynamics of the FoP. To do so, we used a wider range of temporal mismatches that includes the two used in the previous study and every 100 msec step between them. Ultimately, this means, 0 msec, 100 msec, 200 msec, 300 msec, 400 msec and 500 msec of delay.

Two experiments were performed to test this hypothesis. Experiment 1, a behavioral experiment aimed at understanding the temporal dynamics of the FoP and Experiment 2, an EEG imaging study focused on identifying the brain regions responsible for the different subjective experiences of the FoP. The results of Experiment 2 allow the same behavioral analysis done in Experiment 1. In this chapter, we present the methodology, setup and paradigm for both experiments.

5.1 Robotic System

The robotic system is composed by two robots in a master-slave fashion and an interface controlling the interaction protocols between the two. These protocols are the temporal mismatches (delays) used between the movement on front executed by the participants and the touch on the back performed by the slave robot. Force feedback on the finger was always present.

The master robot is a commercial master haptic interface, Phantom Omni SensAble Technologies (figure 5.1 A-B). This robot has a range of movement equivalent to a hand movement pivoting at the level of the wrist, with the possibility of arm allocation, from the center, of 280mm to each side, 170mm down, 300mm up and 210mm from being completely stretched to hitting the virtual wall (force feedback generated by touching the back) in front. Regarding the force feedback, the robot is capable of exerting it at any of the three axis, with mechanical strenght limitations. The slave robot (figure 5.1 C-D) is a patented three degree-



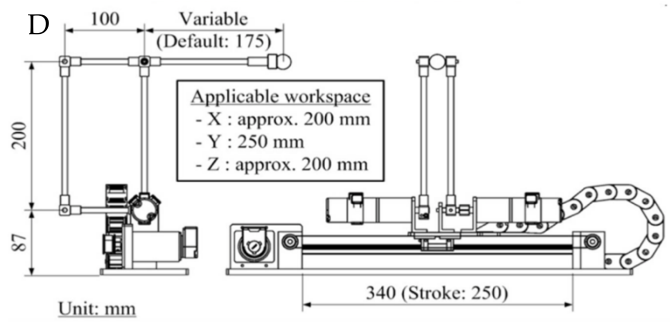


Figure 5.1 Illustrative Examples of the Master-Slave Robotic System
(A) Realistic depiction of master robot being pivoted at the level of the wrist, with arm movement, by a blindfolded participant. The surface on which the robot rests can be adjusted for the height of the subjects. **(B)** Detailed description of the joints of the master robot. Rotations 1, 2 and 3 allow for most of the free movement on the three familiar axes x, y and z, whilst gimbal 1, 2 and 3 allow some movement and rotation at finger level. Although these last movements do not contribute directly to the task movement, they allow for a fluid and natural movement during the pokes. **(C)** Realistic depiction of the slave robot. The ball contact is the part of the robot that touches the subjects on the back. In color, the three movement axis of the slave robot. Not represented here, the slave counterpart also stands in a height adjustable surface. **(D)** Technical representation of the slave robot. Default contact arm (identified as variable) was maintained throughout the experiments. Workspace of the robot is described for each axis in the middle.

of-freedom slave-robot which exact specifications should be consulted in the supplemental information from the 2014 paper [1a]. Regarding the amplitude of movements, it is 200mm in the x direction, 250 in the y direction and 200mm in the z direction. The interface controlling this system is programmed in Visual C++ with a sampling rate of 1kHz. The standard delay between the master robot and the slave counterpart is the time required to map the master's movements and establishing the slave's movements, which is close to 1 msec.

5.2 Participants and Ethical Statement

For Experiment 1, 12 healthy participants were recruited (5 males, mean age 26 [SD ± 5.2] years, all right-handed) and successfully took part in the experiment.

For Experiment 2, 21 participants were recruited. Ultimately, 19 subjects (8 males, mean age 25 [SD ± 4.7] years old and all right-handed) took part in the experiment successfully. None of the subjects reported a history of neurological or mental disorders, or brain injuries. As rejection criteria, we had decided that any participant not experiencing the FoP or having it at very residual levels in the second sessions of the experiments, would have to be excluded from the analysis as there would be no conditions of interest to compare.

Both experimental protocols were approved by the Cantonal Ethical Commission of Genève (GE 15-273). Standard protocols laid down in the Declaration of Helsinki were also followed. All subjects received a compensation of 20.- CHF/hour for their commitment to the experiment.

5.3 Experimental Design

Experiment 1 is composed by two sessions, whereas Experiment 2 is composed by three sessions, being the first two, the same ones as in Experiment 1. The two experiments take place in a sound attenuated room with dimmed lighting. Participants are blindfolded and listening to white noise via headphones throughout the sessions. All the experiments are designed in MATLAB (The MathWorks, Inc.) and stimuli are controlled and presented to the participants using the Psychophysics Toolbox [65] for increased accuracy.

5.3.1 Experiment 1

The first experiment, has the sole purpose of behaviorally assessing the temporal dynamics of the FoP, before starting an imaging study. This is done with two sessions, the first one to replicate some of the results from Blanke et al., 2014 [1], and the second session to address our new objective.

5.3.1.1 Session 1 – Familiarization

Session 1 takes place at the beginning of the experiment and it is aimed at familiarizing the subject with the self-touch robot. This session is divided into two blocks of two minutes each, in which the subject is asked to do poking movements using the master part of the robotic system, which will then make the slave robot touch their backs mimicking their movements. In one of the blocks the slave robot is functioning in synchrony with the master part so that the participant feels the touch on the back and the force feedback on his finger at the same time. The other block requires the participant to perform the same sensorimotor integration task, but this time a temporal mismatch of 500 msec between the poking movement and the touch on the back is present. The blocks in session 1 are presented to the participants in a pseudo-randomized fashion to avoid the introduction of any bias, such as an effect due to the order in which the synchronous and asynchronous conditions are presented. At the end of each block, it is required from the participant to fill in a small questionnaire (table 5.1) regarding subjective sensations he/she might have experienced throughout the block. These questionnaires were mainly used as a control to assess that the FoP was indeed being induced (refer to Q7).

Table 5.1 Questionnaire presented after each block of the first session
The identifier in the first column refers to the order in which the questions were presented. On the middle column, we can see the question itself. On the last column, we see what each question evaluates. The order of the questions was randomized before the first subject and then remained the same for all the remaining subjects. Each question was graded in the sense of how strong the sensation was, on a scale going from 0 to 6 being 0 "not at all" and 6 "very strong".

Identifier	*Questions*	*Assessment*
Q1	"I felt as if I had no body"	Control for suggestibility
Q2	"I felt as if I was touching my body"	Self-touch
Q3	"I felt as if I was touching someone else's body"	Contrast to the one above
Q4	"I felt as if I was behind my body"	Self-location
Q5	"I felt as if I had more than one body"	Control for suggestibility
Q6	"I felt as if someone else was touching my body"	Touched by Other
Q7	"I felt as if someone else was standing behind my body"	FoP
Q8	"I felt as if I was standing in front of my body"	Self-location

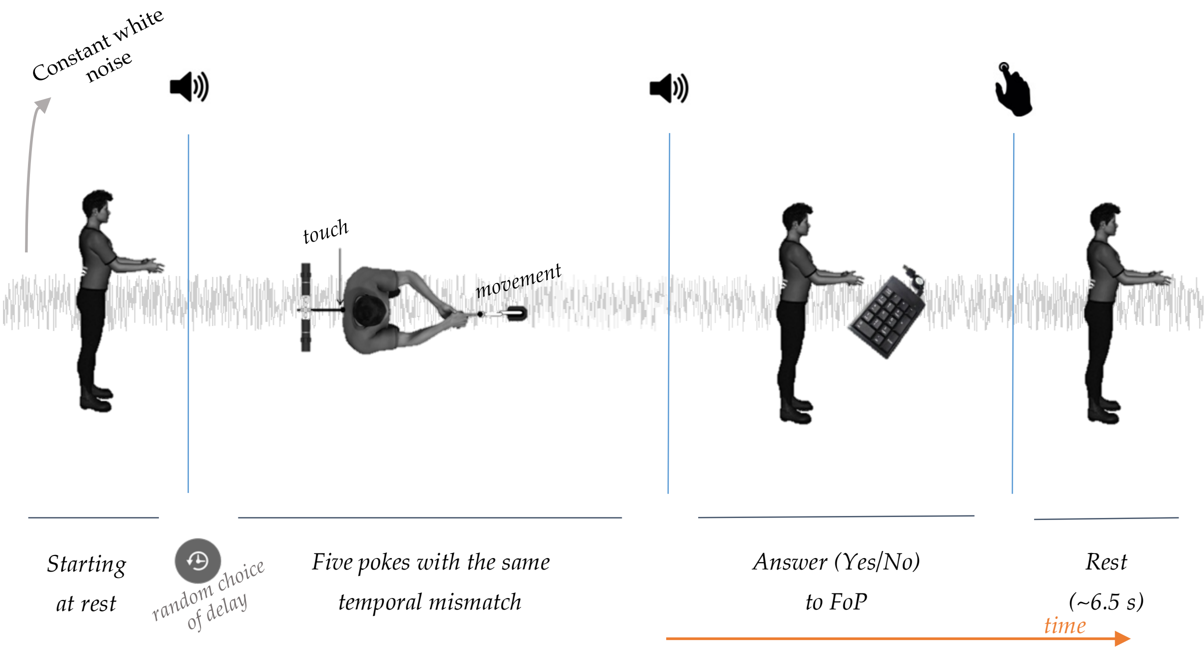


Figure 5.2 Experimental Design - General Representation for One Trial
A participant is blindfolded and hearing constant white noise throughout all the experiment. A vector of delays is randomized prior to each block. Starting at rest, the participant hears a beep with a frequency of 400 Hz for 0.1 seconds on top of the white noise to know that he can start doing poking movements with the master robot, which will then make the slave counterpart touch their back. The participants are instructed not to count the number of pokes. After 5 pokes, another beep is heard (equal to the one before) and the participant stops moving and stands in a position where he doesn't make the slave robot touch his back. He then answers to the question 'Did you feel as if someone was standing behind your body and touching you on the back?' by pressing either 1 (Yes) or 2 (No) on a small keyboard that lies below his left hand. After the button press, there is a waiting period of 6.5 ± 0.5s before the start of a new trial. This happens 30 times per block. In the end, each of the six delays was presented 5 times to the participants (per block).

5.3.1.2 Session 2 – Temporal Dynamics of the FoP

Session 2 takes place right after session 1 and it has 6 blocks. Each block is composed by 30 trials (figure 5.2), which consist of a moving task similar to the one performed in session 1. Trials are initiated by an auditory cue presented on top of the white noise (beep at 400Hz lasting 100 msec, with volume twice as high as the white noise), after which the participant can start to do poking movements on the front, which will generate a touch on the back with a certain delay (remains the same for a full trial). After 5 pokes against the back are counted by the system (participants are instructed not to count the pokes they execute them) a second beep is heard so that the participant stops doing these movements and places his hand and forearm in a way that he is not making the slave counterpart touch his back. The question "Did you feel as if someone was standing behind your body and touching you on the back?" presented verbally to the participants in the beginning of each block is now answered, by pressing buttons 1-Yes or 2-No on a keyboard that stands below the participant's left hand during the all session. Each trial finishes with an answer to this question. After 6.5 seconds (±0.5s) another beep is heard marking the start of a new trial. In case it was the last trial, 5 consecutive beeps are heard in a sequence marking the end of a block. Between blocks participants rest for about 3 minutes. The question to which the participants answer after each 5 pokes is repeated in the beginning of each block.

To be sure that the participants understand the task correctly, six test trials are done in the beginning, one for each delay. In the end of the experiment the trials sum up to 30 per delay, which means about 150 poking movements per delay.

5.3.2 Experiment 2

Experiment 2 was performed after analyzing the results from experiment 1. The main objective of this experiment was to assess the neural correlates of the Feeling of a Presence, deploying EEG and using the same protocols from experiment 1.

Because in this experiment we can also extract the same kind of behavioral results as in experiment 1, the behavioral results from both experiments will be analyzed together in subsequent chapters.

5.3.2.1 Session 1 – Familiarization

This session is identical to the first session of experiment 1, with a slight change in the questionnaire. Participants perform two blocks of two minutes each, randomly starting with either the synchronous or asynchronous condition. The questionnaire presented to the participants after each block, contained only questions Q1, Q2, Q6 and Q7 (refer to table 5.1). Replicating the FoP results from Blanke et. al 2014 [1], could be done with less questions and this way we could also reduce the overall time of this long experiment.

5.3.2.2 Session 2 – Temporal Dynamics and Neural Correlates of the FoP

This session is performed the same way as the second session of experiment 1, but participants are fitted with an EEG system. Participants are blindfolded and listening to white noise via headphones, and take part in 6 blocks composed by 30 trials, in which each trial starts with an auditory cue with a frequency of 400Hz (double volume comparing to white noise) so that the participant knows he can start doing poking movements. After five pokes are performed, a second beep denotes that the participant should now stop and answer the question that was presented to him verbally in the beginning of the block, "Did you feel as if someone was standing behind your body and touching you on the back?". This answer is given by pressing either 1 or 2 (Yes, No) on a keyboard resting below the participant's left hand (figure 5.2). After a resting period of approximately 6.5 seconds another beep will mark the beginning of a new trial, or a sequence of 5 beeps will mark the end of the block.

5.3.2.3 Session 3 – EEG Controls

The aim of this session is to create controls for the EEG data collected. It is composed by 2 blocks of 3 minutes each. In both blocks of this session participants are still blindfolded and listening to white noise via headphones. The blocks are presented to the participants in a pseudo randomized order.

In one of the blocks the participant (standing on the same place as before, without moving) is touched on the back by the slave counterpart of the robotic system, which is now being controlled by the experimenter. This is useful for assessing external touch by the robotic slave counterpart. The other block consists of doing the poking task without having tactile responses on the back (there is still force feedback on the finger). This serves the purpose of analyzing the ERP due to the poking movement and correspondent feedback on the finger. For this block we instruct participants to try and replicate the movements at the same pace as session 2.

6 Temporal Dynamics of the Feeling of a Presence

In this chapter, we present the methods for analyzing the behavioral data collected in the first and second sessions of both experiments, followed by the actual results and a discussion on this topic. We chose to present the behavioral results of both experiments together as to better compare them.

6.1 Behavioral Data Analysis

6.1.1 Questionnaires

To assess the results obtained from the questionnaires performed at the end of the first session of each experiment we used MATLAB's integrated statistical toolbox.

First the answers to the questionnaires were ipsatized, by performing a z-score with the answers of the two conditions put together. This is a general process for data standardization where at each observation, the mean is subtracted and the result is divided by the standard deviation. Then a two-sided t-test was applied to each question to assess statistically significant differences between the mean of the answers of the synchronous and the asynchronous conditions, being 0.05 the threshold for significance.

6.1.2 Psychometric Curve

To analyze the answers to the question 'Did you feel as if someone was standing behind your body and touching you on the back?', which assess the subjective experience of the FoP, we did a psychometric curve fitting evaluation using MATLAB's integrated curve fitting toolbox. This was followed by a one-way [1X6] ANOVA (Factor: delays). The ANOVA (Analysis Of VAriance) is used to analyze if the means among groups divided according to their specific characteristics, are equal or not, therefore generalizing the t-test for more than two groups. Individual two-sided t-tests followed this analysis, as a way to assess for statistically significant differences in terms of FoP rating between neighboring delays.

6.2 Behavioral Results

6.2.1 Experiment 1

The statistical analysis performed on the questionnaires done after each block of session 1, using two-sided t-tests, revealed no statistically significant difference between the synchronous and asynchronous conditions (figure 6.1 A). A trend was observed for Q2 – "I felt as if I was touching my body" ($p = 0.12$), pointing in the direction that participants might feel 'more' self-touch in the synchronous condition.

Regarding the answers to the question 'Did you feel as if someone was standing behind your body and touching you on the back' on session 2, there was a significant increase in answering Yes to the question assessing the FoP with the increase of the temporal mismatch (1x6 ANOVA with $p < 0.025$, figure 6.2 A). The perceived Feeling of a Presence started at 35.85% without any delay and grew until 65.55% with the maximum temporal mismatch used. The point of subjective equality (PSE, 50%) for the FoP was situated at 206 msec.

6.2.2 Experiment 2

The statistical analysis performed to the questionnaires done after each block of session 1 (figure 6.1 B), using two-sided t-tests, revealed significant statistical difference between synchronous and asynchronous conditions for questions Q6 - 'I felt as if someone else was touching my body' ($p < 0.05$) and Q7 – 'I felt as if someone else was standing behind me' ($p < 0.05$). The remaining questions did not show any significance. Once again Q2 – 'I felt as if I was touching my body' showed a trend ($p = 0.15$) to having more self-touch in the synchronous condition.

Regarding the answers to the question 'Did you feel as if someone was standing behind your body and touching you on the back' on session 2, there was a significant increase in answering Yes to FoP with the increase of the temporal mismatch (1x6 ANOVA with $p < 0.001$). At no delay, the perceived FoP was 33.45%, growing until 72.55% with for a delay of 500 msec. The PSE for the FoP was situated at 278 msec (figure 6.2 B).

