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Multisensory processing and agency in VR embodiment: Interactions through BCI and their therapeutic applications

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Multisensory processing and agency in VR embodiment: Interactions through BCI and their therapeutic applications

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“The most exciting phrase to hear in science, the one that heralds new discoveries, is not 'Eureka!' but 'That's funny...'”

Isaac Asimov

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Abstract

Body ownership refers to the experience that this body is my body and is closely linked to consciousness. Body ownership is believed to evolve through multisensory integration processes which has been shown in the rubber hand illusion. This illusion induces ownership over a rubber hand by simultaneously stroking real and rubber hand with a paint brush, while the person's real hand is out of sight. This results in the illusory experience that the rubber hand is part of one's own body. Illusions of body ownership can also be experienced in immersive virtual reality (VR), which was used in all three experiments of this thesis.

The first experiment of this thesis aimed at investigating the underlying mechanisms of body ownership. Experiments on tactile, visual, and auditory perception using electroencephalographic recordings show that spontaneous neuronal activity, which is neuronal activity that cannot be linked to specific inputs or outputs of the brain, can predict the perception of a stimulus. Spontaneous neuronal activity measured with fMRI typically fluctuates between 0.01 and 0.1 Hz and is believed to be organized in networks, also referred to as resting state networks. These networks have been related to cognitive, somatosensory, and sensory functions. Some people who participated in body ownership experiments in our laboratory reported to feel changes in body ownership over time, raising the question whether such fluctuations of the body ownership illusion are present in more people, and if so, whether these illusion-fluctuations can be predicted by spontaneous brain activity. To investigate this, we measured the changes in body ownership illusion with a visuotactile simultaneity task in two different conditions. In one condition participant perceived high and in the other condition low body ownership. We found differences in the simultaneity threshold required for the visuotactile simultaneity task between high and low body ownership conditions. We further found that high and low body ownership both fluctuate over time, which might reflect fluctuations in multisensory integration. The relation between spontaneous brain activity and fluctuations in body ownership remain further exploration. The results are discussed related to the design of the experiment.

The second experiment aimed at investigating the relation between body ownership illusions and pain perception. Looking at one's own body has been demonstrated to have analgesic properties. This well-known effect in people's real hand has been also studied in illusory owned hands with contradictory results. While this analgesic effect of looking at one's own hand has been replicated in VR-embodiment, there are controversial findings in the rubber hand illusion: Some authors find analgesia by looking at the and illusory owned owned rubber hand

and some do not. One crucial difference between the rubber hand illusion and VR-embodiment is that in VR real and virtual hand can be colocated while this is not possible in the rubber hand illusion for obvious reasons. To test whether the distance between the real and the "owned" surrogate hand could explain contradictory findings in the literature, we manipulated distance and visuotactile stimulation in a two-factorial experimental design and measured participants' individual heat pain thresholds (HPT). Our data showed that HPT was higher at colocation than at 30 cm distance, while simultaneity of visuotactile stimulation did not influence HPT. There was further a positive relationship between reported levels of body ownership and HPT. The obtained results are discussed in the light of the recent literature and regarding their therapeutic implications.

When people experience high levels of body ownership over a virtual body which then starts making actions, those actions can be incorrectly attributed to the self. Self-attribution of an action is named agency and it gives us the feeling of control and responsibility over our own actions. Agency has been described as result of a matching between predicted and actual sensory feedback of a planned motor action, a process involving motor areas. However, situations in which strong body ownership gives us the illusion of agency over a surrogate body, raise the question of the involvement of motor areas in the sense of agency. In the third experiment of this thesis we explored this question in the context of brain computer interfaces (BCI). In two conditions participants controlled the movement of an embodied virtual arm through a BCI exploiting activity of either motor or visual areas against a third control-condition, in which participants simply observed the movement. Our data showed that using motor areas led to the highest ratings of agency, visual areas to second highest, and observing the virtual body move to lowest ratings. Interestingly, responsibility over the action's consequences was only induced when controlling the virtual movement through motor areas. Further, the higher the activity in motor areas the higher were the reports of responsibility. The results are discussed in their contribution to our understanding of agency, in the light of how different BCI protocols affect agency, and in their therapeutic implications.

All together these experiments investigated underlying processes of body ownership and its influences on pain perception and agency. The findings have implications in pain management and neurological rehabilitation.

Resumen

La experiencia de saber que este cuerpo es mi cuerpo se entiende por body ownership y está estrechamente relacionada con la conciencia. Se cree que el body ownership emerge de procesos de integración multisensorial, tal y como se ha demostrado a través de la ilusión de la mano de goma. Esta ilusión induce la sensación de ownership sobre una mano de goma tras ocultar la mano real de la persona fuera de su vista y estimulándolas de forma simultánea con un pincel. El resultado es la experiencia ilusoria de que la mano de goma es parte de nuestro propio cuerpo. Las ilusiones de body ownership también se pueden experimentar en realidad virtual (RV) inmersiva, método que se ha utilizado en los tres experimentos llevados a cabo en esta tesis.

El primer experimento de esta tesis tenía el objetivo de investigar los mecanismos subyacentes en el body ownership. Los experimentos sobre la percepción táctil, visual y auditiva mediante registros electroencefalográficos muestran que la actividad neuronal espontánea, que es una actividad neuronal relacionada con inputs u outputs específicos del cerebro, puede predecir la percepción de un estímulo. La actividad neuronal espontánea medida con fMRI típicamente fluctúa entre 0,01 y 0,1Hz y se cree que está organizada en redes, también denominadas redes en estado de reposo. Estas redes se han relacionado con funciones cognitivas, somatosensoriales y sensoriales. Algunas personas que participaron en experimentos de body ownership en nuestro laboratorio reportaron sentir cambios en el body ownership a lo largo del tiempo, planteando la pregunta de si tales fluctuaciones de la ilusión del body ownership están presentes en más personas y si es posible predecir estas fluctuaciones de la ilusión con la actividad espontánea del cerebro. Para investigar esto, medimos los cambios en la ilusión de body ownership con una tarea de simultaneidad visuo-táctil en dos condiciones diferentes. En una condición el participante experimentó un alto grado de body ownership y en la otra un bajo grado. Encontramos diferencias en el umbral de simultaneidad requerido para la tarea de simultaneidad visuo-táctil entre las condiciones de alto y bajo body ownership. También encontramos que la experimentación de un alto y bajo nivel de body ownership fluctúa en el tiempo tiempo, lo que podría reflejar fluctuaciones en la integración multisensorial. Más investigación es requerida para comprender la relación entre la actividad cerebral espontánea y las fluctuaciones en el body ownership. Los resultados se discuten en relación al diseño experimental utilizado.

El segundo experimento tenía el objetivo de investigar la relación entre las ilusiones de body ownership y la percepción del dolor. Se ha demostrado que la observación del propio cuerpo puede tener propiedades analgésicas. Este efecto

ampliamente conocido en relación a nuestra mano real ha sido también estudiado en manos poseídas de forma ilusoria encontrando resultados contradictorios. Mientras que el efecto analgésico de mirar a la propia mano se ha replicado en embodiment inducido en RV, existen hallazgos polémicos en referencia a la ilusión de la mano de goma: algunos autores encuentran un efecto analgésico al mirar la mano de goma poseída y otros no. Una diferencia crucial entre la ilusión de la mano de goma y el embodiment inducido en RV es que en RV se puede colocar la mano real y virtual en la misma localización, mientras que por obvias razones esto no es posible en la ilusión de la mano de goma. Para probar si la distancia entre la mano real y la mano artificial poseída puede explicar los hallazgos contradictorios en la literatura hemos manipulado la distancia y la estimulación visuo-táctil en un diseño experimental bifactorial midiendo los umbrales de dolor individual (HPT) de los participantes. Nuestros datos mostraron que el HPT era mayor cuando ambas manos se colocaban en la misma localización en comparación a cuando estaban situadas a 30 cm de distancia, mientras que la simultaneidad de la estimulación visuo-táctil no influyó en el HPT. También encontramos una relación positiva entre los niveles reportados de body ownership y HPT. Los resultados obtenidos se discuten en referencia a la bibliografía reciente y con respecto a sus implicaciones terapéuticas.

Cuando las personas experimentan altos niveles de body ownership sobre un cuerpo virtual que realiza acciones, esas acciones pueden atribuirse erróneamente al yo. La auto-atribución de una acción se denomina agency y nos da la sensación de control y responsabilidad sobre nuestras propias acciones. La agency ha sido descrita como resultado de una correspondencia entre la retroalimentación sensorial predicha y la real en una acción motora planificada, un proceso que involucra áreas motoras. Sin embargo, situaciones en que la experimentación de body ownership resulta también en una ilusión de agency sobre un cuerpo artificial plantean la cuestión de si también existe la implicación de áreas motoras en el sentido de agency. En el tercer experimento de esta tesis exploramos esta cuestión en el contexto de las interfaces cerebro-ordenador (BCI). En dos condiciones, los participantes controlaron el movimiento de un brazo virtual a través de una BCI que utilizaba la actividad de áreas motoras o visuales contra una tercera condición control en que los participantes simplemente observaron el movimiento. Nuestros datos muestran que las puntuaciones más altas en el sentido de agency fueron obtenidas al utilizar áreas motoras, mientras que las puntuaciones con áreas visuales fueron las segundas más altas y las puntuaciones más bajas sucedieron en la observación del movimiento virtual. Curiosamente, la responsabilidad sobre las consecuencias de la acción sólo fue inducida cuando el movimiento virtual era controlado a través de las áreas motoras. Adicionalmente, mientras más alta era la actividad en las áreas motoras, más altos fueron las puntuaciones reportadas en el sentido de responsabilidad. Se discute la contribución que estos resultados suponen para nuestro conocimiento del sentido de agency en base a cómo diferentes protocolos de BCI afectan el sentido de agency y en sus implicaciones terapéuticas.

En conjunto, estos experimentos investigaron los procesos subyacentes en el body ownership y sus influencias en la percepción del dolor y en el sentido de agency. Los resultados tienen implicaciones en la gestión del dolor y la rehabilitación neurológica.

List of publications

The following publications are associated with this thesis.

Publications in peer-reviewed journals:

- **Nierula, B., Martini, M., Matamala-Gomez, M., Slater, M., and Sanchez-Vives, M.V. (2017).** Seeing an embodied virtual hand is analgesic contingent on colocation. *The Journal of Pain, 18(6)*: 645–655.
- **Nierula, B., Spanlang, B., Martini, M., Borrell, M., Guger, C., Nikulin, V.V., Slater, M., and Sanchez-Vives, M.V. (2017).** Inducing agency and responsibility over virtual body movement through brain computer interfaces. In preparation for submission to the *Proceedings of the National Academy of Sciences of the United States of America.*

Conference proceedings:

- **Nierula, B., Martini, M., Matamala Gómez, M., Sanchez Vives, M.V. (2015).** Are body ownership illusions analgesic? *16th National Congres of the Spanish Society of Neuroscience, Granada.*
- **Nierula, B., Martini, M., Spanglang, B., Borrell, M., Guger, C., Nikulin, V.V., Slater, M., Sanchez Vives, M.V. (2017).** Inducing agency over body movement through brain-computer interfaces. *35th European Workshop on Cognitive Neuropsychology, Bressanone.*
- **Nierula, B., Martini, M., Spanglang, B., Borrell, M., Guger, C., Nikulin, V.V., Slater, M., Sanchez Vives, M.V. (2017).** Inducing agency over body movement through brain-computer interfaces. *5th MindBrainBody Symposium, Berlin.*