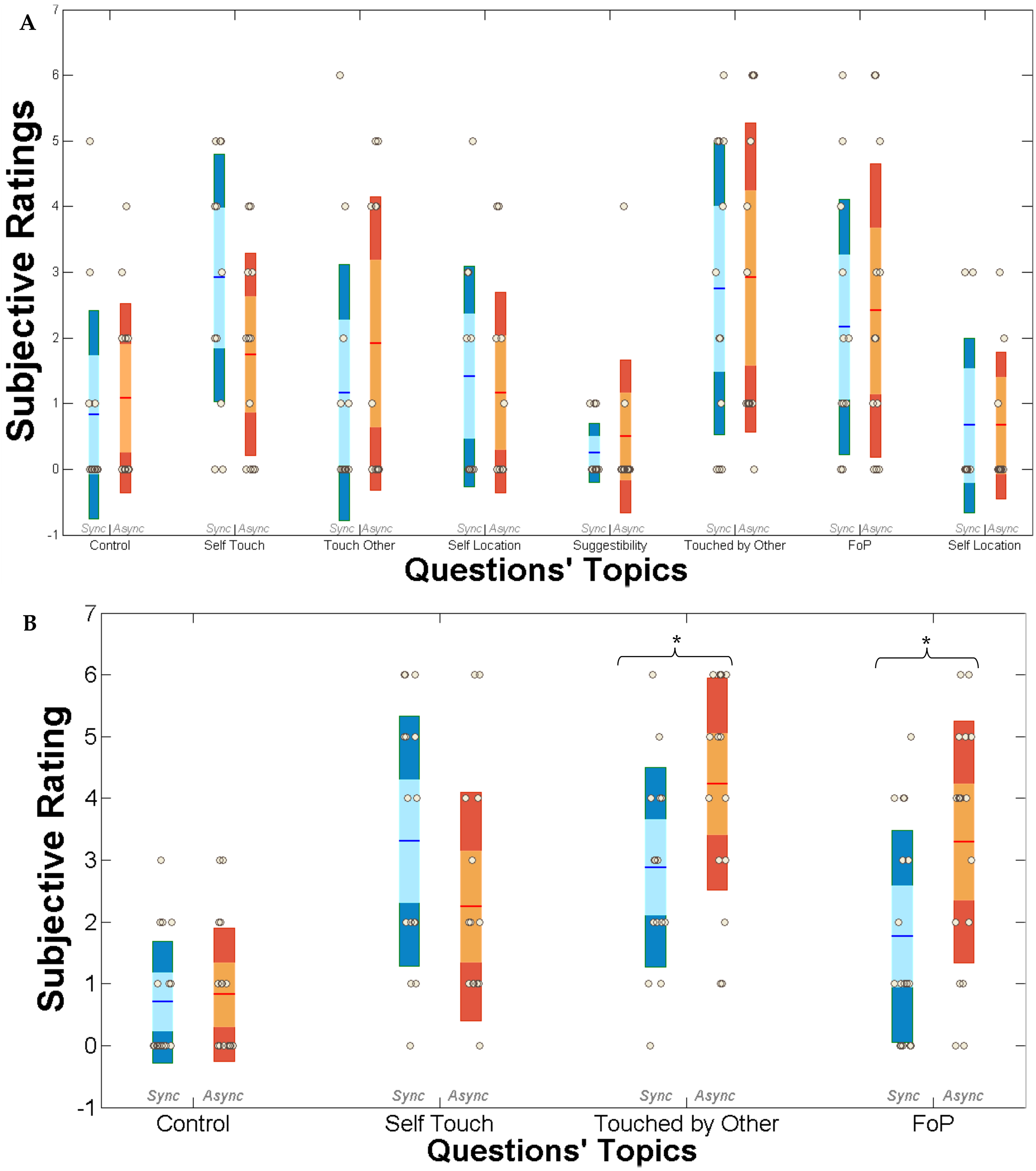


Figure 6.1 Results from the Questionnaires from the First Session of Experiments 1 and 2
The questions' topics refer to the assessment made by each specific question (see table 5.1). The sub-figures are plotted in such a way that the blue patterns refer to the synchronous condition and the red patterns to the asynchronous condition (as it is described below each bar, in grey). On that note, the mean for the scores of each question are in blue (line) for no delay and red (line) for 500 msec of delay, the 95% confidence interval of the mean is in light blue (box) for no delay and orange for 500 msec of delay (box), the standard deviation is in blue (box) for no delay and red (box) for 500 msec of delay. Single subject for each question and condition are plotted in grey.

(A) Raw results from the questionnaires applied in the first session of experiment 1 (N = 12). From the statistical analysis of the normalized data no question shows a statistical difference at a $p<0.05$ level. **(B)** Raw results from the questionnaires applied in the first session of experiment 2 (N = 19). From the statistical analysis performed on the normalized data, only the questions assessing being touched by other and the FoP (Q6 and Q7) show a statistically significant difference.

(*) Statistical analysis to the normalized data with a two-sided t-test reveals significant different answers with $p < 0.05$

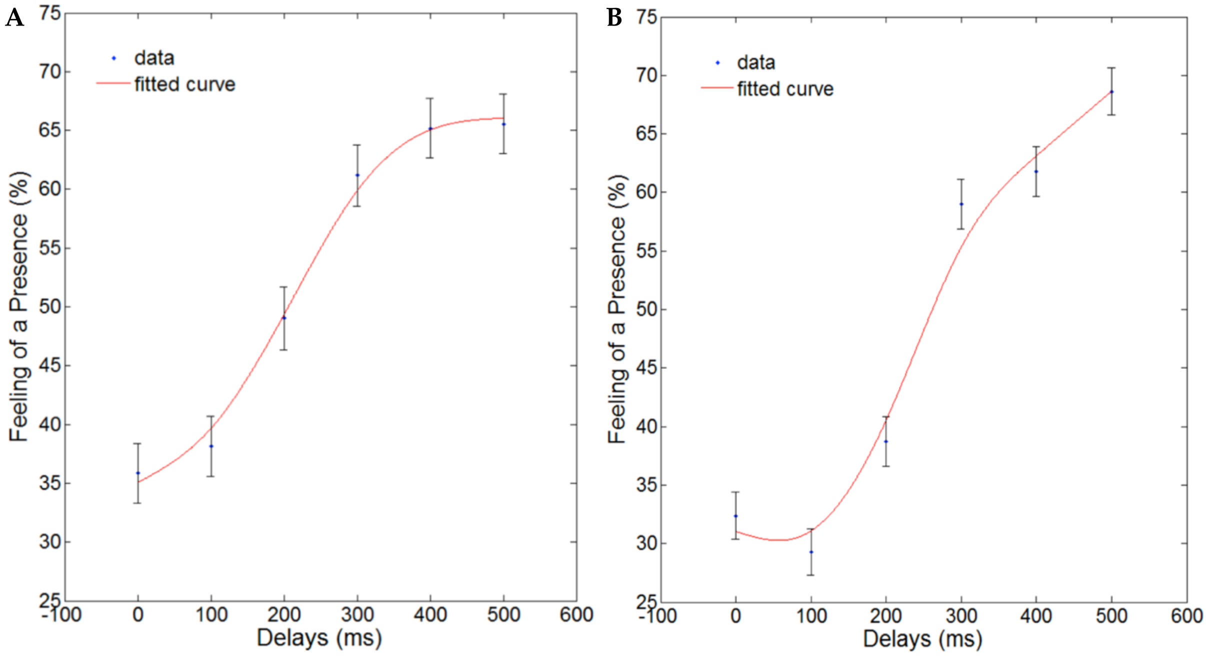


Figure 6.2 Behavioral Performance from the Second Session of Both Experiments
The blue dots represent the mean of all the participants for each delay. The black error bars represent the standard deviation of the mean and in red the fitted curve using the method smoothing spline for the curve fitting toolbox of MATLAB.

(A) Percentage of FoP experienced at specific delays, as the mean of all participants, for the second session of experiment 1 (N = 12). The fitted curve is sigmoidal, starting around 35% of FoP up to 65% for the highest delay. The point of subjective equality is situated at 206 msec. Statistical testing resorting to a [1x6] ANOVA (Factor: delays) shows that delay has a significant effect on answers to the FoP ($p < 0.05$). **(B)** Percentage of the FoP experienced at specific delays, as the mean of all participants, for the second session of experiment 2 (N = 19). The fitted curve is sigmoidal, starting around 32% of FoP up to 70% for the highest delay. The point of subjective equality is situated at 278 msec. Statistical testing resorting to a [1x6] ANOVA (Factor: delays) shows that delay has a significant effect on answers to the FoP ($p < 0.001$).

6.3 Behavioral Discussion

The first session of both Experiment 1 and Experiment 2 aimed at replicating some of the results observed in Blanke et al. 2014 [1], primarily the significant differences on the subjective experience of the FoP observed between the paradigm with no delay and the paradigm with 500 msec of delay. This objective was achieved only in the first session of experiment 2 for both questions that assessed the FoP. We believe that the analysis performed for experiment 1, lacked power due to the low number of participants (N = 12). Nevertheless, replicating these results in experiment 2 shows that the high asynchrony generated by the 500 msec of delay (as opposed to no delay) can generate differences in the subjective experience of the FoP.

Regarding our main objective assessed with session 2, we have showed that it is possible to induce the Feeling of a Presence at different delays, resulting in the pattern of a sigmoidal curve. Just by increasing the delay used, we were able to induce on average, 85% more FoP in experiment 1, and almost 110% more in experiment 2. Moreover, the fact that the FoP is somewhat stable for low delays (0-100 msec) and high delays (400-500 msec), but has a steep increase around 200-300 msec, goes in the direction of previous literature on sensorimotor integration and sensorimotor conflicts [37, 46, 54]. Regarding this pattern, Blakemore et al. 1999 [46] also obtained similar results for an experiment regarding self-generated tickling and external produced tickling. In this setup, participants had to manipulate with the left hand the controls of a robot that produced tactile stimuli on his/her right hand, in conditions ranging from, no delay to 100, 200 or 300 msec of delay. Their results also show a steep increase from 100 msec to 200 msec of delay. At this point, there is no longer any variation in perception, with all the stimuli being perceived as produced by an external agent.

This information on the temporal dynamics of the FoP allowed us to proceed to an imaging study of this phenomenon, as it is of interest to observe in terms of brain activity, the effect of sensing or not the FoP at the exact same delay. In previous experiments [1], having or not the subjective sensation of the FoP was only being achieved separately, with two different experimental conditions.

7 Neural Correlates of the Feeling of a Presence

This chapter addresses the second session of Experiment 2, that was performed with the use of EEG. Starting with specific methodology used for data collection, data processing and data analysis, we will present in this chapter the results of this session. A discussion on this topic will follow.

7.1 Methods

7.1.1 EEG Acquisition System and Processing

EEG signal was recorded with a 64-channels BioSemi EEG system (Behavioral Brain Sciences Center, University of Birmingham). Electrodes were placed according to the 10/20 layout for 64 channels (refer to figure 4.1 B) and referenced to two electrodes placed on the upper back part of the head (CMS and DRL), which drive the Common Mode voltage as close as possible to the ADC reference in the voltage box. Electrode impedance was set below 10kΩ in the beginning of the experiment and the signal was sampled at 1024Hz. Horizontal and vertical electro-oculograms were also placed on the face to detect saccades and blink movements that might occur during the trials, so that we could further eliminate them from the collected data. Actiview (BioSemi) was the selected program to control the EEG acquisition and make the communication between the main computer sending the triggers for respective events and the data being acquired.

The collected EEG data was fully processed with the use of MATLAB® (The MathWorks Inc.) version 2013b, a matrix-based computer language for signal processing, and the external MATLAB-based toolbox Eeglab [66]. The data was down-sampled to 512 Hz and subsequently filtered three times, first with a high-pass at 1 Hz to eliminate very slow wave oscillation, followed by a low pass at 45 Hz to suppress high-frequency noise and unwanted frequencies, and finally a notch-filter at 48-52 Hz to further suppress line noise. Data was re-referenced to the average of all electrodes. Visual inspection of the data was performed before entering the next stage, Independent Component Analysis (ICA), to remove strong or obvious noise components that were not eliminated with the filtering.

ICA was performed using Eeglab and the extended infomax ICA algorithm (binary version). ICA is an algorithm tool to help remove contaminations in the EEG data obtained from participants. This topic is further discussed in the end of this sub-chapter. Nevertheless, once the independent components have been computed, some that are related to noisy

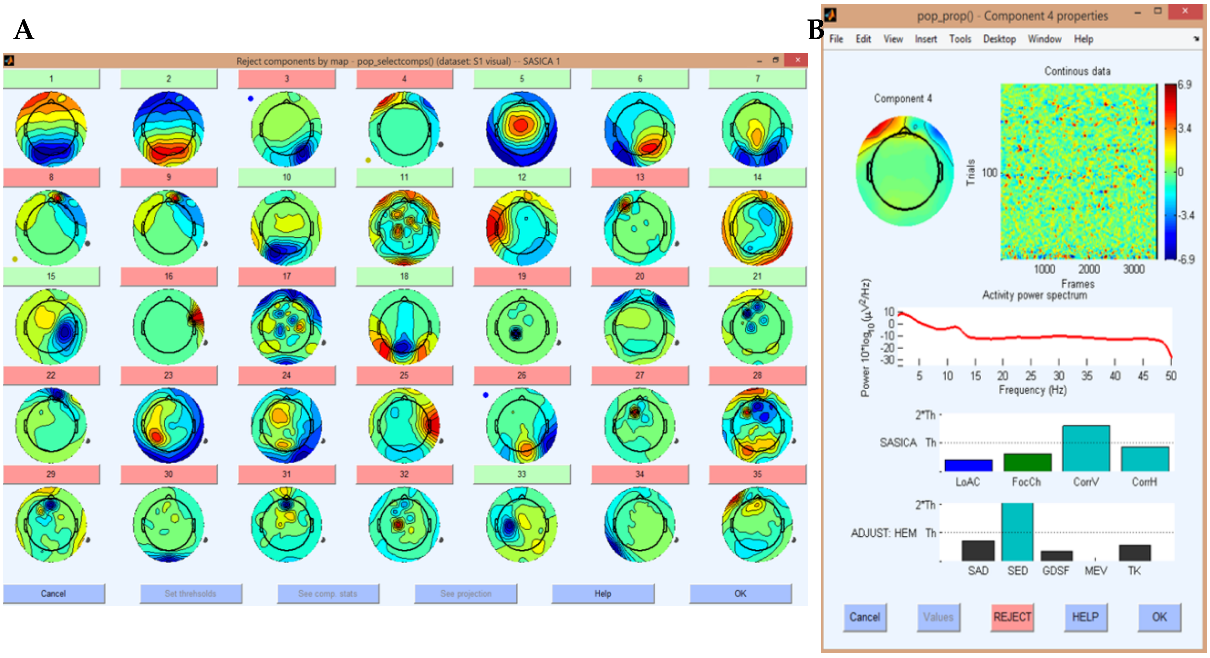


Figure 7.1 Examples of SASICA's Interface
(A) Topographical visualisation of the first 35 independent components computed by the ICA already with suggested rejections and identification of components deemed to be too auto-correlated (components regarding neural activity do not show high-levels of auto-correlation) or with a strong correlation to EOG electrodes, marked with coloured dots. From here, one can analyse each component individually and change the recommendations of accepting or not a component. **(B)** Descriptive characterization of an independent component. On the bottom we can see the results from four methods applied by SASICA and also from another toolbox called ADJUST (see reference for more details on this toolbox). The methods seen from SASICA are LoAC (Low Autocorrelation) for Muscle Artifact detection based among other factors on the fact that these patterns are not trial specific, FocCh (Focal Channel Topography) for detection of bad channels which are mainly associated with extreme focal activity, and CorrV and CorrH for the detection of blinks and horizontal eye movements respectively.

sources, must be eliminated by visual inspection performed by an expert in the field. If this visual analysis is done without any kind of strict criteria, one will end up using different selection criteria for the independent components. SASICA [67] comes into play here. With its semi-automatic methods for component rejection we can establish the same rejection criteria across studies and participants.

SASICA has at its disposal several parameters helping this selection to be done. This includes correlation with vertical and horizontal EOG electrodes, low auto-correlation of time-course (for muscle noise), focal channels topography, focal trial activity, residual variance, correlation with bad channels, among others measures coming also from other toolsets that SASICA uses. All the processing is done in a neat interface supplied by SASICA (figure 7.1).

7.1.1.1 Independent Component Analysis

Independent Component Analysis (ICA) can be described as the search for a linear transformation that maximizes statistical independence between components, as described by Pierre Comon, 1994 [68].

ICA is a fundamental approach in solving the so-called problem of the Blind Separation of Sources (BSS). This problem is better understood with an illustration. For example, an antenna which is capturing signals at a certain band, is receiving input from all the sources which emit in its receptive field. If no previous knowledge of the sources is known this situation becomes a BSS problem [69]. In this case, we would need to identify the sources and pin point the source of interest. ICA would be the best technique too start approaching this problem.

ICA takes the upper hand, by assuming that the sources are independent. Indeed, all emissions in this example have no reason to be correlated. By identifying all the different sources of signals, we can then reject some of the sources based on prior knowledge of noise features and use other methodologies to exclude some sources. After that, the signal can be reconstructed and considered artefact free. The same principles applied on the example can be done for EEG, as seen on figure 7.2.

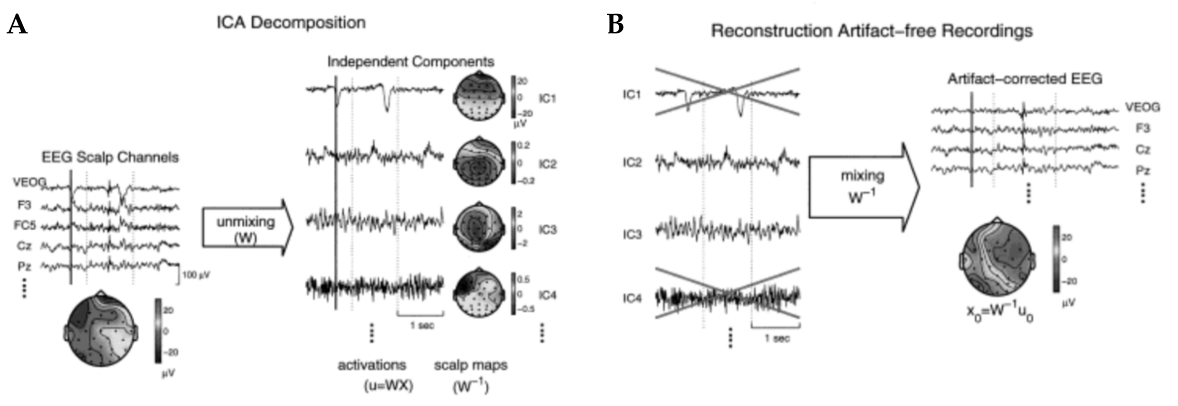


Figure 7.2 Application example for the ICA in the case of EEG Recordings
Adapted from Jung et al., 2001 [103]. **(A)** Raw amplitude over time is shown for exemplary electrodes on the left side. By applying independent component analysis to those electrodes, the sources IC1 to IC4 on the right are obtained. These sources are considered independent. IC1 has the typical shape of a blink artefact and IC4 appears to be noise. On the other hand, IC2 and IC3 are most likely components of interest to one's investigation. Exemplary topographies are shown both for the raw signal and also for the independent sources. **(B)** On the left we can see the selected sources to reconstruct the signal at each electrode. These sources were selected by an expert in the field and are now considered noise free. On the right we can see the reconstructed signals for each electrode, now free of noise. By comparing the exemplary topographies, we can see the changes in the signals due to removing the noise sources.

7.2 EEG Data Analysis

To analyze the EEG data, three consecutive steps are taken. We first apply a Generalized Linear Model (GLM) to try and model our data according to predictors we believe are important for the brain states related to the time-locking event. This is done with a pool of data that has one dataset for each participant, containing all the trials. Statistical analysis is then performed on the results of the GLM, to point us in the right direction for source localization. Finally, source localization methods are used in agreement with the statistical analysis done on the results of the GLM. This last step is performed on a pool of 12 datasets per participant, where all trials are divided per delay and answer (e.g. dataset for 300 msec of delay without FoP).

7.2.1 General Linear Model

The Generalized Linear Model is a method mainly used when analyzing fMRI data, that is now growing in the EEG field. Compared to other methods it has the advantage of allowing the specification of all the parameters of interest on one single model and the analysis at single trial level for each electrode and time-point (referred to from now on as, channel-time pair), while other approaches require the first step to be an average across trials of the same condition in order to increase Signal to Noise Ratio (SNR).

Using a GLM also means using a different approach than most methods of EEG analysis. Instead of trying to extract immediately information regarding significance on the scalp, we first reconstruct the data according to predictors of interest and only after we analyze where those predictors had significant contributions. The already known signal (Y) is therefore reconstructed, based on parameters (or contributions, β) of predictors (X) decided by the researcher. These predictors are usually based on the characteristics of the experimental conditions and on the experimental answers [70, 71]. Because we can never know all the predictors causing variations in the EEG signal, there is always a difference between the adjusted signal and the original one, represented by an error factor (ε) [72]. The resultant equation follows:

$$\underbrace{\underbrace{Y = X\beta}_{\textit{Adjusted}} + \varepsilon}_{\textit{Real}} \tag{7.1}$$

We chose to encode each channel-time pair individually as to preserve independence between consecutive time-points. Consequently, being an analysis at single-trial level at each channel-time pair, Y is a vector of t rows, where t is the number of trials, representing the signal at one channel-time pair for every epoch. In its turn, the predictor X is a 2-D $t * c$ matrix, with t trials and *c* conditions (predictors). X is also referred in literature as the design matrix. The parameters matrix β, is a vector of *c* rows, where *c* stands for the number of conditions (or predictors). Finally, the error matrix is a vector with *t* (trials) rows.

The predictors' matrix X (figure 7.3), is constructed by the researcher based on the conditions he thinks are of interest to the resultant signal. Different ways of coding the predictors' matrix will allow the researcher to assess different effects. In our case when analyzing all trials and all conditions put together, we have four predictors:

- **Intercept:** which is present in most analysis with GLM and has a constant value (either 0 or 1). This predictor accounts for activity that is always present in the data, such as baseline activity or noise;
- **Delays:** this predictor codes the delay at each trial and therefore takes values between -5 and 5 with steps of 1;
- **Feeling of a Presence (FoP):** this predictor codes the answers given by the participants in each trial, with 0 for not having FoP and 1 for having FoP, or 0 for having FoP and 1 for not having FoP, depending on the analysis;
- **Interaction:** a last predictor is created representing the interaction between having FoP and the experienced delay. This is done by multiplying at each row the two previous predictors [72, 73].

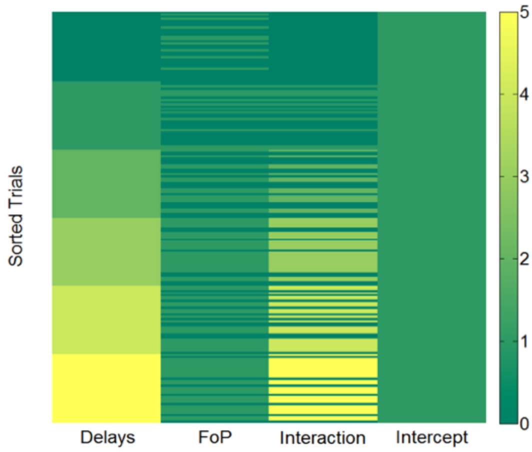


Figure 7.3 Design Matrix for an Arbitrary Participant
Trials were ordered in a descending fashion according to delay, for this exemplary design matrix. The first column represents delays, that are coded from 0 to 5 (being 0, no delay and 5, 500 msec of delay). The second column is related to having FoP coded 0 from answering 'no' and 1 for answering 'yes'. The third column is the interaction between delay and FoP, achieved through multiplying the first two columns. The last column is the intercept, which is a constant term valuing 1.

The meaning of the β parameters changes according to the way the predictors' matrix is coded. Each individual parameter, except the interaction parameter, codes for the action of its predictor's effect when the other conditions are null (coded as 0), therefore, when looking at the parameter for the FoP we have to take into account that it's only assessing the effect of the FoP for the delay coded with zero. With a centering approach, one can center a desired delay at zero to assess the effect of FoP there. The same goes for the delay parameter. It will assess the effect of delay, only at the condition coded as zero on the FoP predictor. Despite requiring re-fitting a model every time one wants to study a different effect and being computationally heavy, this method allows the gathering of a vast amount of information from the EEG data. Finally, the interaction parameter shows the difference between the effect of delay when experiencing FoP and the same effect when not experiencing FoP.

To obtain the optimized β parameters, from equation (1), the method of the ordinary least squares is used. This is a statistical method for estimating unknown parameters from normal sampled data:

$$\hat{\beta} = (X^T X)^{-1} X^T Y \qquad (7.2)$$

Different approaches to solving this equation exist, being the most popular the Moore-Penrose Pseudoinverse [74]. To clarify, the General Linear Model will output to each channel-time pair, four optimized parameters, one for each of the four predictors, by taking into account all the values from all the epochs at a given channel-time pair.

We used custom MATLAB scripts to implement this approach, making use of the Statistics and Machine Learning Toolbox.

The GLM makes some apriori assumptions, that affect and limit the end result. It is considered that the errors, are normally distributed, have the same nature for each measurement and are not correlated in time or data points. On top of this, when the predictors are created, there is no absolute certainty that they accurately model the data. Due to all of this, upon implementing this model, several controls should be performed to assess if the results are trustworthy.

Three assessment strategies were implemented, inspired on recommendations from MathWorks and current literature [70- 72] on how to evaluate the fitted models. Two of these strategies use comparisons with other fitted models to better assess the validity of our results. For further reference, the actual model upon which we base our findings is referred to as the Real Model (RM) and the models against which we compare are referred to as test models. Test Model 1 (TM1) has all its predictors, except the intercept, taken from a random uniform distribution. Test Model 2 (TM2) has the same predictors as the real model plus an added predictor dependent on one of the others in a non-linear fashion (specifically we use the interaction parameter squared).

7.2.1.1 Analysis of the Adjusted Sensory-Motor Evoked Potential

The first step that should be taken when assessing the outcomes of a fitted model is to look at the adjusted sensory evoked potential (SEP). The model used should always fit the data reasonably, or otherwise be discarded.

This step, depending on the number of epochs given to the GLM can be done just by visual inspection or with more objective measures. Usually when the number of repetitions is very high, most models will have a moderate to good fit of the data, meaning one should apply stricter approaches. We fall on this second case, due to the elevated number of epochs every participant has for each time-channel pair.

Error monitoring was chosen as a controlling measure and it is performed at each channel-time pair, for every electrode and every participant, by assessing the difference of the adjusted SEP and the mean of the real data for the condition being predicted, relatively to the standard deviation, in such a way that an error of 100% is equal to the standard deviation of that specific channel-time pair. This allows to relatively compare different models that seem to rank the same in terms of prediction.

7.2.1.2 Estimation of Normal Parameters for the Pearson's Residuals

A strategy that complements the previous assessment, takes use of the Pearson's residuals to evaluate the fitness of our model. Pearson's residuals are one of the equivalent in logistic regressions to the residual sum of squares in linear regression. It is based on subtracting of the fitted value at each observation and dividing by the estimated standard deviation of the fitted values (as seen in equation 3). Note that for normal models such as ours, this is equivalent to just performing the operation on the numerator.

$$r_i^P = \frac{y_i - \hat{\mu}_i}{\sqrt{\mathrm{V}(\hat{\mu}_i)}} \tag{7.3}$$

At each channel-time pair, we have a number of Pearson's residuals equivalent to the number of epochs that are being analyzed. If the assumptions made to fit the data where done properly, then the corresponding normalized Pearson's residuals should have a good standard normal distribution (figure 7.4), as the link between the predictors, the independent and the dependent variables was assumed to be the identity function.

Because we have approximately 1 million fitted points and therefore the same number of groups of Pearson's residuals to analyze, we had to have a way to analyze these results in a less extensive way. To solve this, we estimated the parameters of the normalized Pearson's residuals as if they had a normal distribution and selected, per participant, both the groups with the worst and the best approximation to a normal distribution, according to the expected interquartile range and the expected population at 1 standard deviation from the

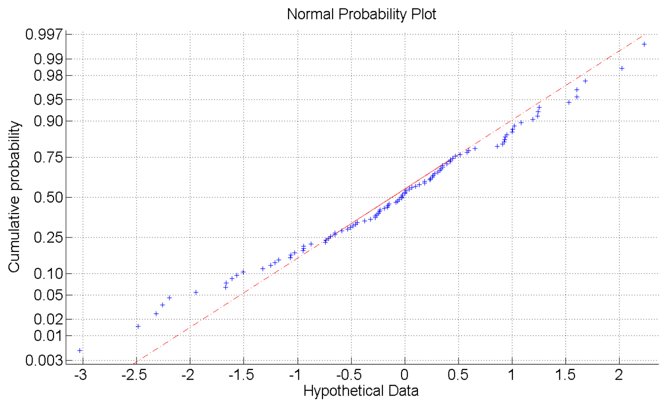


Figure 7.4 Example of a Normal Probability Plot for a Normal Distribution
One hundred points extracted from a normal distribution are presented (in blue) against their expected normal distribution line. In a red solid line, there is the inter-quartile range and in dashed red, the extrapolation of the quartile line. This represents a good normal fitting.

mean. In the end, we would have four groups of Pearson's residuals to analyze per participant, simplifying this assessment of fit.

7.2.1.3 Akaike Information Criterion

The last strategy is a relative measure. It should be applied after analyzing the results from the two first methods and it will tell us which model approximates better reality given the recorded data and the complexity of the model [70], based on the minimization of information loss.

The assumption that a good model should minimize information loss was objectively approached by Kullback and Leibler [75] and subsequently developed as a model selection mechanism by Akaike (1973, cited by [76]), by relating maximum likelihood and the Kullback-Leibler information. The descriptive equation of the Akaike Information Criterion (AIC) for the maximum likelihood case can be observed below:

$$AIC = -2\log\left(\mathcal{L}(\hat{\theta}|y)\right) + 2k \tag{7.4}$$

where, $\hat{\theta}$ is the maximum likelihood estimate of the projection onto the parameter space of the approximating model used, y is data generated by our recordings (or theoretically generated from the real descriptive function of the predictors $f(X)$), $\mathcal{L}$ is the likelihood function and k is the number of estimated parameters.

The model with the lowest AIC is considered the best at minimizing information loss. We can further use the difference in AIC of our models to directly compare the minimization of information between two models, by computing the relative likelihood of a model *i*, as described in equation 5:

$$r\mathcal{L} \propto e^{\left(\frac{AIC_{RM}-AIC_{TM_i}}{2}\right)} \tag{7.5}$$

The obtained relative likelihood computed in this way informs on how better (or worse) Test Model *i* is at minimizing information loss. For example, if the difference between the values of the AIC of the RM and the TM was *-10*, this would mean that TM*i* would be 0.007 times as likely as the real model to minimize information loss.

7.2.2 Cluster Permutation Tests

When making this analysis, a decision was made regarding the period of analysis. Due to the complexity of the arm movement any analysis of possible ERP's clusters is done in a time period from 0 to 400 msec regarding the touch on the back, as anything else before that could be too contaminated with the arm movement.

When performing statistical analysis of EEG data, one has to be aware of the Multiple Comparison Problem (MCP) that arises from the multidimensionality of the data. This problem regards the inability to control for the false alarm rate when using standard statistical methods on such a large number of comparisons, or in other words, the probability of falsely concluding that there is a statistically significant difference across two conditions. This can only be safely done by applying non-parametric statistical procedures [77]. These statistical tests have the upper hand of not assuming any parameters regarding the distribution of the variable being analyzed and therefore have a safer and more conservative approach to this problematic.

This cluster permutation test was not performed directly on the EEG signal but rather on the optimized parameters given by the GLM. A total of 13 parameters, six for the effect of FoP (one at each delay), two for the effect of delay (when having and not having the FoP) and one for the effect of the interaction between the delays and the subjective experience of the FoP.

To correctly implement this statistical analysis, we created custom scripts resorting to functions from the external MATLAB based toolbox FIELDTRIP [77], designed for the analysis of EEG and MEG data, with functions ranging from data pre-processing to connectivity analysis.

Such computations are taken in two important steps:

- ***Cluster-based statistical test:*** parameters of every channel-time pair of a certain predictor are compared by means of a t-value (in our case since every participant experiments all the conditions, the samples are not considered independent) against the null hypothesis, i.e the hypothesis that the parameters are insignificant (all zero - meaning no contribution of any of the predictors established in the GLM). The samples are now selected according to a significance threshold ($p < 0.05$) and clustered based on temporal and spatial connectivity. Clusters are finally considered if they satisfy a number of imposed conditions (e.g. size, max t-value…);

- ***Assess significance probability:*** This step presents the solution for the MCP, by using a Monte Carlo method approach. Here, the data from the parameter being analyzed is put together with the zeros representing the null hypothesis. By randomly taking out a number of samples equal to the number we had for the parameter being analyzed, we create a random subset with the label of condition 1. The cluster based statistical test discussed previously, is now applied to this random partition. These steps are repeated 10.000 times to create a null distribution of cluster-level t statistics (this address the possibility of any difference between the parameters and the hypothesis that they are insignificant, is explained by chance). Finally, for each cluster measured in the data, a p-value is determined based on the number of times that cluster appears randomly in the data versus the number of cluster that appeared in total. To be considered significant this p-value had to be under 0.05.

7.2.3 Source Localization Methods

One of the objectives of this study is to estimate which brain regions are responsible for having or not this subjective experience of the Feeling of a Presence. This was performed using a distributed linear inverse solution which applies the local autoregressive average regularization approach (LAURA), taking physical and biological constraints into account when computing this inverse solution [78, 79]. Activity is computed over 4996 solution points.

To perform this, we first computed the Global Field Power (GFP) on periods of significance determined by the cluster permutation tests. The GFP is a measure of spatial standard deviation of the electrical activity measured in the whole EEG cap. The peaks of the GFP time function, have been previously associated with more stable topographies. This is of interest for the estimation of brain sources, as a stable topography is likely to have the same source over time [80]. Therefore, by computing the GFP function in said periods of significance we can assess where these periods have more stable topographies, and eventually divide these periods into smaller ones to determine the brain sources. We established Periods of Interest (POIs) inside the periods of significance by visual inspection of the GFP function.

Source estimation was performed for all subjects individually, for all conditions of this experiment (6 delays × 2 answers for the FoP), by averaging in time the POIs for each electrode. Statistical analysis was then performed to assess significant differences between conditions at each one of the solution points, with a criteria of $p < 0.01$ for a two-sided t-test. The results are shown on the Montreal Neurologic Institute's average brain using the Talairach and Tournoux coordinates [81].

7.2.3.1 Activity Estimation

Further investigations were performed to assess differences in activation of the estimated brain sources, this time not with the intent of assessing this difference across all conditions but only across delays and the control condition of external touch, as a proofing method that our results were following a similar line in terms of suppression when in conditions of self-touch, as it has been shown in convenient literature [39, 44, 45, 54].

For a correct assessment of brain activity this estimation of activity was performed only in the POIs selected previously through the analysis of the GFP's time function, for the exact same reason explained before, regarding the relationship between the peaks of these functions, stable topographies and common sources [80]. Moreover, two different brain regions were decided to be target of this evaluation. The first, were the ones considered significant as being different for experiencing or not the Feeling of a Presence and the second ones, the ones which presented a peak of activity for the POI when averaging the inverse solutions of all the subjects. For the former, activity was considered to be the mean of the activity at all significant voxels, whereas for the latter, it was considered to be the mean of the three voxels with highest absolute activity.

The mean activities were than compared by means of a two-sided t-test, neighborhood-wise and against the activity for the external touch (control condition).