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List of Abbreviations

ANOVA	**AN**alysis **O**f **VA**riance
CI	**C**onfidence **I**nterval
CSP	**C**ommon **S**patial **P**atterns
EEG	**E**lectro**E**ncephalo**G**raphy
EM	**E**ye **M**ovement
EMG	**E**lectro**M**yo**G**raphy
EOG	**E**lectro**O**culo**G**raphy
ERD	**E**vent-**R**elated **D**esynchronization
ERP	**E**vent-**R**elated **P**otential
fMRI	**f**unctional **M**agnetic **R**esonance **I**maging
GABA	**G**amma-**A**minobutyric **A**cid-**A**gonistic
HPT	**H**eat **P**ain **T**hreshold
ICA	**I**ndependent **C**omponent **A**nalysis
IQR	**I**nter**Q**uartile **R**ange
ISF	**I**nfra **S**low **F**luctuations
MA	**M**uscle **A**ctivity
MNI	**M**ontreal **N**eurological **I**nstitute
n.s.	**n**ot **s**ignificant
PMC	**P**re**M**otor **C**ortex
RLP	**R**un **L**ength **P**robability
SEM	**S**tandard **E**rror of the **M**ean
SMR	**S**ensory**M**otor **R**hythm
SNR	**S**ignal to **N**oise **R**atio
SOA	**S**timulus **O**nset **A**synchrony
SSVEP	**S**teady-**S**tate **V**isual **E**voked **P**otentials
TLP	**T**ime **L**ag **P**robability
TMS	**T**ranscranial **M**agnetic **S**timulation
VR	**V**irtual **R**eality
VTS	**V**isuo**T**actile **S**timulation

Chapter 1

Introduction

The relation between body and self is very complex and has led to ongoing philosophical debates (de Vignemont, 2011). One important aspect of the self is the minimal self, that is, "a consciousness of oneself as an immediate subject of experience, unextended in time" (Gallagher, 2000). The Minimal Self does not include past or future thoughts or actions, it is limited to what is accessible to immediate self-consciousness. Aspects of the minimal self involve the sense of body ownership and agency. Body ownership refers to the attribution of a body to the self, while agency refers to the attribution of an action to the self. The two concepts are closely related and can be lost in clinical conditions such as somatoparaphrenia or anarchic hand syndrome. With the discovery of the rubber hand illusion by Botvinick and Cohen (1998) body ownership became manipulable in an experimental setup and captured the interest of psychologists and neuroscientists. Since then, advances in understanding the underlying processes of body ownership and its relation to agency have been made (Blanke, 2012; Ehrsson, 2012; Tsakiris, 2015). Body ownership and agency have been also studied in immersive virtual reality (VR), where it is possible to feel body ownership and agency over a virtual body (Slater, Perez-Marcos, Ehrsson, & Sanchez-Vives, 2008; Slater, Spanlang, Sanchez-Vives, & Blanke, 2010). The present thesis aimed at studying the underlying processes of body ownership and agency in VR-embodiment and their therapeutic applications. Specifically we were interested on (1) whether spontaneous neuronal activity has an influence on body ownership by investigating fluctuations in the perception of body ownership, (2) whether VR embodiment has possible applications in pain treatment by investigating whether looking at an embodied virtual hand is analgesic as it has been reported for looking at one's real hand; and (3) the brain basis of agency over movements of a virtual body studied through different brain computer interface (BCI) paradigms.

In the following introduction I will first explain the sense of body ownership and the current state of research in this field. I will continue with explaining how spontaneous neuronal activity, which is completely unrelated to the stimulus, can influence the processing of sensory inputs, and why it is interesting to investigate if body ownership is also influenced by spontaneous neuronal activity. Next I will review some work showing possible connections between body ownership and pain perception and explain an ongoing controversy on the analgesic effect of looking at an illusory owned artificial hand, which has been shown in some studies but not in others; the second experiment of this thesis was designed to shed some light into this controversy. I will continue explaining the state of research in the field of agency, showing the connections between body ownership and agency. I will then introduce brain computer interfaces (BCI), and show how previous research combined BCI and immersive VR. I will finish the introduction by describing our last experiment in which we used different BCI methods to control a virtual arm movement and compared the level of agency they induced.

The introduction will be followed by the thesis' objectives, the methodology, where all relevant methods and materials related to the three experiments are described, the results, the discussion, and will finish with the conclusions.

1.1 Body ownership

The following section will introduce the reader to the sense of body ownership and the current state of research in this field. It will explain how underlying sensory integration processes are believed to create this sense, while being influenced by top down processes from higher order concepts. It will further introduce the reader to body ownership illusions, which are used to experimentally investigate the sense of body ownership, I will explain the different measures of body ownership, and its neural correlates. The section will finish by introducing the reader to body ownership in immersive VR.

1.1.1 The sense of body ownership

Body ownership refers to the feeling that this one body is my body and that it is me undergoing a certain experience (Gallagher, 2000). Interestingly we do not have this feeling for all body parts—some body parts we just know they are ours while with others we feel it (de Vignemont, 2007). For example in case of the gallbladder we just know it is part of our body, instead in case of our arms we also feel that they are ours. It might be this feeling rather than the knowledge of body ownership that connects our body to the self (de Vignemont, 2007).

Body ownership is typically taken for granted because it is always there in the background of our consciousness. However, there are several medical conditions in which body ownership is altered or lost. For example patients suffering from damage to frontal and parietal lobes cannot recognize their paralyzed limb as part of their body (Arzy, Overney, Landis, & Blanke, 2006; Berti et al., 2005; Bottini, Bisiach, Sterzi, & Vallarc, 2002; Critchley, 1953; Gerstmann, 1942; Halligan, Marshall, & Wade, 1995). This condition called somatoparaphrenia is independent of the person's ability to perceive tactile stimuli on their affected hand, indicating that it is not their inability to perceive tactile stimuli on that limb which causes somatoparaphrenia, it is rather their inability to perceive that limb as part of their own body. Body ownership is further altered in patients with chronic back pain (Moseley, 2008), complex regional pain syndrome (Moseley, 2005), and acute schizophrenia (Priebe & Röhricht, 2001).

1.1.2 Multisensory integration

Body ownership has been explained to some extent by multisensory integration (Blanke, 2012; Blanke, Slater, & Serino, 2015; Ehrsson, 2012). Multisensory integration is the neural process that is involved in the formation of information derived from stimuli engaging several sensory modalities (Stein & Stanford, 2008), for example when we see another person clapping their hands we also hear the sound of the hand-clapping. So the stimulus of clapping the hands in the external world produces two stimuli to the brain - an auditory and a visual which are combined (integrated) by the brain again. Multisensory integration takes place in multisensory neurons, which respond to stimuli from more than one sense and which are present at all levels in the brain (Stein & Stanford, 2008).

Illusions based on multisensory integration

When we are certain about its visual location, the visual stimulus dominates the auditory one (Alais & Burr, 2004; Sato, Toyoizumi, & Aihara, 2007). This effect is exploited in the *ventriloquist effect*, an illusion in which the voice of a person appears to come from a puppet that is typically held in that person's hand. We perceive this illusion almost every day when hearing the words of the newsreader coming from their lips instead of from the TV speakers.

The *McGurk-effect* (McGurk & MacDonald, 1976) is related to speech perception. When seeing the lip movements of the syllable "ba" while hearing "ga", participants typically report that they heard "da", which is an intermediate sound between the heard and the seen syllable. This effect does not occur when participants only hear the words without seeing the lip movements. In this case they hear the syllables as they were presented.

Illusory flashing occurs when a single visual flash is accompanied by multiple auditory beeps, the single flash is then incorrectly perceived as multiple flashes (Shams, Kamitani, & Shimojo, 2000, 2002). The same effect can also be induced by tactile stimuli—a single visual flash accompanied by multiple tactile stimuli is incorrectly perceived as multiple flashes (van Erp, Philippi, de Winkel, & Werkhoven, 2014).

The *Pinocchio illusion* (Lackner, 1988) is an illusion in which a person touches their own nose while the experimenter applies vibrations to their biceps brachii. This leads to a change in proprioception of the person's arm induced through muscle spindle activity. The person feels that their arm is extended—since this is not possible while touching the nose the person will feel that their nose is elongated up to 30 cm. The same illusion can be also induced if the person touches another person's nose while the experimenter is synchronously touching their own nose.

Body ownership illusions are also based on multisensory integration. Since they are crucial for this thesis they will be described in more depth in Section 1.1.4.

1.1.3 Body perception as multisensory integration process

The perception of one's own body in space critically depends on multisensory integration (Ernst, 2006; Graziano & Botvinick, 2002; Lackner & DiZio, 2005; Makin, Holmes, & Ehrsson, 2008; van Beers, Sittig, & van der Gon, 1999). Information from all different sensory receptors are sent via afferent nerves to the brain and there integrated into one percept. This includes afferent signals from joints, muscles, tendons, and skin as well as visual, vestibular, and auditory signals. Such integration processes related to bodily perception occur in frontal, parietal, and temporal lobes (Angelaki & Cullen, 2008; Avillac, Ben Hamed, & Duhamel, 2007; Graziano & Botvinick, 2002; Graziano & Cooke, 2006; Hagura et al., 2007; Pouget, Deneve, & Duhamel, 2002).

The central body representation in the brain is continuously updated on the basis of actual available input from different sensory modalities and is therefore dynamic (Ehrsson, 2012). This can be seen in the previously described Pinocchio illusion where the brain adapts the central body representation in order to overcome a conflict in sensory information (Lackner, 1988) and research related to body ownership illusions (see Section 1.1.4) shows that one can have the illusion of having a very big belly (Normand, Giannopoulos, Spanlang, & Slater, 2011), a very long arm (Kilteni, Normand, Sanchez-Vives, & Slater, 2012), or even three arms (Guterstam, Petkova, & Ehrsson, 2011). Dynamic multisensory integration processes play also an important role in self-identification of the whole body or body parts (Blanke, 2012; Blanke et al., 2015; Ehrsson, 2012). In the next Section I will show by explaining several body ownership illusions how a feeling of mineness over body parts can be generated by our brain.

1.1.4 Body ownership illusions

Body ownership illusions are illusory perceptions that are driven by multisensory integration processes. The following sections will describe the induction of such illusions.

The rubber hand illusion

Induction In the rubber hand illusion (Botvinick & Cohen, 1998) participants are sitting with their hands resting on a table. A screen was placed so that participants could not see their real left hand. Instead a left rubber hand was placed in front of them (see Figure 1.1). The experimenter started to simultaneously stroke real and rubber hand with paint brushes which made participants refer the perceived touch to the rubber hand. Further most participants reported they felt as if the rubber hand was their own hand. When asked to point under the table with their right index finger at the location of their left hand, the pointed location was shifted towards the rubber hand when participants had experienced the rubber hand illusion before. This did not occur when the stimulation applied to rubber and real hand was asynchronous.

The main contribution of this study was that it provided a paradigm to study body ownership in an experimentally controlled way. Body ownership was previously a field studied mostly by philosophers—the possibility to experimentally manipulated body ownership made it testable in experimental setups and opened the doors of this field of research to neuroscience.