7.3 EEG Results

For a better understanding of the results obtained and for comparison with Sensorimotor Evoked Potentials (SEP) studies, we show SEP in response to the touch on the back. This is obtained by combining all conditions, and by averaging all subjects (figure 7.5).

The conclusions of this work are not based on the visual analysis of these SEPs but rather on the application of a Generalised Linear Model to our data, subsequent permutation test and source localisation methods. The visual inspection of the data independently of the conditions, allows the identification of components typical for SEPs. Immediate processes more related to integration at the level of the sensorimotor cortex can be observed in the data, at P100 (maximum positivity in 100 ± 20 msec) and N140 (maximum negativity in 140 ± 20 msec). Later components are also observed.

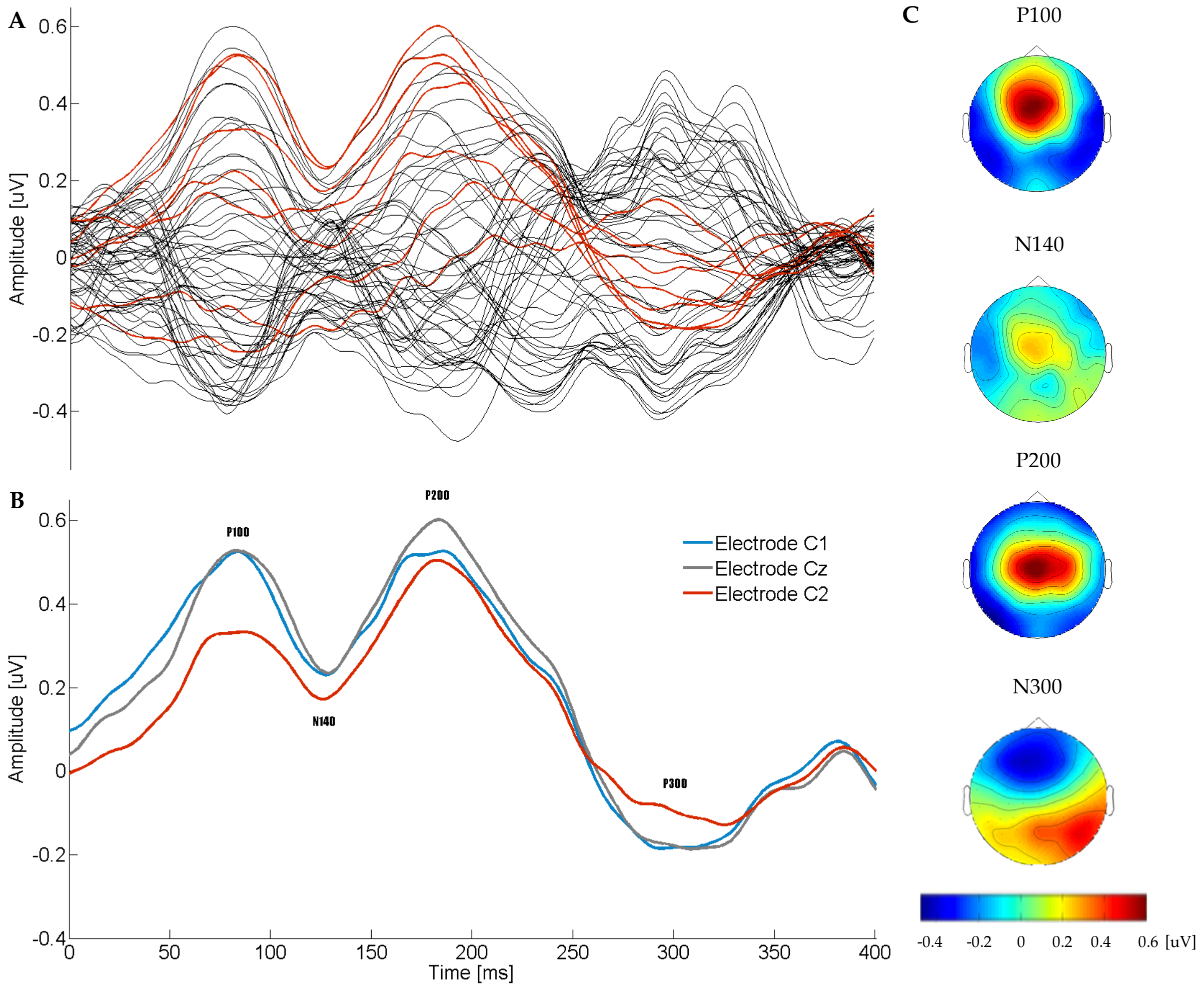


Figure 7.5 Example SEP for the Touch on the Back from the average of All Conditions and Participants
(A) All of the 64 electrodes are shown superimposed, for visual observation. The electrodes directly on top of the sensorimotor cortex are displayed in red. **(B)** Electrodes most likely to react to trunk touches are shown (C1, Cz and C2). The two first components to be observed in the data are the P100 and the N140, most likely to be related with more immediate processes at the level of the sensorimotor cortex. P200 and N300 are late components associated with higher cognitive functions. **(C)** Topographies relative to the identified components, P100, N140, P200 and N300. Each component's topography is the average around the actual latency of the observed component ranging -5 msec and +5 msec from the peak's maximum (or minimum).

7.3.1 General Linear Model Analysis

The collected EEG data were modelled using a GLM approach. The results of interest to us from the application of the GLM are the estimated optimized parameters (β) for each one of the predictors described in the methods section. The intercept assesses the baseline activity present at each condition, including brain activity that is unrelated to the tasks and the part of the SEP that is equal for every condition. We will not focus on this parameter, as the interest of this investigation is to assess differences in the brain that account for differences in the subjective experience of the Feeling of a Presence. Also, note that, a positive cluster of a certain predictor refers to a group of channel-time pairs that, according to the model being used, are contributing positively to the dependent variable (EEG signal). For negative clusters the contribution should be considered to be in the opposite direction.

The delay parameter, for the specific case of assessing the effect of delay when not experiencing the FoP (figure 7.6 A), showed significant difference for three clusters at a level of $p < 0.05$, when comparing the model's parameter against the null hypothesis (figure 7.6 B). This effect lasted from 0-183 msec, with one positive cluster (0-132 msec) and two negative clusters (0-85 msec and 100-183 msec). No significant effect was found for the effect of delay when having FoP, although a trend was verified for a positive cluster at 50 msec ($p = 0.066$).

The effects of delay were expected to occur, as with increasing delay, participants move away from a condition of self-touch and enter the domain of other-touch. This leads to an increase of activity which most likely explains these significant effects. Again, the effects of delay do not address our particular objective, so despite being reported here, no further analysis is pursued.

Permutation tests did not reveal any significant effect for the FoP parameter, for any of the used delays.

The interaction between the predictors for delay and for FoP (figure 7.6 D), showed significant effects for one cluster at $p < 0.05$, when comparing the model's parameter against the null hypothesis (figure 7.6 E). This effect lasted from 52-113 msec, after the touch on the back, with one negative cluster. This parameter is the only one remaining stable for any of the centring approaches. Its normalized values do not change.

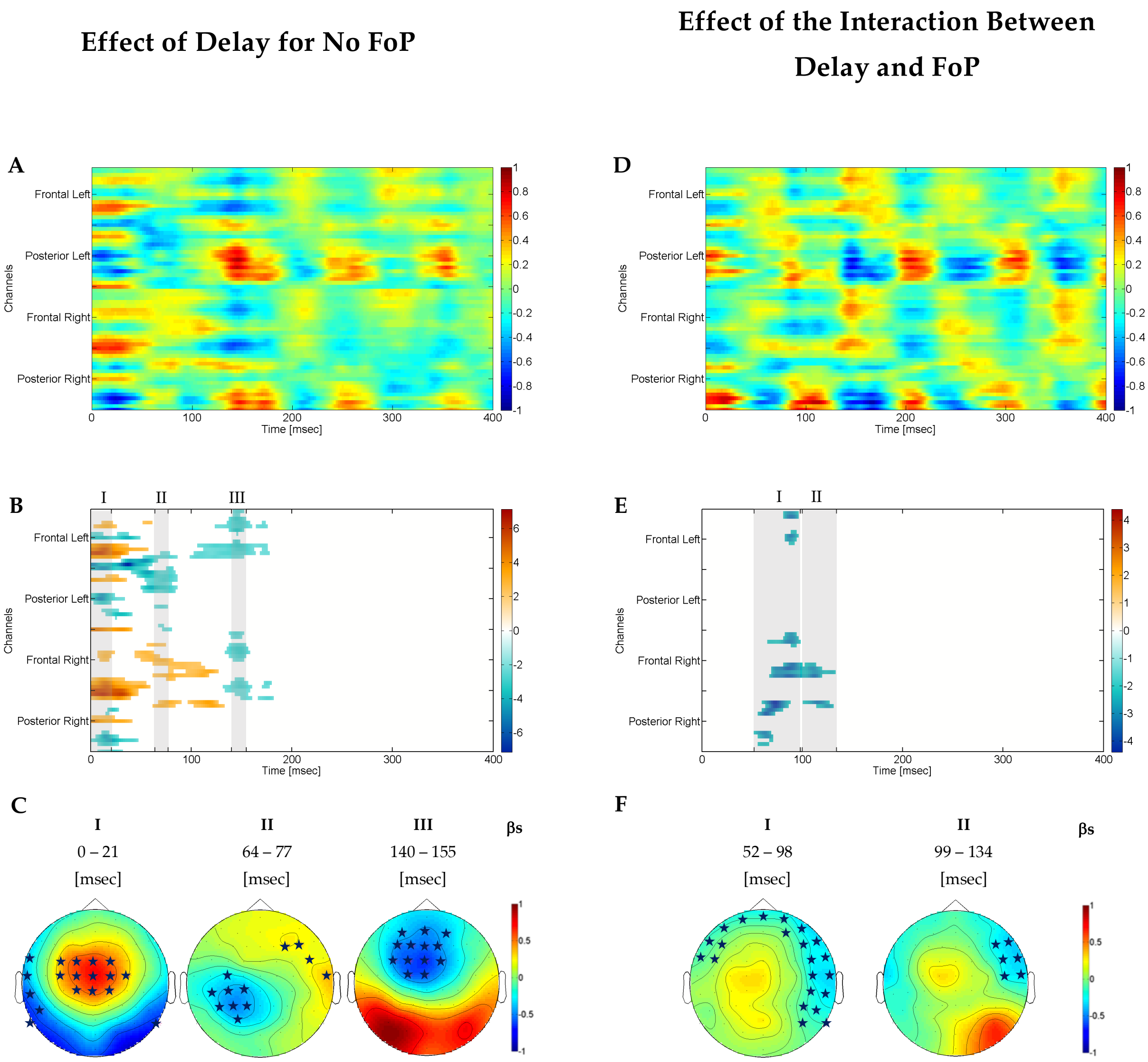


Figure 7.6 Parameters with Significant Effects
(A) Normalized parameters for the effect of delay when participants did not experience the FoP, averaged across all participants. Electrodes are shown in the order of the 10-20 layout for 64 channels. **(B)** T-values for clusters considered significant at $p < 0.05$. A positive cluster was considered significant from 0 to 132 msec, and two negative clusters, one from 0 to 85 msec and another from 100 to 183 msec, regarding the touch on the back (at 0 msec). Periods of interest for computing topographies are identified with a shaded area and have their respective numeral on top. **(C)** Representative topographies for the designated time-periods for all the trials without FoP. The topographies regard the normalised parameters computed for the signal during those periods, not the actual amplitude. Significant electrodes considering the clusters found for these parameters are highlighted with dark blue stars. **(D)** Normalised parameters for the effect of the interaction between delays and FoP, averaged across all participants. Electrodes are shown in the order of the 10-20 layout for 64 channels. **(E)** T-values for clusters considered significant at $p < 0.05$. One negative cluster was considered significant ranging from 52 to 113 msec, regarding the touch on the back (at 0 msec). Periods of interest for computing topographies are identified with a shaded area and have their respective numeral on top. **(F)** Representative topographies for the designated time-periods for all trials independently of condition. The topographies regard normalised the parameters computed for the signal during those periods, not the actual amplitude. Significant electrodes considering the clusters found for these parameters are highlighted with dark blue stars.

7.3.1.1 Model Diagnostics Part 1 – Evaluating the Model's Predictions

The first step after applying a GLM to any kind of data should be to check the adjusted SEP, generated by using the acquired parameters and the designed predictors. This adjusted SEP is separated from the real SEPs by the error that is not explained by any of the predictors. For further reference, the model used to fit the data with what we believe are the true predictors is referred to as Real Model (RM), the comparer model using random uniformly distributed fake predictors is the Test Model 1 (TM1) and the comparer model which consists of the real model with an added predictor (squared interaction) is referred to as the Test Model 2 (TM2).

Predicting the overall signal independently of condition and comparing it to the real one would be meaningless, as there are too many repetitions overall and there would always be a perfect fit. A visual analysis done condition-wise allows a correct assessment of the predictions made. Condition-wise is a more realistic analysis has there are enough repetitions per condition to fit correctly the model and to evaluate the error between real and adjusted SEPs.

The real data is correctly adjusted by the modelled data for both the RM and the TM2 (figure 7.7 A and 7.7 C). The adjusted SEP coming from TM1 is however, fitting the real data in a poorer way, which was naturally expected.

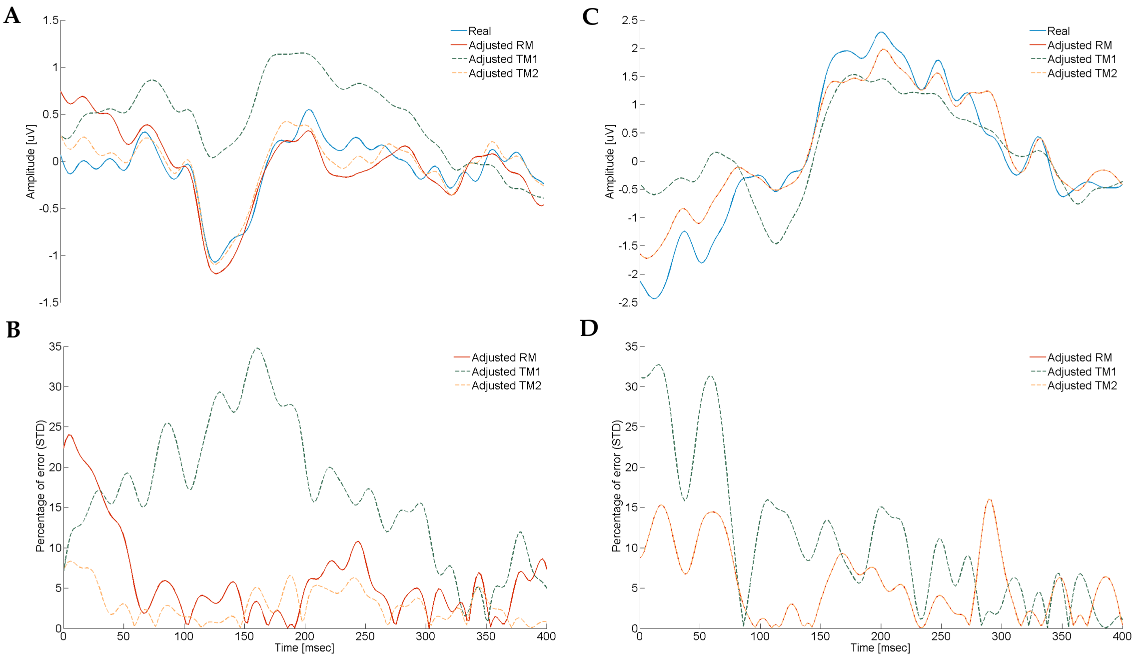


Figure 7.7 Representative Analysis of Real and Adjusted SEPs
For all sub-figures, the blue line regards real acquired data, the red line the real model, the green dashed line, test model 1, and the orange dashed line, test model 2. **(A)** SEPs for the condition of 500 msec of delay independently of the answer for centring approach at 400 msec of delay, for one arbitrary participant at electrode Cz. **(B)** Analysis of the error committed by each one of the models when comparing its adjusted SEP to the real acquired data, relatively to the standard deviation at each channel-time pair (an error of 100% would be committing 1 standard deviation of error). **(C)** SEPs for the condition of no delay independently of the answer for centring approach at 500 msec of delay, for one arbitrary participant at electrode Cz. **(D)** Analysis of the error committed by each one of the models when comparing its adjusted SEP to the real acquired data, relatively to the standard deviation at each channel-time pair.

Regarding the errors performed by the models relatively to the standard deviation of the real data, both the RM and the TM2 seem to perform quite accurately, with a mean error of 6% and 3%, respectively for the first example shown here (figure 7.7 B) and both with a mean error of 5% for the second example (figure 7.7 D). The TM1 however, performed poorly with a mean error of 17% on the first example and 11% for the second one.

The slight differences between the RM and TM2 were expected, as in fact, TM2 contains the RM. Not having a linear relationship with any of the other predictors, it is most likely the case that the extra predictor is modelling some sort of more constant noise that is present in the data, instead of being discarded by the GLM.

Confirming that the model's predictions are approaching the desired SEP, more objective measurements have to be deployed to assess the validity of our assumptions and the relative quality of the applied model.

7.3.1.2 Model Diagnostic Part 2 – Pearson's Residuals

Analysing the normality of the Pearson's residuals (PRs) at each fitted model gives a good perspective, both on the goodness of fit of the model and on the assumptions made regarding the predictors.

The visual analysis according to the inter-quartile range criteria (figure 7.8 A-B), reveals some differences between the best and worst fits to normal distributions. For the majority of subjects (16 out of 19), the best fit of a group of PRs, to its expected normal distribution, is almost perfect (figure 7.8 B), with the worst fit still being a very good fitting with deviances on the edges (figure 7.8 A), but still a clear normal distribution as most of the PR's (groups have about 900 residuals) do not deviate from the extrapolation lines (in red in the figures). Between the best and the worst fitting there are about one million fitted groups, the lack of a big difference between both fits suggests that all the channel-time pairs had the GLM correctly applied. A second visual analysis with the expected population around one standard deviation of the mean, revealed similar results (figure 7.8 C-D). Again, for the majority of the participants there are no significant differences between the fittings, suggesting that all groups of PRs have normal distributions and that again all channel-time pairs have indeed been well modelled by the GLM.

The groups of PR's were also analysed per participant with the Anderson-Darling test. This statistical test, can assess if a given sample originated/belongs to a certain distribution, such as the normal distribution.

The analysis with this test, shows that 15 out of 19 participants have all electrodes being well modelled by the RM from 0 to 400 msec after the time-locked event. From the other four, 2 of them show good modulation mostly for a strip of electrodes (containing mostly central and fronto-central electrodes, e.g. Cz and FCz) while the other 2 show a poor modulation over all electrodes.

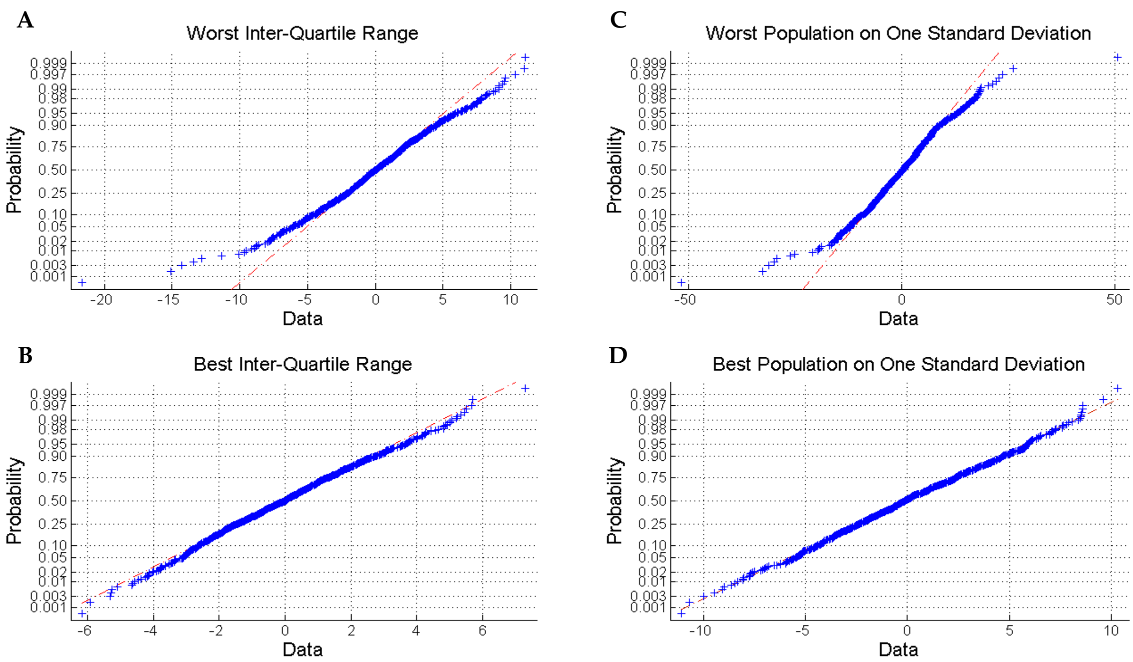


Figure 7.9 Normality Assessment for Two Arbitrary Participants
For all the sub figures, the blue markers represent the individual Pearson's Residuals (PRs) at the respective channel-time pair being modelled, the red dashed line is the extrapolation of the quartile line (that unifies the first and third quartiles) to the minimum and maximum values of x. Probabilities on the y-axis refer to the cumulative probability. **(A)** Worst group of PRs according to the inter-quartile range criteria, for one arbitrary participant. The deviation from the expected normal probability values occurs in the far extremities, in a way that does not suggest a significant deviation from a normal distribution. **(B)** Best group of PRs according to the inter-quartile range criteria for the same participant as in (A). The PRs fit almost perfectly the expected normal distribution. **(C)** Worst group of PRs for the Population on One Standard Deviation criteria for one arbitrary participant. The Pearson's Residual seem to follow a normal distribution although there is a deviation from the extrapolated quartile line. Again the deviations from the expected normal distribution are in the far extremities and do not seem significant. **(D)** Best group of PRs for the Population on One Standard Deviation Criteria for the same participant as in (C).

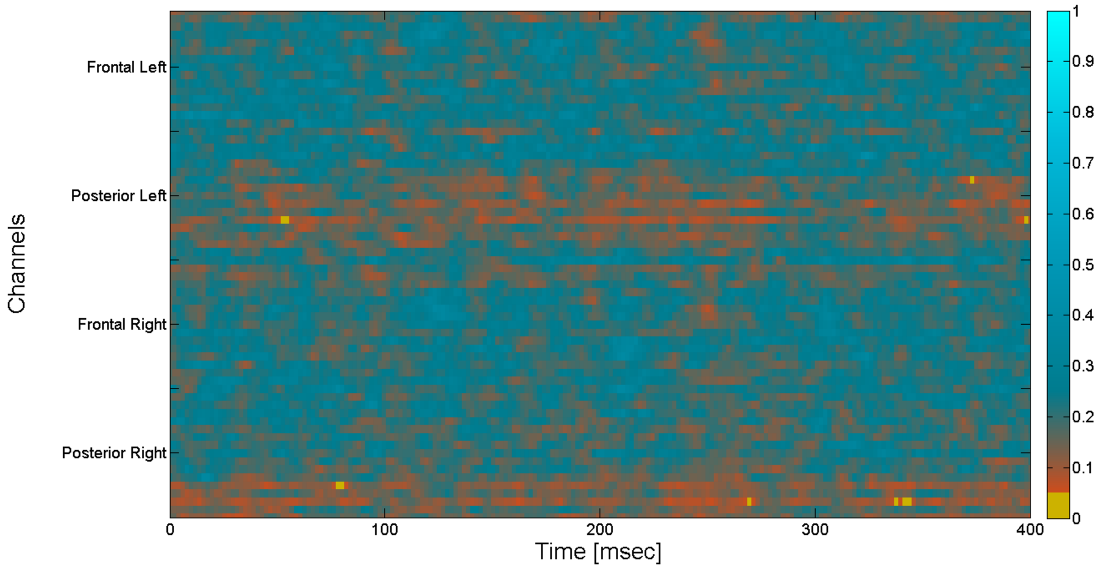


Figure 7.8 Results from the Anderson-Darling Normality Test
Average across participants, of the p-values from the Anderson-Darling test applied to groups of Pearson's Residuals from one of the centring approaches. P-values under 0.2 rapidly increase to a red tone and p-values under 0.05 are identified in yellow. The stripes with highest p-values correspond to the ones on top of the somatosensory cortex and in immediate proximity. Stripes with the lowest p-values correspond mostly to occipital electrodes.

Looking at the average across subjects of the p-values being returned by this statistical analysis, we see that the assumptions made regarding the predictors for our data hold their ground (figure 7.9). We could also hypothesize that this information is already showing us where spatially the effects will occur, as there seems to be groups of electrodes with clearly higher p-values (around 0.4), while other strips (eventually not modelled by our conditions) have p-values closer to 0.05.

In general, according to the normality of the Pearson's Residuals, the assumptions made when fitting the data with the real model seem to hold up quite strongly.

7.3.1.3 Model Diagnostics Part 3 – Akaike Information Criterion

The Akaike Information Criterion (AIC) is a way of comparing models for the same given dataset. Its results should provide an informative measure on the information loss of the different models. This can be achieved by assessing the difference of AIC scores of the different models, as explained in the method section.

The difference of AIC scores between the real model and test model 1 showed that the RM is valued about 1.45 u.a. (units of AIC) less than the TM1. This shows that the TM1 is 0.23 as likely as the RM to be able to minimize information loss (figure 7.10 A). For the comparison with TM2, the results went in the same direction, but the difference was only of 0.72 u.a., which represents a likeliness of minimizing information loss of 0.48 when compared against the RM (figure 7.10 B).

This seems to show that our model (RM) compensates in term prediction versus complexity of the model and therefore should be the main model to explain the data.

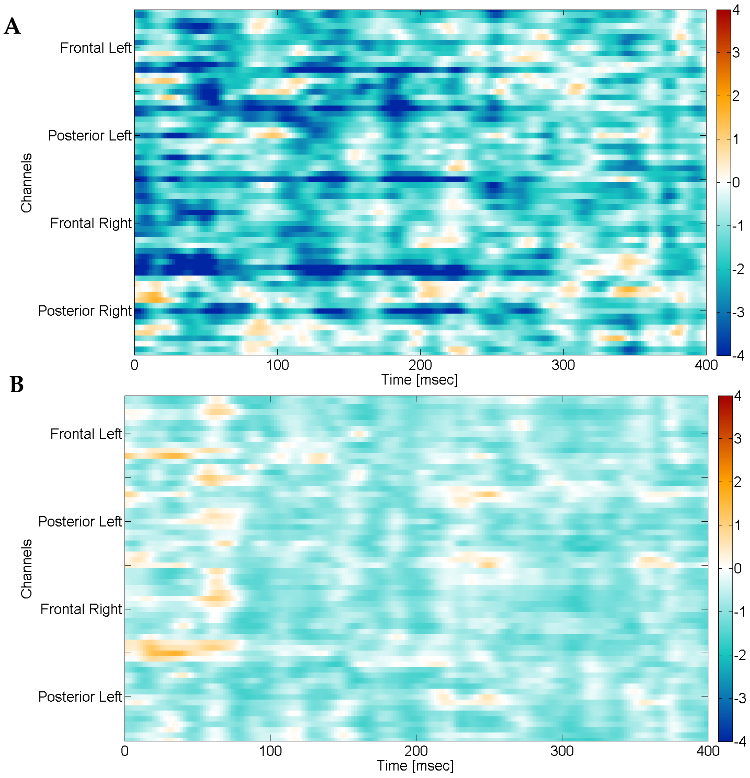


Figure 7.10 Results from the Akaike Information Criterion **(A)** Average of the difference between the AIC values at each channel-time pair for the RM and the ones for TM1, for one of the centering approaches. The mean difference in AIC for the overall average is -1.4517, meaning that test model 1 is about 0.23 times as likely as the real model to minimize information loss. **(B)** Average of the difference between the AIC values at each channel-time pair for the RM and the ones for TM2, for one of the centering approaches. The mean difference in AIC between both models for the overall average is -0.7197, meaning that test model 2 is about 0.48 times as likely as the real model to minimize information loss. It is important to mention that AIC values almost do not vary between different centering approaches of the GLM.

7.3.1.4 Model Diagnostics – Conclusions

According to, all the criteria used, we have seen that we can model the data correctly, have correct assumptions regarding our predictors, as demonstrated by the normality of the Pearson's residuals, none of the other models had significant adding of information to ours, and finally, ours is the best when comparing results and complexity. The model used seems to account correctly for our data and to have trustable parameters.

7.3.2 Source Localisation

Upon observing the results from the cluster permutation test, we observed that only the parameters assessing the general effect of delay, the effect of delay when not having FoP and the interaction parameter had significant clusters (as shown before, refer to figures 7.6 B and 7.6 E). The effects of delay were of course expected but that is not a matter to be addressed on this investigation. To assess the neural correlates of the temporal dynamics of the Feeling of a Presence we are more interested in the effect that the interaction between delays and answer to the FoP, have on the brain.

To analyse which conditions were driving this significant cluster on the interaction effect, a post-hoc analysis on the interaction's significant period was conducted for all the centring approaches, regarding the parameters of the FoP at the different delays. For this analysis, four groups were designed (0 and 100 msec, 200 msec, 300 msec, 400 and 500 msec), each containing one dataset for having the FoP and another for not having the FoP. The motivation to create these groups had to do with the fact that 'Yes' and 'No' on the FoP were very unbalanced on the both ends of the delays, which could undermine statistical comparison of the sources. For two delays to be put together and form a group, they had to be contiguous and the clusters for the effect of the FoP at each one of them could not be statistically different (e.g. the significant clusters for the effect of the FoP at 0 msec of delay are not significantly different from the ones observed at 100 msec). The results of this analysis revealed significant clusters for the effect of FoP when experiencing 400 or 500 msec of delay (figure 7.11 B) ranging from 59 msec to 115 msec, with a p-value < 0.05, not corrected for Multiple Comparisons as this analysis is already justified by the previous findings.

As the period of significant activations is quite large and seems to have two different cluster, we computed the Global Field Power (figure 7.11 C) of the averaged SEP (across subjects) as a way to split the period of interest, as theoretically the peaks of the GFP are, where more stable topographies occur. The joint analysis of the significant electrodes and the GFP's peaks during the significant period of the interaction suggest that a separation should be made creating two intervals, one ranging from 60 msec to 89 msec and the other one from 91 msec to 119 msec. These periods while now be referred to as Interval 1 (I1) and Interval 2 (I2), respectively.

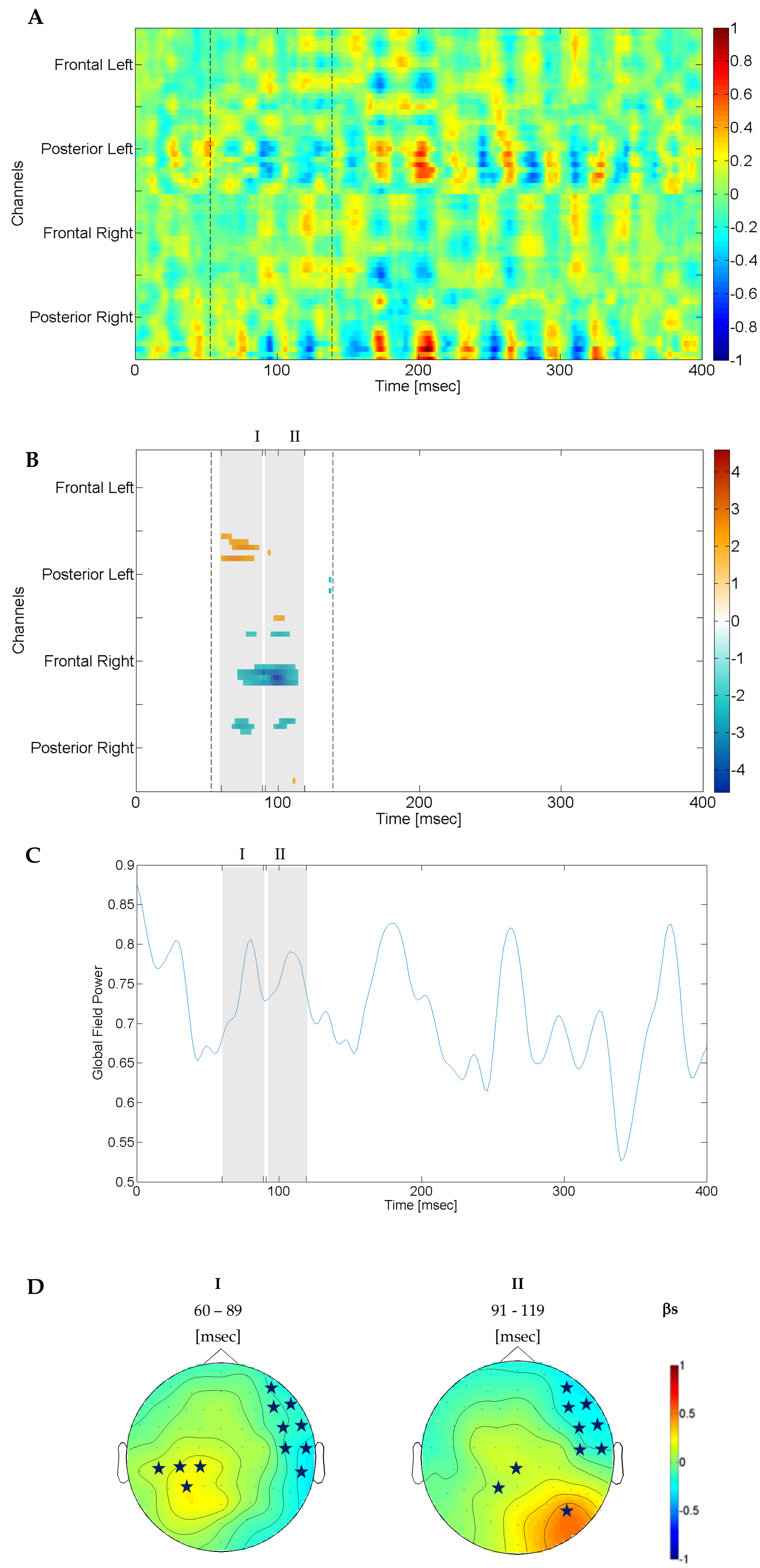


Figure 7.11 Post-Hoc Analysis of the FoP Parameter for the Significant Period of the Interaction

(A) Normalized parameters for the effect of FoP at 400 and 500 msec of delay, averaged across all participants. Electrodes are shown in the order of the 10/20 Biosemi 64 layout. Black dashed lines represent the limits of the significant period of the interaction parameter. **(B)** T-values for electrodes considered significant at p-value < 0.05, for the FoP parameter with delays of 400 and 500 smec. This significance is observed from 60 msec to 115 msec. Dashed blacklines identify the limits of the significant period for the Interaction parameter, and the grey areas identify periods of analysis for source localization. **(C)** Analysis of the averaged GFP for all participants, for the collected data on conditions with 400 or 500 msec of delay independently of the answer to the question assessing the FoP. The grey areas identify the periods of analysis for source localization, based on the GFP peaks happening on the FoP parameter during the significant period of the interaction.