The rubber hand illusion is typically induced within 10 seconds and perceived is experienced in 80% of participants in less than 15 seconds (Lloyd, 2007) and was replicated in many different experiments (Costantini & Haggard, 2007; Costantini et al., 2016; Ehrsson, Spence, & Passingham, 2004; Ehrsson, Wiech, Weiskopf, Dolan, & Passingham, 2007; Hegedüs et al., 2014; Kalckert & Ehrsson, 2014b; Lloyd, 2007; Longo, Schuur, Kammers, Tsakiris, & Haggard, 2008; Mohan et al., 2012; Walsh, Moseley, Taylor, & Gandevia, 2011). It has been shown that the rubber hand illusion cannot only be induced through matching visual and tactile stimulation—it can also be induced through matching between visual and motor

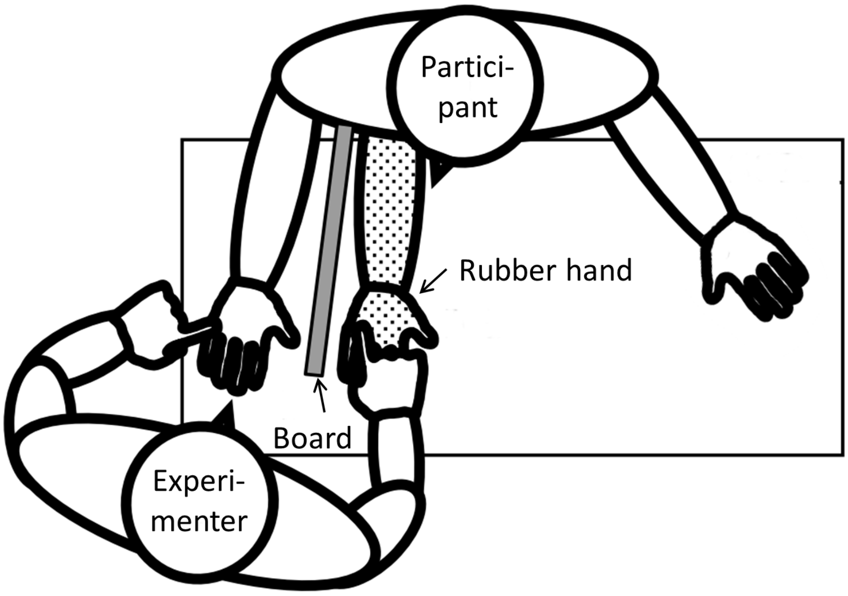

FIGURE 1.1: Experimental setup to induce the rubber hand illusion. Figure modified from Armel and Ramachandran (2003).

stimulation (Kalckert & Ehrsson, 2014a): When participants move their real index finger that is hidden from sight and see the index finger of the rubber hand moving at the same time they feel ownership over the rubber hand in a similar level as when the rubber hand illusion is produced through visuotactile stimulation (VTS). The rubber hand illusion can even be induced in blindfolded people: When the experimenter is moving the participant's left index finger to touch a rubber hand and synchronously touches his/her right hand, induces the feeling as if the person was touching their own hand (Ehrsson, Holmes, & Passingham, 2005).

Limits of the rubber hand illusion The rubber hand illusion has several limits.

(1) *Temporal limits*: ownership over a rubber hand is induced when visual and tactile stimulus are induced with delays up to 300 ms and vanishes with delays starting from 600 ms (Shimada, Fukuda, & Hiraki, 2009). However, the limit of asynchrony seems to be determined by individuals' temporal resolution in multisensory perception (Costantini et al., 2016).

(2) *Spatial limits*: the feeling of ownership over the rubber hand decays when the distance between real and rubber hand exceeds 27.5 cm in the vertical (Lloyd, 2007) and in the horizontal plane (Kalckert & Ehrsson, 2014b). This matches the boundaries of near-peripersonal space (Ehrsson, 2012; Fogassi et al., 1996; Graziano, Hu, & Gross, 1997; Ladavas, Di Pellegrino, Farne, & Zeloni, 1998).

(3) *Corporeal limits*: the feeling of ownership is also reduced when the rubber hand is replaced by a non-corporeal object (Tsakiris, Carpenter, James, & Fotopoulou, 2010), for example a wooden stick.

(4) *Anatomical limits*: ownership over the rubber hand decays when the rubber hand is rotated (Costantini & Haggard, 2007) and vanishes when the rubber hand is in an anatomically impossible position (Ehrsson et al., 2004; Pavani, Spence, & Driver, 2000; Tsakiris & Haggard, 2005b).

Temporal and spatial limits are connected to multisensory integration—the multisensory stimuli will only be integrated if they are within the individual time window of multisensory perception and if they are within the arm's near-peripersonal space to which multisensory neurons have been shown to be sensitive. Corporeal and anatomical limits are driven by the visual input and are connected to higher order concepts such as the shape and the anatomically plausible position of the arm. Indeed it has been suggested that bottom-up multisensory integration processes that drive the rubber hand illusion are necessary but not sufficient to induce it. The illusion is also modulated by top-down processes probably originating from the central representation of one's own body (Tsakiris & Haggard, 2005b).

In experiment 1 of this thesis we applied the corporeal constraint to manipulate body ownership (Body condition versus Object condition); in experiment 2 we applied in a two-factorial design the temporal and the spatial constraint to manipulate body ownership (factor distance: colocation versus distance between virtual and real arm; factor synchrony of VTS: synchronous versus asynchronous stimulation).

Full body ownership illusions

It is also possible to induce full body ownership illusions (Petkova & Ehrsson, 2008). The first experiment that induced full body ownership participants were wearing a head mounted display, that are two computer displays attached to the head—one for each eye, and were asked to look down on their body. Through the head mounted display they saw a video recording from two cameras attached to the head of a life-sized mannequin and recording down the mannequin body. So when the participant saw a video of looking down a mannequin body the experimenter was simultaneously touching the participant's and the mannequin's belly with a stick (see 1.2). This resulted in most of the participants in the feeling that the mannequin body was their body. In section 1.1.7 we will see that VR plays an important role in full body ownership illusions.

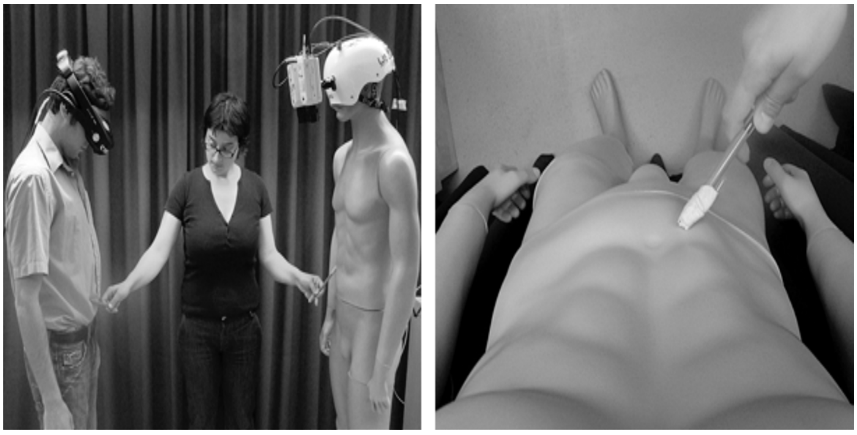

FIGURE 1.2: Experimental setup to induce a full body ownership illusion. Figure from Petkova and Ehrsson (2008).

Out of body illusions

In out of body illusions people experience to be in a different place in the room than their body is. It can be induced in two ways—by changing the feeling of the actual position of oneself (Ehrsson, 2007) or by changing the perceived position of one's body (Lenggenhager, Tadi, Metzinger, & Blanke, 2007).

1.1.5 Measures of body ownership

The level of induced body ownership over a surrogate body or body part can be measured using subjective measures such as questionnaire reports and objective measures such as changes in proprioception, or physiological responses to a threat. These measures will be explained in more detail below.

Questionnaire reports

A very typical and straight forward measure of body ownership is to ask the participant after or during the induction of the rubber hand illusion or the full body illusion how their experience was. Many studies adapted the questionnaire from Botvinick and Cohen (1998), for example Mohan et al. (2012)). Other studies adapted their questionnaire to the one proposed by Longo et al. (2008).

Proprioceptive drift

The idea behind the proprioceptive drift is that when participants feel strong ownership over a rubber hand this should influence their sense of position for their real hand. Participants are typically asked to close their eyes and then point at the position of the index finger of their hand undergoing the illusion with their other hand. In the original study a displacement of position towards the rubber hand had been reported (Botvinick & Cohen, 1998) when rubber and real hand was stimulated synchronously but not in the asynchronous stimulation condition and has been referred to as proprioceptive drift (e.g. Tsakiris and Haggard (2005b)). However, it has been shown that asynchronous stroking can also lead to proprioceptive drift (Rohde, Di Luca, & Ernst, 2011) even when questionnaire reports show low ownership reports. Longer intervals of asynchronous stroking (above 120 seconds) reduce the drift in the asynchronous stroking condition. In the initial study reported feelings of ownership correlated with the proprioceptive drift (Botvinick & Cohen, 1998). However, later work suggested distinct multisensory integration processes for the two phenomena (Kammers, de Vignemont, Verhagen, & Dijkerman, 2009; Rohde et al., 2011).

A measure similar to the proprioceptive drift has been developed for out of body illusions (Lenggenhager et al., 2007). In this case participants are asked to position themselves where they feel their body was positioned during the out of body experience.

Response to threat

When a rubber hand is integrated into one's body as if it was one's real hand one should be affected by a threat to the rubber hand. For example if the rubber hand is strongly bent, a hammer hits the rubber hand or if a knife comes close to it. Typically a threat to one's own hand rises anxiety. It has been shown that a threat to the rubber hand rises skin conductance response (Armel & Ramachandran, 2003) and activates similar areas in the brain as threatening the real hand (Ehrsson et al., 2007). The threat has also been used as measure in full body ownership illusions (Petkova & Ehrsson, 2008).

1.1.6 Neural correlates of body ownership

Multisensory neurons in area 5 of the primate parietal lobe have been shown to encode the position of the monkey's hand while it is covered from view (Graziano, 2000). Interestingly these neurons respond also to the position of a false arm but not to the position of unrealistic substitutes of the arm (i.e. a rectangle) or an anatomically incorrect false arm (i.e. left instead of right arm). These neurons combine visual and somatosensory signals in order to monitor the arrangement of our limbs and have been proposed as the neuronal correlate of body ownership (Makin et al., 2008).

Two main regions within a larger network of cortical areas have been highlighted to be involved in the integration of multisensory arm-related signals—the premotor cortex (PMC) and the intraparietal sulcus. They are part of a larger network including insula, primary somatosensory cortex, lateral occipital complex, temporoparietal junction, supplementary motor area, anterior cingulate cortex, and cerebellum (Blanke et al., 2015).

These findings on multisensory integration in peripersonal space around the hand have been related to the feeling of body ownership over a rubber hand. Inducing the rubber hand illusion through synchronous VTS of real and rubber hand has been shown to activate ventral PMC (Ehrsson et al., 2004), intraparietal sulcus, and cerebellum (Ehrsson et al., 2005, 2004). These brain areas show also deactivation during decreased hand ownership induced through asynchronous VTS (Gentile, Guterstam, Brozzoli, & Ehrsson, 2013). The perceived strength of hand ownership measured with questionnaires was related to activation of PMC, cerebellum (Ehrsson et al., 2004), anterior insular, anterior cingulate cortices (Ehrsson, 2007), right posterior insula, and sensorimotor cortices (Tsakiris, Hesse, Boy, Haggard, & Fink, 2007). Threats to the rubber hand have been shown to activate the supplementary motor area (Ehrsson, 2007) and posterior parietal regions (Lloyd, Morrison, & Roberts, 2006) and proprioceptive drift was correlated with activity in the right insula and left somatosensory cortex (Tsakiris et al., 2007).

1.1.7 Body ownership in virtual reality

Immersive virtual reality

An immersive VR system delivers the participant computer generated sensory input which is updated as a result of the participant's movements and thereby generates the impression of an alternate environment. This sensory input is always visual and can be in addition auditory, tactile, and/or force feedback. One way to induce an immersive VR experience is through a Cave-like system (Cruz-Neira, Sandin, & DeFanti, 1993), another is by wearing a head mounted display. In this thesis I will focus on immersive VR experiences induced through head mounted display. In an head mounted display the visual image is displayed very close to the eyes so participants can only see what is displayed by the head mounted display. Through stereoscopy one can have the illusion of 3-D vision in an head mounted display. This technique consists in presenting two 2-D images rendered from the perspective of two different viewpoints, one for each eye, that are fused into one overall 3D image. In addition, the displayed image is constantly updated with the head movement of the participant. This creates the illusion of looking around while being in a virtual environment. When using a head mounted display the virtual environment can be displayed from the perspective of the eyes of a computer generated body (virtual body) which creates the illusion as if the virtual body was one's own body. Through body tracking the movements of the participant can be captured and mapped on the virtual body which allows the participant to control the movements of the virtual body and enhances the illusion of ownership over that virtrual body.

The quality of the experience in an immersive virtual environment is limited by technological constrains such as graphics frame rate, resolution, how much of the participant's body movements are tracked, the latency of the tracking, the quality of the images, the extent of the field of view, the quality of the rendered scene, how naturalistic objects behave in the scene, and the range of different sensory modalities used besides vision in the immersive VR system (Slater, 2009).

The following three concepts play a crucial role in explaining why immersive VR systems have the power to transform place and self-representation: immersion, place illusion, and the plausibility illusion (Slater, 2009).

Immersion is based on the sensorimotor contingencies the immersive VR system provides. That is when the participant is turning their head the displayed scenario is changing accordingly, or when the participant bends forward to look under a table the system should render the scenario accordingly. However, the possible actions in an immersive virtual environment are limited by the sensorimotor contingencies the system provides. For example when there is no body tracking, movements of the real body will not lead to movements of the virtual body. Or when the person reaches out to manipulate a virtual object but this does not give haptic feedback immersion will be also reduced (Slater, 2009). Basically immersion limited by the sensorimotor contingencies the system can provide.

Place illusion is the feeling of 'being there' in a place in spite of the knowledge that you are not there (Slater, 2009). It is different from immersion in the sense that it is based on the individual experience of the participant. For example, a participant, who is not moving his/her head and body in the immersive VR, may perceive the place illusion less strongly compared to another participant, who is moving around and exploring the environment. Immersion provides the boundaries in which place illusion can occur (Slater, 2009).

Plausibility illusion is the sensation that the displayed scenario is actually happening, although knowing that it is not occurring. Plausibility illusion rises especially when events in the virtual environment that the participant did not cause refer to him/her. For example if the participant sees a character standing in front of her that she knows is not there but when she looks at the character from different angles the background objects that it occludes change as if it was in the real world (this is place illusion). When then the character suddenly looks in the participant's eyes and speaks to them they typically respond to the character although they know it is not there (Pan & Slater, 2007).

When both, plausibility illusion and place illusion, occur the participant is likely to respond realistically to the virtual environment (Slater, 2009).

Body ownership illusions in virtual reality

As described in Section 1.1.7 in immersive virtual environments provided through an head mounted display the participant's body can be replaced by a virtual body. This body is then seen from a first person perspective through the head mounted display. Seeing a virtual body in the same position as your real body and seeing your virtual body's movements match your real ones creates a strong illusion of ownership over the virtual body (Sanchez-Vives & Slater, 2005; Sanchez-Vives, Spanlang, Frisoli, Bergamasco, & Slater, 2010; Slater, 2009). Body ownership illusions in VR using an head mounted display are full body ownership illusions. Full body ownership over the virtual body can be obtained by colocation of real and virtual body, by visuotactile, or by visuomotor contingencies.

Colocation Seeing a virtual body colocated with one's real body from a first person perspective is sufficient to induce a body ownership illusion in VR (Maselli & Slater, 2013; Slater et al., 2010).

Realistic body appearance A realistic body appearance enhances the experience of body ownership over the virtual body (Maselli & Slater, 2013).

Visuotactile contingencies It has been shown that it is possible to induce a virtual version of the rubber hand illusion (Slater et al., 2008). Synchronous VTS enhances the body ownership experience compared to asynchronous VTS (Maselli & Slater, 2013). However, the processing of asynchronous VTS can be influenced by the strength of the body ownership illusion. When the illusion is high asynchronous stimuli are not perceived as incongruent (Maselli & Slater, 2013). On the other side when the virtual body does not appear realistic or when virtual and real body do not spatially overlap synchronous VTS can evoke the illusion (Maselli & Slater, 2013).

Visuomotor contingencies By means of tracking tools attached to the real body, the participant's movements can be captured and mapped onto the virtual body, so whenever the real body moves the virtual one moves in the same way. Seeing a virtual body in the same position as your real body and seeing your virtual body's movements match your real ones creates a strong illusion of ownership over the virtual body (Sanchez-Vives & Slater, 2005; Sanchez-Vives et al., 2010; Slater, 2009). A mirror is typically displayed in VR through which the participant can better see the movements of the virtual body.

Immersive VR and virtual body ownership offer the advantage of a highly controlled experimental setting while preserving ecological validity. Additionally some questions can only be investigated in an immersive VR, for example when the appearance of the body is modified. For example, one can induce the illusion of having a very long arm (Kilteni et al., 2012), having a different race (Peck, Seinfeld, Aglioti, & Slater, 2013), having the body of a child (Banakou, Groten, & Slater, 2013), having a larger belly (Normand et al., 2011), having a female body while being a man (Slater et al., 2010), being in a different posture with respect to the real body (Bergström, Kilteni, & Slater, 2016), or having a tail (Steptoe, Steed, & Slater, 2013). Due to the malleability of our body representation people feel body ownership over these modified bodies, however, most of these modifications can only be done in an immersive virtual environment.

It has been shown that we do not only accept different shapes of the body we feel as ours, changing the body seems to also influence our behavior and attitudes. For example, Caucasian people that are embodied in a dark skinned body tend to have a lower implicit bias than people that are embodied in a light or a purple skinned body (Peck et al., 2013), adults that are embodied in a child's body overestimate sizes of objects (Banakou et al., 2013), and people embodied in a dark skinned musician tend to show greater variety in drumming movements than participants that are embodied in a white skinned person that is wearing a suit (Kilteni, Bergström, & Slater, 2013).

It is further possible to measure the consequences of embodiment using electroecephalography (EEG). For example, one study found that a threat to the embodied virtual hand elicits motor cortex activation (Gonzalez-Franco, Peck, T. C., Rodriguez-Fornells, & Slater, 2014).

1.2 Influences of spontaneous brain activity on sensory processing

In the following section I will describe the relation between spontaneous neuronal activity and perception. Although unrelated to the stimulus, spontaneous activity can predict perception and is operating in networks, of which some might be closely related to body ownership. I will end this section by outlining the idea for the first experiment of this thesis.

1.2.1 Influence of spontaneous neuronal activity on perception

Spontaneous neuronal activity refers to activity that cannot be attributed to specific inputs or outputs of the brain (Fox & Raichle, 2007). Such activity has been related to perception. Specifically it has been shown that spontaneous neuronal activity can predict whether a stimulus is perceived or not in the tactile (Boly et al., 2007; Monto, Palva, Voipio, & Palva, 2008), visual (Busch, Dubois, & VanRullen, 2009; Busch & VanRullen, 2010; Fiebelkorn et al., 2013; Hanslmayr et al., 2007; Hanslmayr, Volberg, Wimber, Dalal, & Greenlee, 2013; Mathewson, Gratton, Fabiani, Beck, & Ro, 2009; Nunn & Osselton, 1974), and auditory (Sadaghiani, Hesselmann, & Kleinschmidt, 2009; Sadaghiani, Poline, Kleinschmidt, & D'Esposito, 2015) domain. Further, spontaneous brain activity in local field potentials (LFP), magneto- or electroencephalographic (M/EEG) recordings predict characteristics of post-stimulus evoked potentials. For example, in anesthetized cats fluctuations of the LFP predict latency and amplitude of the neural response to a visual stimulus (Fries, Neuenschwander, Engel, Goebel, & Singer, 2001) and in macaque monkeys pre-stimulus network power and coherence predict amplitude and latency of early visual evoked potential components (Liang, Bressler, Ding, Truccolo, & Nakamura, 2002). MEG recordings in humans show that pre-stimulus mu-rhythm activity modulates evoked responses to stimuli given at detection threshold (Nikouline et al., 2000), and further that phase resetting of the ongoing spontaneous activity within distinct EEG domains is generating evoked potentials (Makeig et al., 2002). Furthermore, ongoing spontaneous activity can also predict reaction times to supra-threshold stimuli (Cordes et al., 2001; Drewes & VanRullen, 2011; Dustman & Beck, 1965), temporal perceptual discrimination of somatosensory stimuli (Baumgarten, Schnitzler, & Lange, 2015, 2016), and decision making (Wyart, de Gardelle, Scholl, & Summerfield, 2012), and cross-modal integration of vision and touch (van Erp et al., 2014). Such frequencies typically range from 0.01 to 20 Hz (see also VanRullen (2016)).

1.2.2 Spontaneous neuronal activity in resting state networks

Modulations of spontaneous neuronal activity are organized in networks (Cordes et al., 2001; Fox & Raichle, 2007), as revealed by functional magnetic resonance imaging (fMRI) studies. These networks appear as blood oxygen level-dependent (BOLD) signal fluctuations at frequencies ranging from 0.01 Hz to 0.1 Hz. It is assumed that such oscillations at the same frequency functionally connect distant brain areas. Multiple of these resting state networks have been identified and can be divided into networks reflecting cognitive function and networks reflecting sensorimotor and sensory function. Among these networks the default mode network (DMN) has been studied the most (Heine et al., 2012) and its activity has been linked to self-related and internal processes such as mind wandering (Mason et al., 2007), introspection (Goldberg, Harel, & Malach, 2006), and monitoring of the "mental self" (Lou et al., 2004). The DMN can also be assigned to specific cognitive functions, especially frontal areas of the network seem to be important for self-reference (for review on resting state networks and consciousness see (Heine et al., 2012)). Also in the EEG domain oscillations between 0.01 and 0.1 Hz have been shown to predict whether a stimulus applied at the individual tactile threshold is perceived or not (Monto et al., 2008). In this thesis I will refer to oscillations between 0.01 and 0.1 Hz that were measured with EEG as infra-slow fluctuations (ISF).

1.2.3 Spontaneous neuronal activity and body ownership

At the end of experiments on body ownership conducted in our lab some participants reported fluctuations in the feeling of body ownership. Some participants felt body ownership over the virtual body to be sometimes stronger and other times weaker.

In the first experiment presented in this thesis we were interested whether the experience of body ownership is stable or fluctuating, and in the case that it fluctuates, whether those fluctuations can be predicted by ISF. To test this we asked participants to continuously report their level of body ownership (approximately every 4 seconds through a simultaneity detection task explained in the methods in Section 3.2.3) in two experimental conditions—one in which they felt body ownership over a virtual body and a control condition in which they had no body and instead saw a virtual object at the location of their hand.

1.3 Body ownership and pain perception

There are at least two ways through which body ownership and pain perception might be linked. One is through the interoceptive system proposed by Craig (2003), another is through the finding that looking at one's own body reduces pain. Because of its therapeutic implications, several research groups have investigated whether this holds also true for an illusory owned surrogate body or body part with controversial findings. The following section will explain the possible links between the interoceptive system and pain as well as the findings on the analgesic effect of looking at one's own body. It will further explain the controversial findings on the analgesic effect of looking at an illusory owned surrogate body and finish with the outline of experiment two, which was designed to shed some light into this controversy.

1.3.1 Pain

The International Association for the Study of Pain defines pain as "an unpleasant sensory and emotional experience associated with actual or potential tissue damage, or described in terms of such damage" (Merskey & Bogduk, 1994). Following this definition pain is a sensory percept that gets elicited specifically to tissue damage and is always perceived as a damage of tissue even when such damage is not (or not anymore) present. So while pain perception is a conscious percept of senses and emotion, the term nociception is concerned with objective processes—information about noxious stimuli which the nervous system receives and processes. Nociception can exist outside of conscious awareness whereas this is not the case for pain because it is a percept created by our brain (Moseley & Flor, 2012).

1.3.2 Interoception

Pain has been proposed to be part of the interoceptive system, a hierarchical system proposed to subserve homeostasis, the awareness of emotion and of feelings related to the physiological condition of the body (Craig, 2003). In the following I briefly describe this system. The interoceptive system represents all aspects of the physiological conditions in the body. It receives afferent input from the solitary nucleus, a series of purely sensory nuclei in the brainstem, and generates a direct thalamocortical representation of the physical body's state. This representation is crucial for temperature, pain, itch and other somatic feelings in primates. The contralateral afferent homeostatic input from the solitary nucleus is processed in the ventromedial nucleus of the thalamus and from there projected to the mid/-posterior part of the dorsal insula and then re-represented in the anterior insula of the non-dominant hemisphere. Here, in the anterior insula, the interoceptive cortical representation forms an evaluation of one's condition, that is, an evaluation of how you feel.