(D) Topographies of the chosen intervals for source localization analysis, showing the normalized FoP parameters. The first interval ranges from 60 msec to 89 msec regarding the touch on the back and the second interval from 91 msec to 119 msec. Significant electrodes happening in those time periods are identified in dark blue stars.

The results of the source localisation methods for I1 (figure 7.12), reveal a significant difference in activation within the Inferior Post-Central Gyrus (Talairach [TAL] coordinates for the maximum difference: x = -61, y = -22, z = 15), with $p < 0.01$, an area also associated with the Secondary Somatosensory Cortex (SII). A negative difference shows that this region is more activated for the condition of not having FoP at 400 and 500 msec of delay.

In the case of I2, the source localisation methods pointed out a significant difference in activation within the Inferior Parietal Lobule (TAL for the maximum difference: x = -48, y = -35, z = 39), with $p < 0.01$. Again, a negative difference points out that this region is more activated for the condition of not experiencing FoP at 400 or 500 msec of delay.

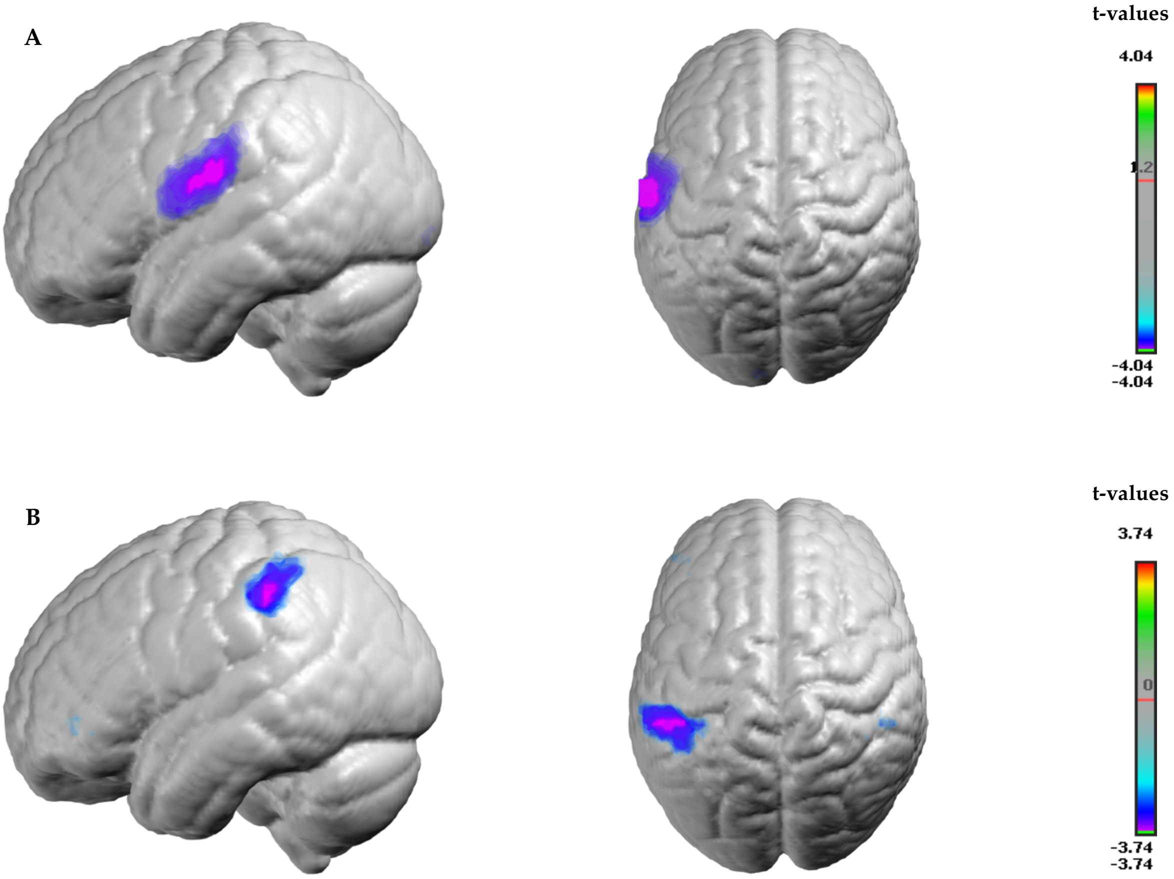


Figure 7.12 Brain Regions With Significant Differences in Activation for FoP Versus No FoP When Experiencing 400 and 500 msec of Delay

All sub-figures show T-values interpolated around the voxels that were considered significant with a p-value under 0.01. **(A)** Statistical analysis of the difference in the activated sources during Interval 1 for FoP versus No FoP, when experiencing 400 or 500 msec of delay, revealed a significant difference in one region, Inferior Post-Central Gyrus (TAL coordinates: x = -61, y = -22, z = 15). **(B)** Statistical analysis of the difference in the activated sources during Interval 2 for FoP versus No FoP, when experiencing 400 or 500 msec of delay, revealed a significant difference in one region, Inferior Parietal Lobule – Broadmann Area 40 (TAL: x = -48, y = -35, z = 39).

7.3.3 Activity Analysis

To see if our results are in line with previous literature on sensory attenuation during self-touch, we investigated the underlining activity during I1, for the region with the biggest peak activity (Medial Frontal Gyrus, TAL: x = -2, y = -25, z = 65, figure 7.13 A), across delays and independently of the answers to the FoP. This region matches with the center of the primary somatosensory cortex, where trunk touches are coded. The activity in this region varied significantly with the increase of delay, from 200 msec to 400 msec and then plateauing at 400 msec and 500 msec (figure 7.13 B). This analysis was performed with a two-sided t-test, that revealed a significant difference, with p-value under 0.005 when comparing 200 and 300 msec, and a significant difference between 300 and 400 msec, with $p < 0.05$.

The same comparison of activity across delays was performed in the identified regions, for their respective latencies, as a way to test if these effects could be related to delay as well. None of the regions showed significant differences in activation when analysed across delays and independently of the answer to the FoP (Figure 7.14 A-B).

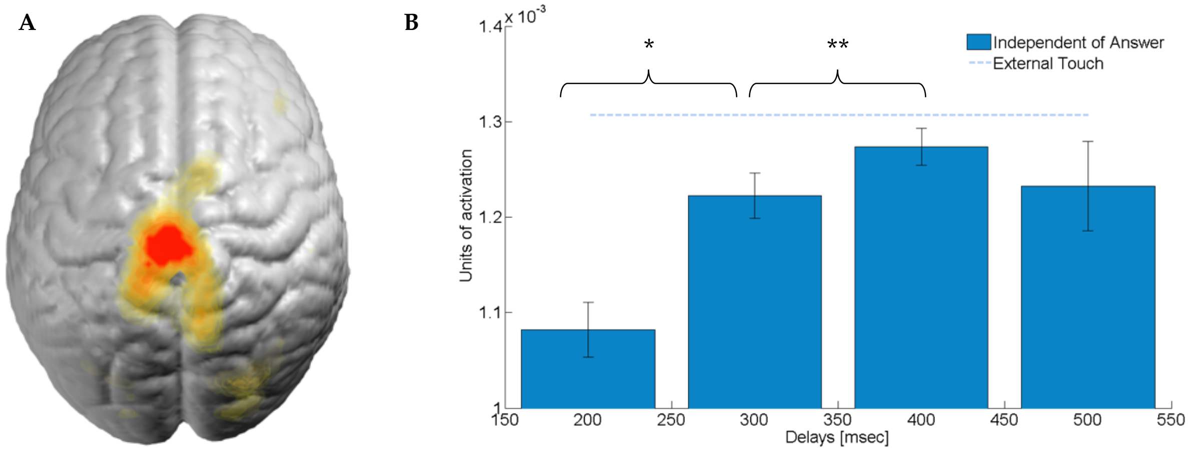


Figure 7.13 Activity in the Center of the Primary Somatosensory Cortex for Interval 1
(A) Brain region identified as having the activity peak for I1, it is the Medial Frontal Gyrus (TAL maxima: x = -2, y = -25, z = 65).

(B) Activity on the peak of activity for Interval 1. The bars in blue represent the mean activity at the given region, the grey dashed line the mean activity during the control condition of external touch and in black the standard deviation. It is observed that the activity increases with delay, reaching a plateau at 400 msec.

(*) Two-sided t-test reveals a significant difference in activity with $p < 0.005$.

(**) Two-sided t-test reveals a significant difference in activity with $p < 0.05$.

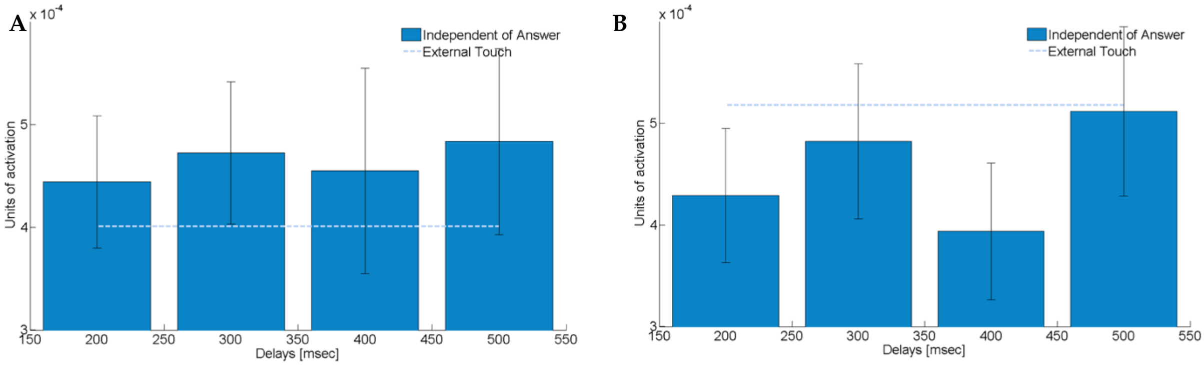


Figure 7.14 Activity for the Identified Regions in their Respective Intervals Across Delays
For both activity barplots, the bars in blue represent the mean activity at the given region, the grey dashed line the mean activity during the control condition of external touch and in black the standard deviation.

(A) Activity on the Inferior Post-Central Gyrus during I1 across different delays independently of the experienced FoP. No significant difference in activity was observed between any of the delays. **(B)** Activity on the Inferior Parietal Lobule during I2 across different delays independently of the experienced FoP. No significant difference in activity was observed between any of the delays.

7.4 Discussion

With electroencephalography, our main objective with experiment 2 was to determine, where in the brain the subjective experience of the Feeling of a Presence appears. To do so, we modelled the data with a GLM approach and started by analyzing the parameters for our predictors of interest, namely, delays, subjective experience of the FoP and interaction between the two. A post-hoc analysis to the effect of the FoP at specific delays based on the interaction results, followed by source localization methods, was able to fulfill this goal, identifying the Inferior Post-Central Gyrus (SII) and the Inferior Parietal Lobule as the main sources of the FoP.

7.4.1 Somatosensory Evoked Potentials

The expected somatosensory evoked potentials were seen in the average of all conditions and all trials. P100 and N140 are extensively observed in literature [82-85]. P100 has been shown to reflect the bilateral activation of the secondary somatosensory (SII) cortex in literature regarding finger stimulation [85], while N140 is suggested to be a transformation from the tactile sensory experience to perceptual awareness, which in other words means that it would be, the step taking the touch from low level processing (unconscious) to conscious awareness of having been touched [84]. P200 and N300, are more complicated to interpret due to their late latency, however, for this exact reason, they should be associated with higher order functions [82, 84, 86]. P200 is likely to be the result of an accumulation of activity from SI and SII. It has been suggested to be a comparison of the current touch with a ‘touch template’ that the brain keeps in working memory [84]. The presence of the N300 has been linked with stronger stimuli being applied among the rest [86]. Although earlier components exist, they are usually observed only when experiments are conducted with electrical stimulation of the medial nerve. With tactile stimulation such as ours, they are not observable (P50 could eventually be visible with more trials). Moreover, the literature regarding SEP from tactile stimuli exists mostly for finger and wrist. To our knowledge, convenient literature on trunk stimulation is not available yet.

7.4.2 Sensorimotor Mismatches and the Effect of Delay

Analyzing the different predictors for our modelled data revealed significant clusters for two different effects. Here, we will start by addressing the effect of the delay on the signal, when not experiencing FoP. This analysis showed significant clusters with a latency going from 0 msec to 183 msec regarding the touch on the back. Within this time-period there are three clusters. The earliness of the only positive cluster, 0 to 132 msec, and of one of the negative ones, 0 to 85 msec, is likely to be related to the motor preparation and motor commands required to do the task. Since we are addressing the effect of delay, one should consider that at no delay the presence of the arm movement would be substantial around 0 to 50 msec, while at 500 msec of delay it would not be seen, meaning that when comparing trials based on the delay used, it is natural to see effects already at 0 msec. Moreover, this effect is consistent with previous literature on self-touch, showing how healthy people have an attenuated SEP when experiencing a condition of self-touch versus a condition perceived as an external touch (such as conditions with no delay or 100 msec of delay versus conditions with a higher delay) [45, 46, 87].

Following the observation of this effect in the modelled data, an important task before analyzing the neural correlates of the FoP was to verify that we could indeed see the main effect of delay extensively observed in literature [87, 88]. Once again, this effect consists in a significant attenuation of activity when in a condition of self-touch versus a condition of external touch. In our case, this would translate into seeing attenuation in the no delay condition, while observing higher levels of activity for 500 msec of delay. This was performed by measuring the activity on the most active part of the brain, which was the primary somatosensory cortex, on a latency consistent with the observed P100 (60-89 msec) across delays and independently of the subjective experience of the FoP. By doing this in such a latency we are assessing the attenuation due to self-touch on the time range where convenient literature found most significant effects [87-90]. Moreover, this spatial distribution (SI) can be explained by the fact that the areas of the sensorimotor cortex encoding the trunk are situated in the medial regions [91-94] and the receptive fields of the back are represented bilaterally in the primary somatosensory cortex [95]. Because our task requires a more complex movement than the usual paradigms assessing self-touch versus other touch [45, 57, 87, 96], we did not perform this for the trials without delay and with 100 msec of delay as they would be too confounded due to the tapping moving required to perform the experiment. For the rest of the delays used, we found significant increases of activity on the top of the somatosensory cortex, suggesting that sensory attenuation decreases with increasing delay. Or in others words, that activity increases the more the touch on the back is perceived as external, as expected.

Notwithstanding the report of this effect, we did not engage in further explorations of this effect, as the effect of delay without considering the FoP does not give any information on the neural bases of the FoP.

7.4.3 Sensorimotor Mismatches and the Feeling of a Presence

Our results on the modelled data, show an interaction between delays and the rating for the subjective experience of the Feeling of a Presence. This effect occurred from 52 to 134 msec from the touch on the back and it is far more interesting than the previous one, since it is a direct result from both the experimental condition and subjective experience of the FoP. This compelled us to conduct a post-hoc analysis to assess the effect of the FoP at specific delays, revealing an effect of the Feeling of a Presence when experiencing 400 and 500 msec of delay. The significant cluster observed ranged from 60 to 119 msec. Divided into periods of interest (60 – 89 msec and 91 – 119 msec), we can observe a match between said periods and the latency of the observed early components, P100 and N140. Some of the effects of self-touch debated throughout this thesis' introduction occur within the identified periods of interest. Specifically, perception attenuation (the attenuation of a sensory input due to self-touch) occurs within the first time-period [88], as we have just seen in the previous sub-chapter. Acknowledging that the FoP might be a problem of distinguishing self-produced stimuli from external stimuli, it is positive to see that our paradigm produces an effect that seems to contain the differences observed between self and other touch observed consistently in previous literature [45, 87, 88], even when looking at effects specific to the FoP.

More interesting however, is that the observed latencies also match previous results of attenuation deficits in schizophrenic patients. For this specific purpose, we will address a study regarding auditory hallucinations by Ford, Roach and Faustman (2007) [89, 90]. Note that, as said by these authors, and other such as Frith, Fletcher [53] and Blakemore [10], the assumptions for the forward model across different sensory modalities, such as vision and hearing, should be the same. In brief, for the specific case of hearing, the efference copies come from speech or own thoughts and then are used to attenuate auditory input [90]. In Ford, Roach and Faustman's experiments [89, 90], participants would have trials of speaking, where they would utter vowels for a short time, and trials of listening where they would listen to their uttered vowels which were previously recorded. Researchers found in both studies [89, 90], that while healthy participants have attenuation on the N100 auditory component of the speaking task (when compared to the listening one), schizophrenic patients have the same activity for both tasks. The interesting fact, is that the latency of our effects on the first POI matches the one observed on this study. This starts to show us, a small link between the FoP and mechanisms of psychotic states, which we will debate further in this discussion and in the final conclusions

7.4.3.1 Brain Sources – Feeling of a Presence

The results from the interaction parameter and subsequent post-hoc analysis allowed the identification of two different brain regions as being responsible for the FoP. We found a significantly lower activation of the Secondary Somatosensory Cortex for the group of 400 and 500 msec of delay when participants reported having the Feeling of a Presence, regarding the first POI (60-89 msec), and the same significant difference for the Inferior Parietal Lobule in the second POI (91-119 msec).

Our findings regarding the SII go in the same direction as a study performed with healthy participants and schizophrenic patients, that also found the SII has one of the main brain regions displaying differences in activation when synchronous stimuli were presented to healthy individuals vs. schizophrenics [54]. In the referred study, participants had to perform a task similar to the matching force task described in chapter '2.3.1 - Considerations on Self-Touch' from the introduction, however, here they would tap on a pressure sensor with their right index finger and a force would be presented to their left index finger either synchronously, asynchronously, not presented at all or even presented without the button press.

The inferior parietal lobule has previously been associated with agency [96], a process which we believe plays a more secondary role in the subjective experience of the FoP, mainly due to it being a higher cognitive process. However, the dysfunctions of this brain region affecting agency, have been correlated with the severity of hallucinations in schizophrenia [97]. A PET study where healthy participants had to manipulate a joystick and see a virtual hand move according to the participant's movements, deployed 4 conditions to study the cerebral anatomy of agency. Participants would see the virtual hand moving, as it was in reality, with a 25º disturbance to one side, with a 50º disturbance to one side, or performed by the experimenter. The results showed that the right inferior parietal lobule would increase activity the more the participant lost agency over the task [98]. A follow-up on this study, done by the same authors, found that in schizophrenic patients, congruency between the hand movement and the observed movement of the virtual hand was not a modulating factor for activity of the inferior parietal lobule as seen in healthy participants [97]. Moreover, current literature has shown that resting state activity in this brain region is higher in schizophrenic patients than in healthy people [99, 100]. Putting these studies together we could argue that the inferior parietal lobule in schizophrenics, is more prompt to higher levels of activity, potentially impairing their agency, as increases of activity in this region are related to the loss of agency.

Finally, in regards to the direction of our effect, we were expecting to see a bigger activation in the scenario of experiencing the FoP, as we hypothesized that actually feeling that a presence was doing it instead of oneself, could create a more salient stimulus than just dissociating your actions from the touch on the back (situations of high delays with FoP versus situations of high delays without FoP, respectively). However, the fact that our effect is observed when looking at conditions in the same group of delays, and the expected attenuation pattern (across delays) is on the top of the SI, means that our results are specifically related to the FoP and therefore, as no literature exists on this matter, no direction of the effect should be assumed in the first place. We will present a speculatory hypothesis for this in the next chapter.

8 General Conclusions

The Feeling of a Presence has been described in literature for more than a century and probably made its way into tales of the occult long before it was even acknowledged as a psychotic symptom. This dissertation set out to study the temporal dynamics and the neural correlates of the Feeling of a Presence, following the first study ever to induce the FoP in healthy individuals [1]. With these goals in mind, we designed a new protocol deploying more delays than what was previously used in 2014 [1] and with EEG as an imaging technique. Furthermore, in the first session of both experiments we replicated the results from Blanke et al., 2014 [1] for significant differences on perceiving the FoP when comparing 500 msec against 0 msec, as a proof of concept.

The temporal dynamics of the Feeling of a Presence were found to correspond to a sigmoidal curve, having the perceived FoP increasing with higher delays. A pattern that was partially expected as we knew that the FoP had to be related to the distinction between self-touch and other-touch. After all it seems crucial to the identification of the presence, that one must perceive the touch as external. Blakemore has demonstrated that this distinction follows a step-wise pattern, with the interval between 200 and 300 msec of delay marking the threshold, in which self-touch becomes indistinguishable from an external one [46]. Notably, our paradigm managed to accurately englobe this phenomenon and to almost double the perceived FoP in both experiments, by increasing the delay used.

For the neural correlates of the FoP, we must point out a remarkable feat. Our protocol was able to induce different subjective experiences with the exact same experimental conditions, in every participant, something that was not achieved previously and allowed to compare differences in brain sources, that could only be explained by the subjective sensation of the FoP, isolated from other confounding factors. This analysis revealed the Secondary Somatosensory Cortex and the Inferior Parietal Lobule as responsible parties for the arousal of the FoP. By comparing the conditions of having the subjective experience of the FoP versus not having it, at 400 and 500 msec of delay, we found a negative cluster in both the mentioned areas, at the latency of P100 for SII and at the latency of N140 for the inferior parietal lobule.

Some of the most interesting aspects of our discoveries, aside from the findings themselves, are the links we can observe between the latencies and brain areas of the FoP, and literature on self-touch and psychotic states.

Starting with self-touch, the first link we can see is immediately the similarity between the threshold for high ratings on the perceived FoP and the threshold described by Blakemore that distinguishes self from other touch [46]. The latency of our first POI, 60-89 msec, englobes

P100, a component found to be modulated by self-touch [87]. The brain region, SII, we identified in this specific latency as being modulated by whether or not one perceives the FoP, has been linked in previous literature with the distinction of self versus other-touch [44, 101]. Moreover, the SII has also been linked with the forward model for sensorimotor integration described in chapter '2.3.2 The Predictive Brain' [101]. Despite not being our main focus, it is interesting to see these connections between our results and this literature, as the paradigm we used to elicit the FoP has a strong core in manipulating BSC through self-touch and sensorimotor mismatches, similar to what has been used in self-touch experiments.

We will now approach a much more relevant and interesting aspect for the FoP, which is the possible link with psychotic states, based on our findings and current literature. Being a part of psychotic states, we expected, as presented in chapter '2. *Background in Neuroscience*', that the FoP shared some of its mechanisms with the ones seen on such psychotic events. In fact, our paradigm aimed at disturbing BSC precisely because there is a strong hypothesis that some of the positive symptoms of schizophrenia can be explained by a poor sense of self [10, 96]. Fletcher and Frith give an insightful explanation on the positive symptoms of schizophrenia and their connection with sensorimotor integration deficits [53]. The deficit theory assumes that the major problem causing these psychotic event is the improper distinction between relevant and irrelevant stimuli [10, 53]. We have seen this in the introduction of this dissertation both for healthy individuals, where we presented studies showing how sensory predictions are used to attenuate incoming sensory feedback in the case of self-touch [44-47, 88, 101], and in the case of schizophrenics from whom it is widely believed that those sensory predictions have deficits which impair the expected sensory attenuations [52, 54]. In our case, identifying the SII as one of the brain regions responsible for the FoP is something that goes perfectly with these demonstrated studies. As the SII is related to the forward model for sensorimotor integration [101], to the sensory attenuations in self-touch [44, 101] and especially to the disturbances of the predictions that should cause these attenuations in schizophrenics [54], it makes all sense to see it involved in a process such as the FoP. Another fact stated by Fletcher and Frith, and by Judith Ford [90], is that these models of attenuation for self-performed actions are similar in functioning for different sensory domains, as they are based on corollary discharges (estimates of sensory feedback through efference copies of the command that generates an action). With this said we point a last remark to the finding of the SII involvement in the FoP. The study by Ford et al., 2007, mentioned in chapter '*7.4.3 – Sensorimotor Mismatches and The Feeling of a Presence*' showed that in the case of auditory hallucinations, schizophrenic patients have less attenuation when hearing their own voice, in the N100 component [90]. This matches the latency where our effects were observed for the SII, that is believed to be exactly one of the responsibles for the forward model in sensorimotor integration.

The presence of the inferior parietal lobule, also corroborates the link with psychotic states. This area has shown in healthy individuals to increase its activity with loss of agency [98]. Such cannot be said for delusional psychotic patients which in fact, have this region unmodulated by agency [96, 97].

Lastly, we will address the direction of our effects, regarding the observed brain regions responsible for the FoP. The fact that both brain regions were less activated when experiencing the FoP is a subject hard to address, due to the novel nature of this topic and consequent lack of directly related literature. However, a speculatory hypothesis can be discussed if we compare healthy individuals with psychotic patients, as done before. In the review linking positive symptoms in schizophrenia with sensorimotor integration deficits, Fletcher and Frith (2008), also pose solid evidence that when presented with salient stimuli schizophrenic patients have significantly lower levels of activation in the midbrain if compared against healthy controls [53]. Unfortunately, the study they address, uses stimuli outside the sensorimotor domain and does not use self-generated actions to create the non-salient stimuli like in sensorimotor attenuation literature, which puts an obvious distance between our experiment and the one bring addressed. However, this is not the only study of this kind. Shergill et al., 2014, a study we have already address in this thesis, where researchers compare activations in the brain between healthy people and schizophrenic patients during the matching force task (described in chapter '*2.3.1 - Considerations on Self-Touch*'), gives a brief note on the differences they observed in the activation of SII between healthy people and schizophrenics. They state that the patient group has a diminished cerebral activity on the SII when compared to healthy controls, for the salient condition [54]. Moreover, we can observe from their results that despite showing the lack of attenuation in the condition of self-touch (so, having the SII largely more activated than healthy controls), the activity over SII then diminishes when in the presence of a salient stimuli, which is the opposite of what happens in a healthy person. Finally, our speculation for the direction of our effect is exactly based on this. Considering that in the situations in which we assessed these brain regions, the touch on the back should always be perceived as external (400 and 500 msec of delay are perceived as external touch [46]), we hypothesize that by inducing a psychotic-like state we have a decrease in activity on SII, just as Fletcher and Frith, and Shergill observed a diminished activity when comparing healthy people with schizophrenics for salient stimuli. This hypothesis is nonetheless a very speculative one, which would need further experiments in order to be corroborated, or disproved.

To the best of our knowledge, the results presented both for the temporal dynamics of the FoP and for its neural correlates are a novelty in literature, marking a solid contribution for the understanding of this hallucination. With these results we hope to advance the knowledge on the mechanisms of the Feeling of a Presence and to contribute to the understanding of hallucinations in psychosis. The present findings can also be viewed in the light of bodily self-consciousness and help to understand how these processes are modulated in the brain.

8.1 Limitations

Our study had two main limitations. Both of them are related to accuracy in time of the touch on the back and existed even though we recalibrated the participant's position after every resting period.

The first limitation is related to the way we identified the touch on the back. The triggers for this event are time-locked to the movement performed at the front, in such a way that if a participant is in a condition of 300 msec of delay and he/she touches the virtual wall in front, the trigger for the touch on the back will appear 300 msec after the tapping of the wall was performed. This is not a relevant problem because the position is recalibrated at the beginning of each block and the position of the participants is monitored during the blocks. However, there could be room for improvement, by eventually adding a circuit for a pressure sensor on the slave robot. It would still have to be calibrated for each participant in terms of sensitivity. In any case, we consider that isolated this poses little to no problem for our experiment.

The second and last limitation we will address has to do with postural control. To the extent of our possibilities we tried to maintain participants in the exact same position during the blocks, however, even with the resting periods, participants would grow tired of being in the same standing position for almost 2 hours. Ultimately this meant that most of them would do small readjustments of posture, probably even involuntarily, such as switching their body weight more to one leg, then to the other and so on, causing their backs to deviate slightly from the initial position. For this problem, there is no immediate solution, as we do not want to constraint their backs, cannot predict their movements before they do it, and even with a sensor on the slave robot, if the participants moved, they would either increase or reduce the delay being used. Fortunately, the effects caused by these movements were very small and thanks to the monitoring being done, we could exclude trials with big movements from the participants.

Put together, we believed that these limitations had a small effect on the accuracy of the back-touch trigger, nevertheless dropping it from the desired 1 msec to a maximum 8-10 msec in the estimated worst scenarios.

8.2 Future Directions

Our study focuses mostly on SEPs analysis and source localization, mostly due to the time restraints of this thesis, to the time necessary to implement the new approach we used with the GLM and to the time that would be necessary to implement the approaches we are about to suggest.

Frequency analysis is clearly a step that should be taken in the future. This includes coherence analysis and connectivity analysis. It has been shown in literature that one of the aspects that is commonly impaired in psychotic patients is the 'communication' between brain regions [89, 102]. Therefore, it would be important to assess that aspect for the FoP as well.

In the light of the direction of our effect, we would consider relevant to conduct a study, eventually with fMRI for more spatial precision and to better compare with reference literature, to assess the level of activity in the brain regions we have identified, in four groups of participants. Healthy individuals not experiencing the FoP but performing a self vs. other touch task, healthy individuals experiencing the FoP according to our paradigm, psychotic patients experiencing our paradigm and psychotic patients that often report the FoP experiencing our paradigm. The final goal would be to correlate the lower activation of the SII and inferior parietal lobule of healthy individuals experiencing FoP with the lower activity of psychotic patients (as compared to healthy controls) on the midbrain and SII when presented with salient stimuli.

Bibliography

[1] O. Blanke, P. Pozeg, M. Hara, L. Heydrich, A. Serino, A. Yamamoto, T. Higuchi, R. Salomon, M. Seeck, T. Landis, S. Arzy, B. Herbelin, H. Bleuler, and G. Rognini, "Neurological and robot-controlled induction of an apparition" *Curr. Biol.*, vol. 24, no. 22, pp. 2681–2686, 2014.

[1a] O. Blanke, P. Pozeg, M. Hara, L. Heydrich, A. Serino, A. Yamamoto, T. Higuchi, R. Salomon, M. Seeck, T. Landis, S. Arzy, B. Herbelin, H. Bleuler, and G. Rognini, "Neurological and robot-controlled induction of an apparition" *Curr. Biol.*, vol. 24, supplemental information, 2014.

[2] O. Blanke and C. Mohr, "Out-of-body experience, heautoscopy, and autoscopic hallucination of neurological origin: Implications for neurocognitive mechanisms of corporeal awareness and self-consciousness," *Brain Res. Rev.*, vol. 50, no. 1, pp. 184–199, 2005.

[3] T. Brugha, N. Singleton, H. Meltzer, P. Bebbington, M. Farrell, R. Jenkins, J. Coid, T. Fryers, D. Melzer, and G. Lewis, "Psychosis in the community and in prisons: A report from the British National Survey of Psychiatric Morbidity," *Am. J. Psychiatry*, vol. 162, no. 4, pp. 774–780, 2005.

[4] G. Fénelon, T. Soulas, LC. De Langavant, I. Trinkler and A-C Bachoud-Lévi. "Feeling of presence in Parkinson's disease". *Journal of Neurology, Neurosurgery, and Psychiatry*. Vol. 82, no. 11, pp. 1219-1224, 2011.

[5] W. James, "Lecture III – The Reality of the Unseen" in The Varieties of Religious Experience: A Study in Human Nature. New York and London: Longmans, Green and Co, 1902

[6] K. Jaspers "Über leibhaftige Bewußtheiten (Bewußtheitstaüschungen)", in Psychopathologisches Elementarsymptom. Z Pathopsychol: Vol. 2, pp.150-161, 1913.

[7] M. Shermer, "The Sensed-Presence Effect". *Scientific American*. p. 34, 2009.

[8] O. Blanke, S. Ortigue, A. Coeytaux, T. Landis, A. Coeytaux, M. Martory, and T. Landis, "Hearing of a Presence". *Neurocase*. Vol. 9, No. 4, pp. 329-339, Oct. 2003.

[9] S. Arzy, M. Seeck, S. Ortigue, L. Spinelli, and O. Blanke, "Induction of an illusory shadow person" *Nature*, vol. 443, no. 7109, p. 287, Sep. 2006.

[10] S. Blakemore, D. M. Wolpert, and C. D. Frith, "Abnormalities in the awareness of action". *TRENDS in Cognitive Sciences*, Vol. 6, No. 6, pp. 237–242, 2002.

[11] P. Brugger, M. Regard and T. Landis. "Unilaterally-Felt 'Presences': The Neuropsychiatry of One's Invisible Doppleganger". *Neuropsychiatry, Neuropsychology and Behavioral Neurology*, Vol. 9, No. 2, pp. 114-122, 1996.

[12] A. Strindberg. "From an Occult Diary" in *Inferno*. 1897. New York: Penguin Books, 1979.

[13] O. Blanke, "Multisensory brain mechanisms of bodily self-consciousness.," *Nat. Rev. Neurosci.*, vol. 13, no. 8, pp. 556–71, 2012.

[14] A. Serino, A. Alsmith, M. Costantini, A. Mandrigin, A. Tajadura-Jimenez, and C. Lopez, "Bodily ownership and self-location: Components of bodily self-consciousness," *Conscious. Cogn.*, vol. 22, no. 4, pp. 1239–1252, 2013.

[15] JE Aspell, B. Lenggenhager and O. Blanke. "Multisensory Perception and Bodily Self-Consciousness: From Out-of-Body to Inside-Body Experience" in *The Neural Bases of Multisensory Processes*. Boca Raton (FL): CRC Press/Taylor & Francis; 2012. Chapter 24.

[16] M. Hara, R. Salomon, W. van der Zwaag, T. Kober, G. Rognini, H. Nabae, A. Yamamoto, O. Blanke, and T. Higuchi, "A novel manipulation method of human body ownership using an fMRI-compatible master-slave system," *J. Neurosci. Methods*, vol. 235, pp. 25–34, 2014.

[17] V. I. Petkova, M. Björnsdotter, G. Gentile, T. Jonsson, T. Q. Li, and H. H. Ehrsson, "From part- to whole-body ownership in the multisensory brain," *Curr. Biol.*, vol. 21, no. 13, pp. 1118–1122, 2011.

[18] H. H. Ehrsson, "Touching a Rubber Hand: Feeling of Body Ownership Is Associated with Activity in Multisensory Brain Areas", *J. Neurosci.*, vol. 25, no. 45, pp. 10564–10573, 2005.

[19] B. Lenggenhager, T. Tadi, T. Metzinger, and O. Blanke, "Video Ergo Sum: Manipulating Bodily Self-Consciousness", *Science*, vol. 317, no. 5841, p. 1096 LP-1099, Aug. 2007.

[20] H. H. Ehrsson, "The experimental induction of out-of-body experiences.," *Science*, vol. 317, no. 5841, p. 1048, 2007.

[21] H. H. Ehrsson, "That's My Hand! Activity in Premotor Cortex Reflects Feeling of Ownership of a Limb," *Science,* vol. 305, no. 5685, pp. 875–877, 2004.

[22] O. Blanke, M. Slater, and A. Serino, "Behavioral, Neural, and Computational Principles of Bodily Self-Consciousness," *Neuron*, vol. 88, no. 1, pp. 145–166, 2015.

[23] J. E. Aspell, B. Lenggenhager, and O. Blanke, "Keeping in touch with one's self: Multisensory mechanisms of self-consciousness," *PLoS One*, vol. 4, no. 8, pp. 25–27, 2009.