Nociceptive and thermoceptive neurons have been identified in the ventromedial nucleus of the thalamus in humans (F. A. Lenz et al., 1993) which is part of the interoceptive system as described above. Its projection fields in the dorsal part of the mid/posterior insular cortex are activated by temperature, pain and numerous interoceptive modalities that cause bodily feelings. Lesions in this area distort homeostatic processing and bodily feelings and further cause loss of discriminative thermal sensation.

The insular cortex has been identified as part of the larger network activated during multisensory processing in peripersonal space (Blanke et al., 2015). Further, activity in anterior and right posterior insular cortex has been shown to correlate with the perceived strength of ownership over a rubber hand (Ehrsson, 2007; Tsakiris et al., 2007). And proprioceptive drift has been shown to correlate with activity in the right insular cortex (Tsakiris et al., 2007). The rubber hand illusion has been shown to influence autonomic regulation. When a hand is undergoing the rubber hand illusion the real hand shows a drop in skin temperature (Hohwy & Paton, 2010; Moseley et al., 2008), however, this finding is still controversial as another study found that this drop in skin temperature is just related to manually induced stroking independent of the perceived level of ownership (Rohde, Wold, Karnath, & Ernst, 2013). Other findings show that the experience of body ownership is modulated by the accuracy of detecting interoceptive states, such as heartbeats. People with lower interoceptive accuracy feel the body ownership illusion stronger than people with higher interoceptive accuracy (Tajadura-Jimenez & Tsakiris, 2014; Tsakiris, Tajadura-Jimenez, & Costantini, 2011). Further in people with lower interoceptive accuracy, changes in body ownership can improve their interoceptive accuracy (Filippetti & Tsakiris, 2017). Although the exact mechanisms are not clear yet, there seems to be a relation between body ownership and the interoceptive system which might be based on the interaction of internal and external bodily signals (Filippetti & Tsakiris, 2017; Tsakiris et al., 2011).

1.3.3 Analgesic effect of looking at one's own body

Looking at one's own body has been reported to have analgesic properties. Painful stimuli applied to the hand are rated as being less painful when looking at that hand (Longo, Betti, Aglioti, & Haggard, 2009; Longo, Iannetti, Mancini, Driver, & Haggard, 2012; Mancini, Longo, Canzoneri, Vallar, & Haggard, 2013) and heat pain thresholds (HPT) increase (Mancini, Longo, Kammers, & Haggard, 2011). Besides these behavioral insights, these studies also revealed signatures of this effect at a neurophysiological level. Activity in primary and secondary somatosensory cortices (SI and SII) has been shown to be reduced during the processing of painful stimuli while looking at one's own body: Reduced Blood-Oxygen-Level Dependent (BOLD) signal was reported in SI and the operculoinsular cortex in fMRI (Longo et al., 2012) and reduced power of event-related beta oscillations (Mancini et al., 2013), as well as reduced laser-evoked potentials (Longo et al., 2009) were reported in SI and SII. However, there are controversial findings in the literature when looking at an illusory owned hand. These findings will be shown in the next paragraph.

1.3.4 Body ownership illusions and pain processing

Since looking at one's own body has been shown to have analgesic effects, researchers got interested to see whether this effect holds true for body ownership illusions. Mohan and coworkers (2012) were the first ones to investigate this and showed no changes in pain perception during the rubber hand illusion, indicating that the analgesic effects of looking at one's own body would not hold true when the body part is artificial, even though it is attributed to oneself. In contrast, other studies showed that while perceiving a rubber hand as part of one's body, looking at this "owned" rubber hand leads to increased HPT (Hegedüs et al., 2014) and higher resistance to painfully cold stimuli (Giummarra, Georgiou-Karistianis, Verdejo-Garcia, & Gibson, 2015; Siedlecka, Klimza, Łukowska, & Wierzchoń, 2014). Similar, when feeling ownership over a virtual arm HPT increased when participants looked at the embodied virtual arm compared to two different control conditions (looking at a non-corporeal object in a virtual environment or at a fixation point in the real world; Martini, Perez-Marcos, & Sanchez-Vives, 2014).

To understand these controversial findings in the literature we looked into the methodological differences between these five studies. Three studies leading to controversial findings used heat stimuli (Hegedüs et al., 2014; Martini et al., 2014; Mohan et al., 2012). Among them are two studies that reported modulation of HPT by body ownership (Hegedüs et al., 2014; Martini et al., 2014). While in the study by Mohan et al. (2012) the position of the rubber hand during synchronous and asynchronous stimulation conditions was kept the same, Hegedüs et al. (2014) rotated the rubber hand during the asynchronous stimulation condition in order to further reduce the strength of body ownership during this control condition. A major difference between the studies involving a rubber arm versus a virtual arm illusion is the relative location of the real with respect to the illusory-owned arm. While a virtual arm can be colocated or not with the real arm, a rubber arm can never be colocated with the real arm for obvious reasons. The distance between real and fake limb has been identified as critical factor for body ownership, in the vertical (Lloyd, 2007) and in the horizontal plane (Kalckert & Ehrsson, 2014b).

In the second experiment I present in this thesis we aimed at testing whether the distance between real and virtual hand could explain why some researchers report an analgesic effect of looking at one's illusory owned hand while others don't. In four different conditions participants reported their HPT and rated their feeling of ownership over the virtual body. Conditions differed in VTS – synchronous or asynchronous – and in distance between real and virtual arm, which could be either 0 cm (colocated) or 30 cm apart. We hypothesized that during colocation there is an analgesic effect and thus higher HPT than when there is distance between the real and the virtual arm. The results of this experiment were published in the Journal of Pain (Nierula, Martini, Matamala-Gomez, Slater, & Sanchez-Vives, 2017). Note that descriptions in this thesis related to this experiment have been adapted from this article.

1.4 Agency

Agency and Body ownership are closely related. In this section I will first explain what is understood when talking about the sense of agency, and then describe what we know so far about the link between agency and body ownership. I will next present the comparator model, which is widely used in the field to explain agency, and go through its limitations, and I will show under which conditions we can perceive illusory agency over a movement we did not perform ourselves. I will continue by outlining how other processes can influence agency, and then describe what is known about the neural correlates of agency. I will finish this section by explaining brain computer interfaces (BCI). I will then outline the third experiment of this thesis in which we compared two different BCI protocols in their level of agency they can induce in an immersive VR setup, and to better understand the involvement of motor areas in agency.

1.4.1 The sense of agency

The sense of agency is the experience of controlling one's own motor actions and therefore events in the external world (Haggard, 2017). There are two aspects of agency—an objective and a subjective one (Haggard & Eitam, 2015). The objective aspect refers to one's capacity to initiate, perform, and control an action that is in accordance with one's goals and desires. This is even reflected in our criminal law where those who act in line with their felonious goals have to expect harder punishment than those who performed a criminal action by accident.

The subjective aspect of agency refers to the subjective experience of how it feels to control one's actions and thereby influence the external world. This feeling occurs before, during and after muscular movement. A core part here is the association between a voluntary performed action and its outcome. Another part of the subjective aspect of agency is the feeling of responsibility, that is, the experience on how one's actions affect the outside world. When referring to agency in this thesis, I refer only to the subjective aspect of agency.

1.4.2 Body ownership and agency

Body ownership can be perceived during voluntary actions, during passive movements and during rest (Longo & Haggard, 2009; van den Bos & Jeannerod, 2002). In contrast, only voluntary actions should result in a feeling of agency. For example, when my arm is passively moved I feel that this is my arm in movement but I do not feel agency over that movement because I did not cause it. However, when I voluntarily move my arm, I will feel agency over that movement. Although in healthy people the two senses of body ownership and agency seem to both contribute to a coherent perception of body awareness, schizophrenic patients with delusions of control report that another person or authority is controlling the actions that their body performs. In this case the feeling of control is separated from the feeling of body ownership (Tsakiris, 2015), which makes the relationship between body ownership and agency ambiguous. For instance, behavioral results and questionnaire reports suggest an additive relationship between body ownership and agency (Tsakiris & Haggard, 2005a). As we can willingly control only the movements of our own body, but not those of other bodies or objects, agency offers important information which might be used to update the sense of body ownership. However, the literature still does not give a clear picture about the relationship between them. One study showed that when seeing a rubber hand move while actively moving one's real hand synchronously, people perceive stronger ownership over the rubber hand (Dummer, Picot-Annand, Neal, & Moore, 2009). A different study, however, showed that synchronous passive or active movement led to similar levels of body ownership over a rubber hand (Kalckert & Ehrsson, 2014a). It has further been suggested that when mismatching visuomotor information is available, this information is used over other information to attribute a body part to the self (van den Bos & Jeannerod, 2002). For example, when moving one's hand while seeing a hand moving differently, people make their judgment of whether the hand they see is their own hand exclusively on the non-matching movement cue and independent from other cues such as the orientation of that hand.

On the other hand, insights from fMRI studies support an independent relationship between body ownership and agency because they rely on separate underlying brain mechanisms. The strength of body ownership has been associated with activation in the premotor cortex (bilateral) and the right posterior insula (Ehrsson et al., 2004; Tsakiris et al., 2007), while actions attributed to the self activated right posterior insula (Farrer et al., 2003), and actions that are not attributed to the self activated right dorsolateral prefrontal cortex, right inferior parietal lobe, and temporoparietal junction (Farrer et al., 2003; Farrer et al., 2008; Fink et al., 1999; Leube et al., 2003; for review see Tsakiris, 2015).

1.4.3 The comparator model

As described in Section 1.4.1, we feel agency when planned motor actions and their outcome match. Agency has been explained with comparator models, a group of computational models that had been originally developed to explain motor control (Sperry, 1950; von Holst & Mittelstaedt, 1950). These models assume that in case of a planned motor action, the brain does not only send create the motor command of this action, it also predicts the action's sensory feedback. When the motor command is sent to the muscles, an efference copy of this motor command is used to compute a forward model which is a prediction of the expected sensory feedback given this action. The actual sensory feedback when performing the movement is then compared with the predicted feedback resulting in a prediction error. Neural signaling of prediction errors can be used to adjust and improve performance, and to learn how to improve future predictions (Haggard, 2017). If an action is caused by oneself and the forward model is correct, then forward model and actual feedback should match, and the prediction error should be zero. Thus a zero prediction error should lead to a very high sense of agency over that action. Several versions of the comparator model have been suggested to explain agency (de Vignemont & Fourneret, 2004; Frith, Blakemore, & Wolpert, 2000; Haggard, 2017; Tsakiris & Haggard, 2005a). Figure 1.3 displays the model proposed by Haggard (2017).

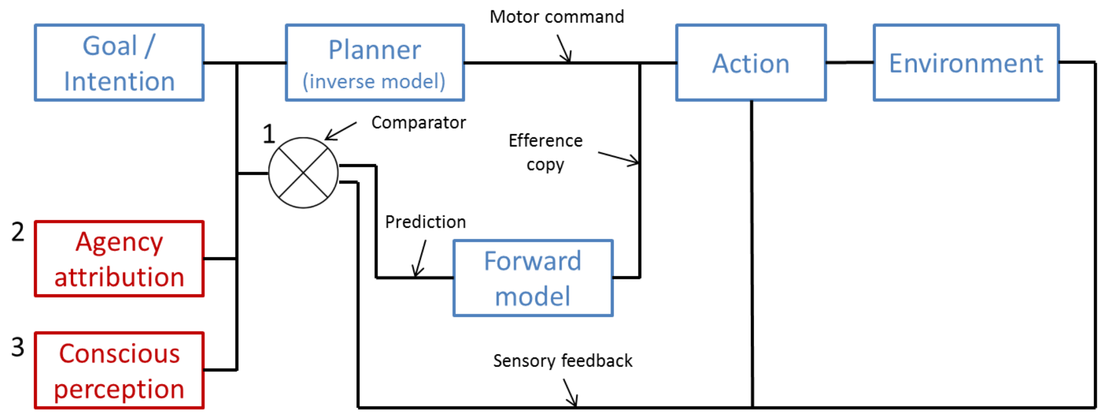

FIGURE 1.3: Comparator model for neural control of action and agency (Haggard, 2017). Each voluntary action begins with a goal or an intention which is then transformed into a motor command by a planner (or inverse model). An efference copy of the motor command is used to compute a forward model that holds the expected feedback given the intended motor action. The predictions of the forward model are then compared with the actual sensory feedback. The prediction error from this comparison can be used to (1) improve the inverse model, (2) attribute the action to the self (the conscious component of this is the feeling of agency) and (3) adjust conscious perception (attenuation of self-produced sensory input). Figure is adapted from Haggard (2017).