[24] A. Serino & P. Haggard, "Touch and The Body", *Neuroscience and Biobehavioral Reviews*, *34*, pp. 224–236, 2010.

[25] S. Schütz-bosbach, J. Jiri, and P. Haggard, "Touchant-touché: The role of self-touch in the representation of body structure", *Conscious. Cogn.*, vol. 18, no. 1, pp. 2–11, 2009.

[26] M. Tsakiris, M. D. Hesse, and C. Boy, "Neural Signatures of Body Ownership: A Sensory Network for Bodily Self- Consciousness," no. October, pp. 2235–2244, 2007.

[27] M. Jeannerod, "The mechanism of self-recognition in humans," *Behav. Brain Res.*, vol. 142, no. 1–2, pp. 1–15, 2003.

[28] S. Ionta, L. Heydrich, B. Lenggenhager, M. Mouthon, E. Fornari, D. Chapuis, R. Gassert, and O. Blanke, "Multisensory Mechanisms in Temporo-Parietal Cortex Support Self-Location and First-Person Perspective," *Neuron*, vol. 70, no. 2, pp. 363–374, 2011.

[29] G. M. Stratton, "IV. - The Spatial Harmony of Touch and Sight.," *Mind*, vol. VIII, no. 4, pp. 492–505, Jan. 1899.

[30] M. Botvinick and J. Cohen, "Rubber hands 'feel' touch that eyes see.," *Nature*, vol. 391, no. 6669, p. 756, 1998.

[31] H. H. Ehrsson, K. Wiech, N. Weiskopf, R. J. Dolan, and R. E. Passingham, "Threatening a rubber hand that you feel is yours elicits a cortical anxiety response.," *Proc. Natl. Acad. Sci. U. S. A.*, vol. 104, no. 23, pp. 9828–33, 2007.

[32] Youtube.com, 'Rubber Hand Illusion, take 2', 2009. [Online]. Available: https://www.youtube.com/watch?v=nzF_DfOafKw.

[33] A. Morin, "Levels of consciousness and self-awareness: A comparison and integration of various neurocognitive views", *Consciousness and Cognition*, vol. 15, pp. 358–371, 2006.

[34] V. I. Petkova and H. H. Ehrsson, "If I Were You: Perceptual Illusion of Body Swapping," vol. 3, no. 12, 2008.

[35] H. E. van Stralen, M. J. E. van Zandvoort, and H. C. Dijkerman, "The role of self-touch in somatosensory and body representation disorders after stroke.," *Philos. Trans. R. Soc. Lond. B. Biol. Sci.*, vol. 366, no. 1581, pp. 3142–52, 2011.

[36] F. De Vignemont, H. H. Ehrsson, and P. Haggard, "Bodily Illusions Modulate Tactile Perception," vol. 15, pp. 1286–1290, 2005.

[37] D. Wolpert, Z. Ghahramani & M. I. Jourdan. "An Internal Model for Sensorimotor Integration". *Science* 269: 1880-1882, 1995.

[38] L. Weiskrantz, J. Elliott, and C. Darlington, "Preliminary observations on tickling oneself.," *Nature*, vol. 230, no. 5296, pp. 598–599, 1971.

[39] S. Shergill, P. Bays, C. Frith and D. Wolpert, "Two Eyes for an Eye: The Neuroscience of Force Escalation," *Science*, Vol. 301, No. July, p. 187, 2003.

[40] A. Bubic, D. Y. von Cramon, and R. I. Schubotz, "Prediction, cognition and the brain.," *Front. Hum. Neurosci.*, vol. 4, no. March, p. 25, 2010.

[41] Z. Ghahramani, D. Wolpert and M.I. Jordan, "Computational Models of Sensorimotor Integration", *Self-Organiaztion, Computational Maps and Motor Control*, Elsevier Press.

[42] R. C. Mial, D. M. Wolpert, "Forward Models for Physiological Motor Control", *Neural Networks*, Vol.9, No. 8, pp.1265-1279, 1996.

[43] D. M. Wolpert, & M. Kawato, "Multiple Paried Forward and Inverse Models for Motor Contro", *Neural Networks*, *11*, pp.1317–1329, 1998.

[44] S. J. Blakemore, D. M. Wolpert, and C. D. Frith, "Central cancellation of self-produced tickle sensation.," *Nat. Neurosci.*, vol. 1, no. 7, pp. 635–640, 1998.

[45] M. D. Hesse, N. Nishitani, G. R. Fink, V. Jousmäki, and R. Hari, "Attenuation of somatosensory responses to self-produced tactile stimulation," *Cereb. Cortex*, vol. 20, no. 2, pp. 425–432, 2010.

[46] S.-J. Blakemore, C. D. Frith, and D. M. Wolpert, "Spatio-Temporal Prediction Modulates the Perception of Self-Produced Stimuli", *J. Cogn. Neurosci.*, vol. 11, no. 5, pp. 551–559, 1999.

[47] P. M. Bays, D. M. Wolpert, and J. R. Flanagan, "Perception of the consequences of self-action is temporally tuned and event driven," *Curr. Biol.*, vol. 15, no. 12, pp. 1125–1128, 2005.
[48] O. L. Kay SR, Fiszbein A, "The Positive and Negative Syndrome Scale for schizophrenia," *Schizophr Bull.*, vol. 13, no. 2, pp. 261–276, 1987.
[49] P. Byrne, "Managing the acute psychotic episode.," *BMJ*, vol. 334, no. 7595, pp. 686–692, 2007.
[50] L. A. Sass, "Schizophrenia, Consciousness, and the Self," pp. 427–444, 1998.
[51] C.S. Mellors, "First-rank symptoms of schizophrenia", *Br. J. Psychiatry* 117, 15-23, 1970.
[52] S. S. Shergill, G. Samson, P. M. Bays, C. D. Frith, and D. M. Wolpert, "Evidence for sensory prediction deficits in schizophrenia," *Am. J. Psychiatry*, vol. 162, no. 12, pp. 2384-2386, 2005.
[53] P. C. Fletcher and C. D. Frith, "Perceiving is believing: a Bayesian approach to explaining the positive symptoms of schizophrenia", *Nature Reviews*, vol. 10, January, 2009.
[54] S. S. Shergill, T. P. White, D. W. Joyce, P. M. Bays, D. M. Wolpert, and C. D. Frith, "Functional magnetic resonance imaging of impaired sensory prediction in schizophrenia", *JAMA psychiatry*, vol. 71, no. 1, pp. 28–35, 2014.
[55] G. Xue, Z. Lu, I. P. Levin, and A. Bechara, "The impact of prior risk experiences on subsequent risky decision-making: The role of the insula," *Neuroimage*, vol. 50, no. 2, pp. 709–716, 2010.
[56] A. D. (Bud) Craig, "How do you feel — now? The anterior insula and human awareness," *Nat. Rev. Neurosci.*, vol. 10, no. 1, pp. 59–70, 2009.
[57] P. Capotosto, C. Babiloni, G. L. Romani, and M. Corbetta, "Modulation of Anticipatory Alpha Rhythms," vol. 29, no. 18, pp. 5863–5872, 2008.
[58] R. Saxe and N. Kanwisher, "People thinking about thinking people: The role of the temporo-parietal junction in 'theory of mind,'" *Neuroimage*, vol. 19, no. 4, pp. 1835–1842, 2003.
[59] H. Berger, Über das Elektroenkephalogramm des Menschen. 1^{st} Report. Arch. Psychiatr. Nervenkr. *87*, 527–570, 1929
[60] P. L. Nunez and R. Srinivasan, "Brain Structures and Scalp Potentials" in *Electric Fields of the Brain: The Neurophysics of EEG*, Oxford University Press, 2006.
[61] E. A. Curran and M. J. Stokes, "Learning to control brain activity: A review of the production and control of EEG components for driving brain - computer interface (BCI) systems", *Brain and Cognition*, Vol. 51, pp. 326–336, 2003.
[62] R. Seeley Rod, D. Trent and P. Tate. "Functional Organization of the Nervous System" in *Anatomy & Physiology*, McGraw-Hill Companies, 2005
[63] F. Lopes da Silva, "EEG and MEG: Relevance to neuroscience", *Neuron*, *80*(5), 1112–1128, 2013.
[64] G.Buzsáki, C. A. Anastassiou and C. Koch, "The Origin of Extracellular Fields and Currents – EEG, ECoG, LFP and Spikes", *Nature Reviews Neuroscience*, Vol. 13, No. 6, pp. 407-420, 2016.

[65] D. H. Brainard, "The Psychophysics Toolbox", *Spatial Vision*, Vol. 10 pp. 433–436.
[66] A. Delorme and S. Makeig, "EEGLAB : an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis," vol. 134, pp. 9–21, 2004.
[67] M. Chaumon, D. V. M. Bishop, and N. A. Busch, "A practical guide to the selection of independent components of the electroencephalogram for artifact correction," *J. Neurosci. Methods*, vol. 250, pp. 47–63, 2015.
[68] P. Comon, "Independent component analysis, A new concept?", *Signal Processing*, vol. 36, no. 3, pp. 287–314, 1994.
[69] C. Jutten and J. Herault, "Blind seperation of sources, part I: an adaptive algorithm based on neuromimetic architecture," *Signal Processing*, vol. 24, pp. 1–10, 1991.
[70] S. K. Herbst, M. Chaumon, T. B. Penney, and N. A. Busch, "Flicker-Induced Time Dilation Does Not Modulate EEG Correlates of Temporal Encoding", *Brain Topogr.*, vol. 28, no. 4, pp. 559–569, 2015.
[71] A. B. Sekuler, "Healthy aging delays scalp EEG sensitivity to noise in a face discrimination task", *Frontiers in Psychology*, vol. 1, no. July, pp. 1–14, 2010.
[72] C. R. Pernet, N. Chauveau, C. Gaspar, and G. A. Rousselet, "Research Article LIMO EEG : A Toolbox for Hierarchical LInear MOdeling of ElectroEncephaloGraphic Data", *Computational Intelligence and Neuroscience*, vol. 2011, 2011.
[73] T. Tsai and J. Gill, "Interactions in Generalized Linear Models: Theoretical Issues and an Application to Personal Vote-Earning Attributes", *Soc. Sci.,* pp. 91–113, 2013.
[74] R. Penrose, 'A generalized inverse for matrices', *Mathematical Proceedings of the Cambridge Philosophical Society*, Vol. 51, No. 3, pp. 406–413, 1955.
[75] S. Kullback, and R. A. Leibler, On information and sufficiency, *The Annals of Mathematical Statistics* Vol. 22, No. 1, pp. 79-86, March 1951.
[76] K. P. Burnham and D. R. Anderson, "Kullback-Leibler information as a basis for strong inference in ecological studies", *Wildlife Research* Vol. 28, pp. 111-119, 2001.
[77] R. Oostenveld, P. Fries, E. Maris, and J. Schoffelen, "FieldTrip : Open Source Software for Advanced Analysis of MEG , EEG , and Invasive Electrophysiological Data", vol. 2011, 2011.
[78] C. M. Michel, M. M. Murray, G. Lantz, S. Gonzalez, L. Spinelli, and R. Grave De Peralta, "EEG source imaging", *Clin. Neurophysiol.*, vol. 115, no. 10, pp. 2195–2222, 2004.
[79] R. G. D. P. Menendez, S. G. Andino, G. Lantz, C. M. Michel, and T. Landis, "Noninvasive localization of electromagnetic epileptic activity. I. Method descriptions and simulations," *Brain Topogr.*, vol. 14, no. 2, pp. 131–137, 2001.
[80] W. Skrandies, "Global field power and topographic similarity," *Brain Topogr.*, vol. 3, no. 1, pp. 137–141, 1990.
[81] J. Talairach and P. Tournoux, "Co-planar stereotaxic atlas of the human brain: a 3-dimensional proportional system, an approach to cerebral imaging". New York: Theme Medical, 1988.

[82] R. C. Josiassen, C. Shagass, R. A. Roemer, S. Slepner, and B. Czartorysky, "Early cognitive components of somatosensory event-related potentials," *Int. J. Psychophysiol.*, vol. 9, no. 2, pp. 139–149, 1990.

[83] J. E. Desmedt, Nguyen Tran Huy, and M. Bourguet, "The cognitive P40, N60 and P100 components of somatosensory evoked potentials and the earliest electrical signs of sensory processing in man," *Electroencephalogr. Clin. Neurophysiol.*, vol. 56, no. 4, pp. 272–282, 1983.

[84] D. A. E. Bolton, W. E. McIlroy, and W. R. Staines, "The impact of light fingertip touch on haptic cortical processing during a standing balance task," *Exp. Brain Res.*, vol. 212, no. 2, pp. 279–291, 2011.

[85] H. Hämäläinen, J. Kekoni, M. Sams, K. Reinikainen, and R. Näätänen, "Human somatosensory evoked potentials to mechanical pulses and vibration: contributions of SI and SII somatosensory cortices to P50 and P100 components," *Electroencephalogr. Clin. Neurophysiol.*, vol. 75, no. 2, pp. 13–21, 1990.

[86] P. T. Michie, H. M. Bearparic, J. M. Crawford and L. C.T. Glue, "The Effects of Spatial Selective Attention on the Somatosensory Event-Related Potential", *Psychophysiology*, Vol. 24, pp. 449–463, 1987.

[87] H. Hogendoorn, M. Kammers, P. Haggard, and F. Verstraten, "Self-touch modulates the somatosensory evoked P100," *Exp. Brain Res.*, vol. 233, no. 10, pp. 2845–2858, 2015.

[88] X. C. E. Palmer, X. M. Davare, and J. M. Kilner, "Physiological and Perceptual Sensory Attenuation Have Different Underlying Neurophysiological Correlates", *The Journal of Neuroscience*, vol. 36, no. 42, pp. 10803–10812, 2016.

[89] J. M. Ford, D. H. Mathalon, T. Heinks, S. Kalba, W. O. Faustman, and W. T. Roth, "Neurophysiological evidence of corollary discharge dysfunction in schizophrenia," *Am. J. Psychiatry*, vol. 158, no. 12, pp. 2069–2071, 2001.

[90] J. M. Ford, B. J. Roach, W. O. Faustman, and D. H. Mathalon, "Synch before you speak: Auditory hallucinations in schizophrenia," *Am. J. Psychiatry*, vol. 164, no. 3, pp. 458–466, 2007.

[91] W. Penfiel and H. Jasper, "Epilepsy and the functional anatomy of the human brain", B*oston: Little, Brown*, pp. 122-126, 1954.

[92] J. H. Kaas, R. J. Nelson, M. Sur, C. S. Lin and M. M. Merzenich, "Multiple representations of the body within the primary somatosensory cortex of primates". *Science*, Vol.*204*, No. 4392, 521-523, 1979.

[93] R. P. Lesser, H. Lüders, G. Klem, D. S. Dinner, H. H. Morris, J. F. Hahn and E. Wyllie, "Extraoperative Cortical Functional Localization in Patients with Epilepsy", *Journal of Clinical Neurophysiology*, Vol. 4, No. 1, 1987.

[94] R. Kakigi, M. Hoshiyama, M. Shimojo, D. Naka, H. Yamasaki, S. Watanabe and A. Nakamura, "The somatosensory evoked magnetic fields", *Progress in neurobiology*, Vol. 61, No. 5, pp. 495-523, 2000.

[95] S. B. Eickhoff, C. Grefkes and K. Zilles, "The Somatotopic Organization of Cytoarchitectonic Areas on the Human Parietal Operculum", *Cerebral Cortex*, Vol. 17, No. 8, pp. 1800-1811 August 2007.

[96] M. Jeannerod, "The sense of agency and its disturbances in schizophrenia: A reappraisal", *Exp. Brain Res.*, vol. 192, no. 3, pp. 527–532, 2009.

[97] C. Farrer, N. Franck, C. D. Frith, J. Decety, N. Georgieff, T. D'Amato, and M. Jeannerod, "Neural correlates of action attribution in schizophrenia", *Psychiatry Res. - Neuroimaging*, vol. 131, no. 1, pp. 31–44, 2004.

[98] C. Farrer, N. Franck, N. Georgieff, C. D. Frith, J. Decety, and M. Jeannerod, "Modulating the experience of agency: A positron emission tomography study," *Neuroimage*, vol. 18, no. 2, pp. 324–333, 2003.

[99] S. A. Spence, D. J. Brooks, S. R. Hirsch, P. F. Liddle, J. Meehan, and P. M. Grasby, "A PET study of voluntary movement in schizophrenic patients experiencing passivity phenomena (delusions of alien control)", *Brain*, vol. 120, no. 11, pp. 1997–2011, 1997.

[100] H. C. Whalley, E. Simonotto, S. Flett, I. Marshall, K. P. Ebmeier, D. G. C. Owens, N. H. Goddard, E. C. Johnstone, and S. M. Lawrie, "fMRI correlates of state and trait effects in subjects at genetically enhanced risk of schizophrenia", *Brain*, Vol. 127, No. 3, p. 478–490, 2004.

[101] S. S. Shergill, T. P. White, D. W. Joyce, P. M. Bays, D. M. Wolpert, and C. D. Frith, "Modulation of somatosensory processing by action," *Neuroimage*, vol. 70, pp. 356–362, 2013.

[102] J. M. Ford, D. H. Mathalon, S. Whitfield, W. O. Faustman, and W. T. Roth, "Reduced communication between frontal and temporal lobes during talking in schizophrenia," *Biol. Psychiatry*, vol. 51, no. 6, pp. 485–492, 2002.

[103] T. Jung, S. Makeig, M. Westerfeild, J. Townsend, E. Courchesne, and T. J. Sejnowski, "Analysis and Visualization of Single-Trial Event-Related Potentials", *Human Brain Mapping*, vol. 14, pp.166-185, 2001