According to the comparator model, the sense of agency is the conscious component of this comparator mechanism and is produced retrospectively. The strength of the comparator model is its simplicity, but the model has its limitations. For example, it cannot explain why there is a positive experience of agency at all, it cannot explain agency over thoughts (Synofzik, Vosgerau, & Newen, 2008), and it neither explains by itself how people can feel agency for actions they did not perform. Such illusions of agency will be addressed in the following paragraph.

1.4.4 Illusion of agency

Under certain circumstances people can perceive actions performed by another agent as their own. For example, when a previously learned connection between an action (e.g. a button press) and a response (e.g. a tone) happens randomly, we can feel illusory agency for the response ("I produced the tone") (Sperry, 1950). Further, it has been shown that the movements of another person can be perceived as one's own movement, especially if seen from a first person perspective, if one can preview the movement, or if own subtle movements are performed at the same time (Wegner, Sparrow, & Winerman, 2004). When feeling body ownership over a virtual body, it has been shown that the speaking of that virtual body can be attributed to oneself (Banakou & Slater, 2014) or the walking of the virtual body can be attributed to oneself while one's real body is sitting (Kokkinara, Kilteni, Blom, K. J., & Slater, 2016). These studies show that strong body ownership over a surrogate body plays a crucial role in attributing the actions of that body to oneself.

The comparator model and the findings on illusory agency both suggest that the sense of agency is generated through retrospective inference about the authorship of one's own action (Wegner, 2002). Wegner and Wheatley (1999) proposed that one perceives ownership over an action when three preconditions are met: (1) "The thought should precede the action at a proper interval" (priority principle), (2) "the thought should be compatible with the action" (consistency principle), and (3) "the thought should be the only apparent cause of action" (exclusivity principle). However, other findings suggest that the sense of agency also depends on the brain's prosepctive expectation of the action's sensory consequences (Gentsch & Schütz-Bosbach, 2011). Experiment 3 of this thesis was conducted to further investigate illusory agency.

1.4.5 Measures of agency

Questionnaire responses

Subjective agency ratings are typically gathered with questionnaire responses. There are two types of questions targeting the sense of agency. (1) Questions that focus on the effect (e.g. "Did you produce the tone?", Haggard & Tsakiris, 2009) and (2) questions that focus on the experience (e.g. "How much control did you feel you had over the arm's movements?", Wegner et al., 2004).

Intentional binding

The intentional binding effect has also been used as an objective measure of agency (e.g. Barlas & Obhi, 2013; Cavazzana, Begliomini, & Bisiacchi, 2014; Jo, Wittmann, Hinterberger, & Schmidt, 2014; Moore & Obhi, 2012). People perceive an action and its sensory effect as being closer together in time when they produce the effect intentionally compared to when the effect is produced by an unintended movement (Haggard, Clark, & Kalogeras, 2002). To measure this, participants are asked to look at a so-called Libet-clock and report the position where the clock handle was when they performed the action and when they perceived its sensory effect.

1.4.6 Influences on agency

Agency can be influenced by other ongoing processes such as volition, action selection, and body ownership, which are described here.

Volition

Volition is the process of willingly transforming goals and intentions into results. This includes preparing, initiating and executing an action under one's own control (Haggard, 2017). The readiness potential (Kornhuber & Deecke, 1965) is a slow negative EEG potential originating in cognitive motor areas that precedes voluntary movements and its early component is believed to reflect subconscious preparation for a forthcoming movement (Shibasaki & Hallett, 2006). It has therefore been used as a marker of volition (Shibasaki & Hallett, 2006; but see also Schurger, Sitt, & Dehaene, 2012). A recent study showed that people with larger negative amplitudes in the early component of the readiness potential reported stronger intentional binding between the action and its effect (Jo et al., 2014). It is not, however, the readiness potential alone that influences intentional binding. When an intention is interrupted by a superimposed involuntary action (induced by a transcranial magnetic stimulation (TMS) pulse), no intentional binding occurs (Haggard & Clark, 2003), highlighting how important it is for the intention to match the resulting movement in order to induce agency.

Action selection

The freedom to choose one's actions is strongly linked to agency. The number of possible action alternatives from which a person can choose has been shown to be directly linked to their perceived sense of agency as measured by intentional binding (Barlas & Obhi, 2013). The more options people can choose from, the higher their sense of agency. Further, subliminal visual priming has been shown to systematically influence action selection (Schlaghecken & Eimer, 2004) and explicit judgments of agency (Wenke, Fleming, & Haggard, 2010). These results suggest that agency is linked to action selection processes, where agency is strongest when the selection process is smooth and conflict-free.

Body ownership

Body ownership has also been shown to influence agency. For example, people can perceive illusory agency over the walking of a virtual body seen from a first person perspective while their real body is sitting (Kokkinara et al., 2016), and people can feel illusory agency over the talking of a virtual body while not speaking themselves (Banakou & Slater, 2014). The underlying mechanism of this finding is still unclear. One possible explanation is that when body ownership over a virtual body is very strong and the virtual body performs an action, an intention to do this action might have been created a few moments after that, thus leading to an attribution of the virtual body's action to the self (Banakou & Slater, 2014; Kokkinara et al., 2016).

Another explanation is that body ownership might retrospectively influence the predictions made by the forward model. While feeling ownership over a rubber hand, touching only the rubber hand (but not the real hand) leads to a feeling of numbness or senselessness. This feeling has been shown to be enhanced when people are touching the rubber hand themselves with their other hand compared to when another person is touching the rubber hand (Aymerich-Franch, Petit, Kheddar, & Ganesh, 2016). This shows that body ownership does indeed influence the brain's sensorimotor predictions, however, the underlying mechanism is not yet clear.

1.4.7 Neural correlates of agency

As mentioned in Section 1.4.2, different brain areas are active when an action is self- or externally attributed (Sperduti, Delaveau, Fossati, & Nadel, 2011). The only area that was consistently associated with agency in fMRI or positron emission tomography studies was the anterior insula (Haggard, 2017; Sperduti et al., 2011), an area that has been proposed to have a general role in ongoing self-awareness (Craig, 2009).

Other areas have been associated with non-agency—among them the temporoparietal junction area (including the angular gyrus) and dorsomedial prefrontal cortex (Sperduti et al., 2011). Both areas are not domain specific and are therefore most likely not directly associated with non-agency; they might rather reflect outcomes in the process of identifying the agent. The temporoparietal junction has been proposed to represent the comparison of internal predictions with external events while the dorsomedial prefrontal cortex has been connected to decision making under uncertainty (Sperduti et al., 2011).

Frontal and pre-frontal areas play a key role in planning and initiating voluntary action, however, their contribution to the sense of agency is less clear (Haggard, 2017). Two studies temporally inhibited the pre-supplementary motor area with transcranial direct current stimulation or theta-burst TMS and found a causal contribution of this area on the sense of agency (Cavazzana, Penolazzi, Begliomini, & Bisiacchi, 2015; Moore, Ruge, Wenke, Rothwell, & Haggard, 2010).

Sensory attenuation has also been related to agency (Timm, SanMiguel, Keil, Schröger, & Schönwiesner, 2014; Windt, Harkness, & Lenggenhager, 2014). In the auditory domain the N100 event-related potential (ERP) is an electrophysiological marker for sensory attenuation (Baess, Jacobsen, & Schröger, 2008) that gets elicited in response to self-generated movements, irrespective of agency experience. However, peak-to-peak amplitude between auditory N100 and P200, the P200, and the P300a have been shown to be reduced when experiencing agency (Kühn et al., 2011; Timm et al., 2014; Timm, Schönwiesner, Schröger, & SanMiguel, 2016).

1.5 Brain computer interfaces (BCI)

A brain computer interface (BCI) allows a person to communicate with a machine or computer by changing their neurophysiological signal. BCI systems record, decode, and translate features of the neurophysiological signal into device actions without using peripheral physiological pathways (Birbaumer, Ramos Murguialday, Weber, & Montoya, 2009; Takeuchi & Izumi, 2013). Most BCI systems record brain signals with EEG because it has high time resolution, is non-invasive, and relatively inexpensive (Daly & Wolpaw, 2008).

BCI technology is based on feedback; it decodes an intention (Salvaris & Haggard, 2014) and couples it with a feedback. It has therefore the potential to couple intention and action.

1.5.1 BCI protocols

Mainly three different neural correlates have been used in the literature: Steady-state-visual-evoked potentials (SSVEP), ERP, and changes of the sensorimotor rhythm (SMR) (Wolpaw, Birbaumer, McFarland, Pfurtscheller, & Vaughan, 2002).

The difference in BCI protocols are the underlying neural correlates they employ and the analysis necessary to extract and classify those neural correlates.

SSVEP-based BCI protocols

These protocols exploit visual stimuli that are flickering at a specific frequency. When centered in the fovea, such stimuli produce oscillations at the simulation frequency over the visual cortex that the BCI algorithm can detect with relatively high accuracy.

ERP-based BCI protocols

These protocols exploit ERP. The most widely used ERP-component is the P300, a late ERP component that is modulated by attention (Guger et al., 2009; Mak et al., 2011). P300-based BCI systems typically present a fast sequence of different visual stimuli (for example different letters) and ask the participant to attend to the one matching their intention. The increase of the P300 amplitude can be detected by the BCI algorithm.

SMR-based BCI protocols

These protocols rely on changes in alpha- and/or beta-oscillations over somatosensory areas. These changes can be seen in a decrease in band power relative to a baseline, called event-related desynchronization (ERD), or an increase, called event-related synchronization (Pfurtscheller & Lopes da Silva, 1999). Alpha and/or beta-ERD can be observed during motor planning, imagination, execution, and observation of a movement (Neuper, Wörtz, & Pfurtscheller, 2006; Nikulin, Hohlefeld, Jacobs, & Curio, 2008; Pfurtscheller & Aranibar, 1979; Pfurtscheller & Neuper, 1997). SMR-based BCI protocols use motor imagery to produce changes in the SMR. Based on the somatotopic layout of the sensorimotor cortex, the BCI algorithm can distinguish whether the participant was imagining a foot, hand or lip movement.

The introduced BCI protocols employ different neural systems: SSVEP- and ERP-based BCI protocols employ mainly visual areas, while SMR-based BCI protocols employ sensorimotor areas.

1.5.2 Brain computer interfaces in immersive virtual reality

Several studies have shown that immersive VR and BCI can be used in combination, e.g. to move an avatar through a virtual environment (Lalor et al., 2005), to navigate through a virtual city (Touyama, 2008), or to control a wheelchair in a virtual environment (Leeb et al., 2007) (for reviews see Lécuyer et al., 2008 and Lotte et al., 2013). Such studies have shown that that the combination of the two influences both the VR and the BCI experience. For example, when controlling a virtual body with motor imagery in a Cave system, participants reported feeling more control over that body when imagined movements of one body part resulted in an outcome on the same body part in the virtual body—i.e. when imagined hand movement resulted in a waving movement of the virtual arm and imagined foot movement in walking compared to when it was vice versa (Friedman et al., 2007). The traditional feedback for SMR-based BCI is typically a moving bar on a computer screen. When giving the feedback through controlling a virtual body, people find this more intuitive, natural, and enjoyable than the traditional feedback (Friedman, Leeb, Pfurtscheller, & Slater, 2010). It has further been shown that SMR-based BCI can induce body ownership over a virtual arm (Perez-Marcos, Slater, & Sanchez-Vives, 2009) and even embodied humanoid robots can be controlled through SSVEP-based BCI (Kishore et al., 2014).

1.5.3 Brain computer interfaces and agency

Because of the BCI's ability to couple intention with outcome it should be possible to induce a sense of agency over BCI-induced actions (Haggard, 2017; Vlek, van Acken, Beursken, Roijendijk, & Haselager, 2014). A recent pilot study that replicated the helping hands experiment (Wegner et al., 2004) with BCI supports this claim, although no conclusions could be drawn from the data due to small sample size (van Acken, 2012).

As described earlier (see Section 1.4.3), the comparator model explains agency as a result of a matching comparison between predicted and actual sensory feedback of a planned motor action (Frith et al., 2000; Haggard, 2017), suggesting a necessary involvement of motor areas in the sense of agency. However, as described in Section 1.4.4, we can have, under certain circumstances, the illusion of agency over another person's movement while not moving ourselves (Banakou & Slater, 2014; Kokkinara et al., 2016; Wegner et al., 2004). This happens when one perceives the other person's body as if it were one's own body, which in turn raises the question on the involvement of motor areas in the sense of agency.

To test this we conducted the third experiment of this thesis. Participants could control the right arm of an embodied virtual body through a brain computer interface (BCI), which was either exploiting motor areas (through motor imagery) or visual areas (through SSVEP). In a control condition participants simply observed the movement of the arm. We hypothesized that movements induced through activity in sensorimotor areas would lead to higher agency levels than when controlling the same movement through SSVEP, and to the lowest agency ratings when simply observing the virtual arm move.

1.6 Summary

In this chapter the sense of body ownership was introduced to the reader. It explained that body ownership is based on multisensory integration and its processing is influenced by top-down processes, of which one is an internal representation of one's body. It further explained how body ownership illusions can be induced over body parts and over whole bodies, and that VR plays an important role in full body illusions. The chapter presented then specific background for each of the three experiments conducted for this thesis and explained their connected to body ownership.

In the first experiment we were interested whether the feeling of body ownership over a virtual body is fluctuating over time and whether these fluctuations can be predicted by spontaneous neuronal activity. The novelty of this study is that although several studies have investigated underlying processes of body ownership, this is the first study that investigates the perception of body ownership over time.

In the second experiment we were interested whether looking at the hand of an embodied surrogate body is analgesic similar to looking at one's own hand. The rubber hand illusion is widely-used and accepted as experimental paradigm to study body ownership. The novelty of this study is, that it investigates whether body ownership illusions are analgesic by taking into account the distance between real and surrogate hand, which is always induced in the rubber hand illusion but not necessarily in virtual body ownership illusions, and which could explain controversial findings in the literature.

In the third and last experiment of this thesis we investigated illusory agency, which is closely related to body ownership. We were interested whether BCI can induce agency over movements over a virtual body while the participant feels body ownership over that virtual body but is not moving the real body. The novelty of this study is, that it is to our knowledge the first study that investigates the feeling of agency in the context of BCI.

The following Chapter 2 will list the objectives of this thesis in bullet points.

Chapter 2

Objectives

The objectives of this PhD Thesis can be summarized as follows:

1. To identify key principles of body ownership

   - To determine if the feeling of body ownership over a surrogate body part is a stable percept or if it is fluctuating.
   - To identify a possible connection between the feeling of body ownership and slow oscillatory spontaneous brain activity (ISF).

2. To explore the application of embodiment on pain studies and treatment

   - To determine if body ownership illusions are analgesic and have therefore potential therapeutic value.
   - To determine the impact of distance between the real and virtual owned body on HTP.
   - To shed light to an ongoing controversy in literature regarding whether body ownership over a surrogate body part is analgesic or not.

3. To understand agency in VR embodiment

   - To determine the involvement of motor areas in the sense of agency.
   - To test if BCI-induced movements lead to higher levels of agency than motor observation.
   - To compare agency levels induced by different BCI methods (SMR- vs. SSVEP-based BCI).
   - To investigate the potential therapeutic value of SMR- and SSVEP-based BCI methods.

The following Chapter 3 will outline our hypothesis for each experiment and explain in detail the selected methodology.

Chapter 3

Methodology

In order to meet the objectives outlined in Chapter 2 the following three experiments have been conducted:

1. **Experiment 1: Influence of spontaneous brain activity on body ownership**. In this experiment we used a visuotactile simultaneity task to capture fluctuations of body ownership while manipulating the level of body ownership in two conditions—a Body and an Object condition. We further measured neural activity using EEG. Our hypothesis were:

   (1) Responses in the visuotactile simultaneity task are fluctuating.

   (2) The fluctuations in the visuotactile simultaneity task differ in the Body compared to the Object condition.

   (3) The phase of ISF is correlated with the fluctuations in the visuotactile simultaneity task.

2. **Experiment 2: Influence of distance between real and surrogate virtual hand on the analgesic effect of looking at a virtual hand**. In this experiment we systematically manipulated two factors—the distance between real and virtual arm and the synchrony of VTS; the latter is a typical way to manipulate body ownership in the rubber hand illusion. We measured individual HPT and experienced body ownership in four different conditions (colocation + synchronous VTS, colocation + asynchronous VTS, distance + synchronous VTS, and distance + asynchronous VTS). Our hypothesis were:

   (1) HPT is highest during colocation + synchronous VTS and lowest during distance and asynchronous VTS.

   (2) There is a positive relationship between HPT and body ownership—the higher the body ownership illusion the higher the HPT.

3. **Experiment 3: Influence of BCI in general and BCI method in particular on perceived levels of agency over the movements of an embodied virtual avatar**. In this experiment we induced agency over the movements

of an embodied virtual avatar while the participant was not moving. In order to understand the involvement of sensorimotor areas in the sense of agency we compared two BCI methods—one that employs sensorimotor areas (MotorImagery condition) and another that employs visual areas (SSVEP-condition)—against a third Control condition in which participants only observed the movement. We captured brain activity with EEG and measured experienced levels of control and responsibility with questionnaires. Our hypothesis were:

(1) BCI induces higher levels of control and responsibility over the movement of a virtual body than simply observing it.

(2) SMR-based BCI (motor imagery) induces higher levels of control and responsibility over the movement of a virtual body than SSVEP-based BCI.

(3) There is a relationship between activity in sensorimotor areas and reported control and responsibility ratings.

In the following section I will explain materials and methods used in these three experiments. Some material has been similar for all three experiments and will be described in one common section in the beginning. Other parts are different between experiments and will be described separately for each experiment.

3.1 Common material and methods

3.1.1 Participant recruitment and ethics

Participant recruitment Participants for all experiments were mostly students and were recruited through the participant pool of our laboratory or from Campus Mundet of the Universitat de Barcelona. In experiment 1 some participants were also recruited through the participant pool of Universitat Pompeu Fabra Barcelona. All participants were naïve to the research question and gave written consent before starting the experiment (see Appendix sections A.1.1, B.1.1, and C.2.3 for consent forms).

Ethical approval All experiments were approved by the local ethics committee (Comité Ético de Investigación Clínica de la Corporación Sanitaria Hospital Clínic de Barcelona) and were in accordance with the declaration of Helsinki.

Post-experiment questionnaire Approximately two weeks after the experiment we contacted participants by email for a follow up questionnaire in which we checked if participants experienced any after effects related to the experiment. This questionnaire was not part of the experiment but rather a policy we follow in our laboratory to be aware of any after-effects regarding VR exposure.

3.1.2 Virtual reality system

The virtual environment was programmed and controlled using the Unity game engine (Unity Technologies, www.unity3d.com) and displayed through a head mounted display (Oculus Rift Development Kit 2, www.oculus.com), which had a nominal field-of-view of 100° and a resolution of 960 × 1080 pixels per eye (see Figure 3.1). The virtual environment was displayed at a 75 Hz frame rate. The virtual male or female bodies were taken from the Rocketbox library (Rocketbox Studios GmbH). Further details about the laboratory's setup to create and measure virtual embodiment illusions can be found in Spanlang et al. (2014). The specific setup of the virtual environment will be described separately for each experiment.

FIGURE 3.1: head mounted display used in all three experiments.

3.1.3 Vibrotactile stimulators

In experiments one and two we applied vibrotactile stimuli, which were controlled by Unity through an Arduino (www.arduino.cc) MEGA board and delivered though cell phone micromotors based on electromagnets (78 cm^2, 1200 pm 300 r.p.m., 3 V, 100 mA, 50 Ω).

3.2 Experiment 1: Body ownership fluctuations

As described in the introduction, spontaneous neuronal activity (1) influences perception and (2) is organized in networks at oscillation frequencies around 0.1

Hz. These networks are called resting state networks and are assumed to functionally connect distant brain areas. Resting state networks have further been connected to consciousness (Heine et al., 2012). Body ownership, by some authors also described as bodily self-consciousness (Blanke, 2012; Blanke & Metzinger, 2009), is closely linked to consciousness and might therefore be influenced by the activity of resting state networks. The motivation of this experiment was to investigate if the experience of body ownership is fluctuating and further if these fluctuations are linked to ISF as found with EEG (Monto et al., 2008).

In order to test this, we used a visuotactile simultaneity task, in which always the same stimuli were presented to participants, and measured changes in their response.

In the first part of this section I will describe our pilot experiments that helped us to develop the task we used to capture fluctuations in the experience of body ownership. I will then continue describing the experiment's methodology.

3.2.1 Pilot experiments

Pilot 1—direct ratings of body ownership illusion In the first pilot we tried to capture fluctuations in perceived body ownership strength by asking participants to directly rate their level of body ownership. The pilot was done with four participants from our laboratory including myself. We asked participants to sit comfortably in an armchair and to put their legs on a foot rest. They had four vibrators attached to their body—one to the dorsal part of each hand and one to the frontal medial part of each shinbone. Through a head mounted display they saw a virtual environment with a gender-matched virtual body sitting in an armchair and being in the same position and co-located with their real body. The pilot started with an embodiment phase in which they saw four virtual balls bouncing off their arms and legs. The virtual balls were touching the virtual body at the same positions where participants had the vibrators, so whenever they saw a ball touching the virtual body they felt a vibration in the corresponding position on their real body. This embodiment phase lasted for about 1 minute. Then the VTS stopped but participants continued seeing the virtual scene. After that, we asked them every 2–20 seconds (the interval length was random) to rate the intensity of the illusion ("It felt as if the virtual body was my body.") on a Likert scale between 1 and 7. Participants were asked not to move throughout the experiment.

It was very difficult for participants to answer this question—they reported that although the illusion might not have been constant, they were not able to give it a rating. Some even described it felt as if they had no access to giving the experience a concrete rating. We concluded from this pilot that we needed a more simple way for participants to respond. This led us to pilot 2 which is described in the following paragraph.

Pilot 2—rating body ownership with Yes/No-responses Pilot 2 was very similar to pilot 1 except that this time participants rated the illusion with a mouse button—right button press for "yes, I felt it" and left button press for "no, I didn't feel it". Instead of presenting the virtual scene the whole time as in the previous pilot, we showed the virtual environment only for a very brief time window directly before they were asked to give the rating. The rest of the time the screen was black. We started with a time window of 2 seconds for presenting the virtual environment. The intervals to rate the body ownership experience where again random between 2–20 seconds.

Also in this pilot participants rated either always yes or always no. We next tried to reduce the time window of presenting the virtual environment but this had no change on the response behavior—except when the stimulus was presented so brief that participants could not perceive the virtual environment anymore. When debriefing participants they reported that while feeling the ownership illusion it was too strong to give a no-response. We concluded from this pilot that we needed a different task to capture the fluctuations of body ownership. This led to the pilot 3 in which we found the task we were finally using in the experiment.

Pilot 3—capturing body ownership through a visuotactile simultaneity task Instead of the whole body we concentrated in this pilot only on the feeling of body ownership over the right arm. We used a visuotactile integration task in which a ball touched the virtual finger and participants felt a brief vibration on the corresponding location on their real hand and participants had to report if they felt the two stimuli at the same time or not by using the two mouse buttons. We introduced a delay between tactile and visual stimulus and identified in each participant the length of this delay at which they would perceive the two stimuli at the same time in 50% of the trials. The idea was that when body ownership was stronger, participants should report the two stimuli more often to be simultaneous than when body ownership is less strong. The assumption behind this task is that body ownership temporally binds visual and tactile stimulus, a feature of body ownership that has been shown in a recent study (Maselli, Kilteni, López-Moliner, & Slater, 2016). We used this task, which is described in more detail below, to capture changes in body ownership. 25 participants from our laboratory were piloted to modify small aspects of the task (e.g. the threshold procedure, the presentation of visual and tactile stimuli) until we had a working procedure which we tested on 4 further participants using 2 EEG electrodes (Fpz and Cz). These electrodes were selected based on another study (Monto et al., 2008). Figure 3.2 displays the responses from one participant overlaid by the EEG signal filtered between 0.01 and 0.1 Hz and its amplitude envelope.

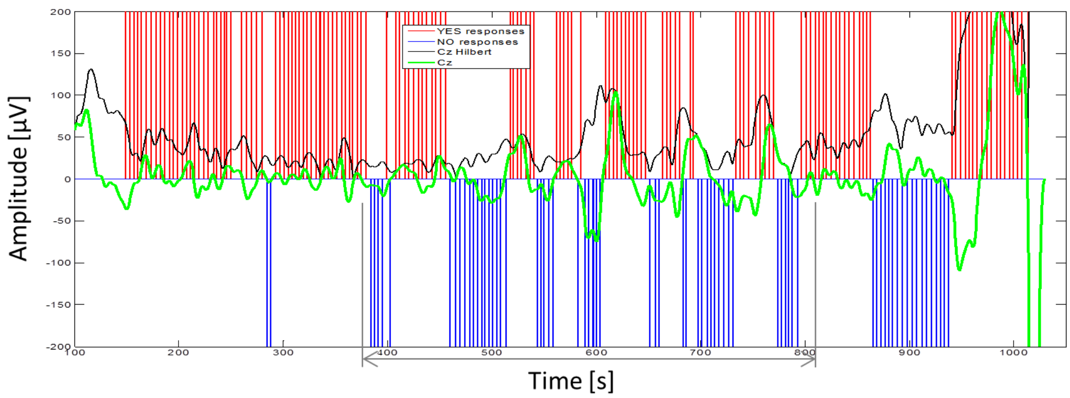

FIGURE 3.2: Yes-responses (red) and No-responses (blue) overlaid by ISF real part (green) and amplitude envelope (black) from electrode Cz. The interval indicated by the gray lines displays a time window where there seems to be a correlation between the signal and the response behavior.

The following sections describe the final experimental methodology that has been used in experiment 1.

3.2.2 Participants

Fourteen healthy female participants (age: *Mean* = 21.1; *SD* = 2.9) with normal or corrected to normal vision and no history of psychological or neurological diseases took part in the experiment. All participants were right-handed according to the Edinburgh Handedness Inventory (laterality quotient: *Mean* = 65.8; *SD* = 19.4). One participant was excluded from further analysis due to technical and protocol related problems leaving a final number of 13 participants (*Mean age* = 21.2; *SD* = 3.0; laterality quotient: *Mean* = 66.4; *SD* = 20.0). Participants were reimbursed for their participation with 35 euro.

3.2.3 Experimental protocol

Participants sat in an armchair with head support. Their right arm was resting comfortably in front of them on foamed material and their fingers were supported

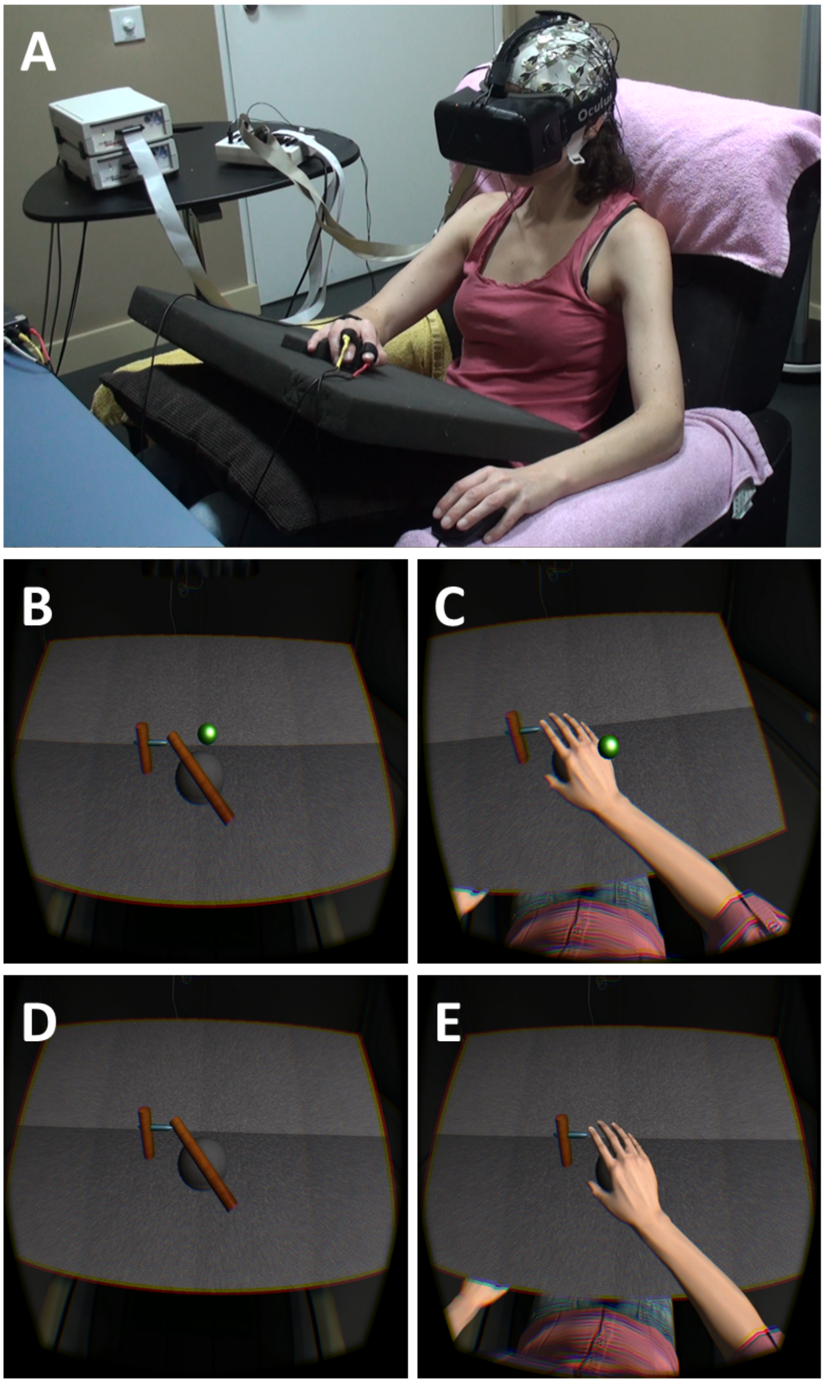

FIGURE 3.3: Experimental setup. (A) Participants were sitting in an armchair with their right hand resting on a foam support in front of them and their left hand at the side giving Yes/No responses by pressing one of two mouse buttons. Throughout the experiment participants were asked not to move their right arm. Embodiment phase (B and C). Depending on the experimental condition participants saw a green ball touching either (B) the virtual hand or (C) the virtual object while feeling a vibration at the corresponding location on their real hand. Figures (D) and (E) show the actual task, in which a virtual cylinder touched either the virtual body or the object. (D) Displays the position of the object when it didn't touch and (E) when it touched the virtual body/object. The tactile stimulus on the participant's right index finger was delivered first and the visual stimulus second, the delay between the stimuli was defined previously.

(see Figure 3.3 A). This position was selected in order to allow the participants to comfortably see the virtual arm in the virtual environment while resting their head on the armchair's head support. Three vibrators were attached to their right arm: one on the palm side of the index finger (distal phalanx) and two others on the dorsal side of the hand (one on the distal phalanx of the middle finger and the other on the back of the palm). The first vibrator was delivering the tactile stimulus for the simultaneity judgment task, while the other two vibrators were used in the initial part of each condition to provide the tactile stimuli to enhance the body ownership illusion. After completing the EEG preparation, the head mounted display was carefully donned (see Figure 3.3A) through which participants could see a virtual environment which was a custom made replica of a VR-laboratory.

There were two experimental conditions—a Body and an Object condition. In the Body condition they saw a virtual female body colocated with their real body and sitting in an armchair from a first person perspective (Figures 3.3 C and E). In the Object condition there was no body, instead they saw a stick lying at the same position as their forearm (Figures 3.3 B and D). Participants were asked to relax and keep their body posture static throughout the experiment. There were four recording sessions conducted on two different days (two recording sessions per recording day; number of days between recordings: *mean* = 3.3; *range* = 1–7). One condition consisted of two recording sessions. On each recording day one Body and one Object session were recorded in counter-balanced order. Each experimental session started with 1 minute visual exploration of the virtual environment, in which participants were asked to turn their head and describe what they saw. This was followed by an embodiment phase during which participants saw a virtual ball tapping the back of the virtual hand at two positions (distal middle finger and back of the hand) and synchronously felt a vibration on their real hand at the according position. In the Object condition participants saw the stick being tapped by the ball while feeling synchronous vibration on their real hand. At the end of the embodiment phase the green ball disappeared.

Visuotactile simultaneity task

The visuotactile simultaneity task was a forced-choice-task in which participants had to report as fast as possible whether a tactile and a visual stimulus were simultaneous or not. The tactile stimulus was always delivered first and consisted in a 50 ms long vibration of a piezoelectric transducer; the visual stimulus consisted in a cylindrical virtual object making a small (0.5 cm) and brief (100 ms) movement to touch either the virtual index finger (Body) or the wooden stick

(Object). Participants used a mouse to provide responses. Each recording session included 240 trials divided into four blocks. Between blocks participants could take a pause until they felt ready to continue with the task. During this pause the screen of the head mounted display went black and participants were allowed to move their body. These pauses were necessary because keeping a fixed posture for several minutes while concentrating on the task was highly demanding. Before each recording session, we ran a threshold defining procedure to determine the subjective stimulus onset asynchrony (SOA), that is, the amount of time between the onset of the tactile stimulus and the onset of the visual stimulus. We searched with an adopted truncated staircase method (Treutwein, 1995) for the threshold of perceived simultaneity at which participants rated in 50% $\pm$ 10% of the trials the two stimuli as simultaneous. The procedure started with a SOA which participants perceived as either always simultaneous (SOA = 50 ms) or never simultaneous (SOA = 700 ms, in some participants even higher) and progressively converged towards intermediate SOA-values for which responses started to alternate. The SOA was then progressively increased until the average rate for simultaneous perceived stimuli, which was calculated over 20–30 trials, converged to a Yes-rate of 0.5 ± 0.1. Defining the simultaneity threshold was extremely challenging because it was influenced by adaptation effects. Once set, the subjective simultaneity threshold was kept constant throughout the whole experimental run, independently on the participant's actual performance.

Response time and direction

We further recorded participants' responses and their response times.

EEG recordings

EEG data were recorded with a 60-channel EEG cap (Easycap GmbH, Herrsching, Germany) using active Ag/AgCl electrodes (actiCAP, Brain Products GmbH, Gilching, Germany). All electrodes had standard positions in accordance with the 10-10 system and were referenced to FCz during acquisition (see Figure 3.4). Of the four electrooculographic (EOG) electrodes one was placed at the outer canthi of the right eye, another in the center below the right eye, the third on the right and the fourth on the left mastoid. Impedances were kept below 10 kΩ. Data was recorded with BrainAmp amplifiers and BrainVision Recorder 1.2 software (Brain Products GmbH) and digitized at 500 Hz. Event triggers were sent from the VR-scenario via a separate Arduino board to Brain Vision recorder through a parallel port.

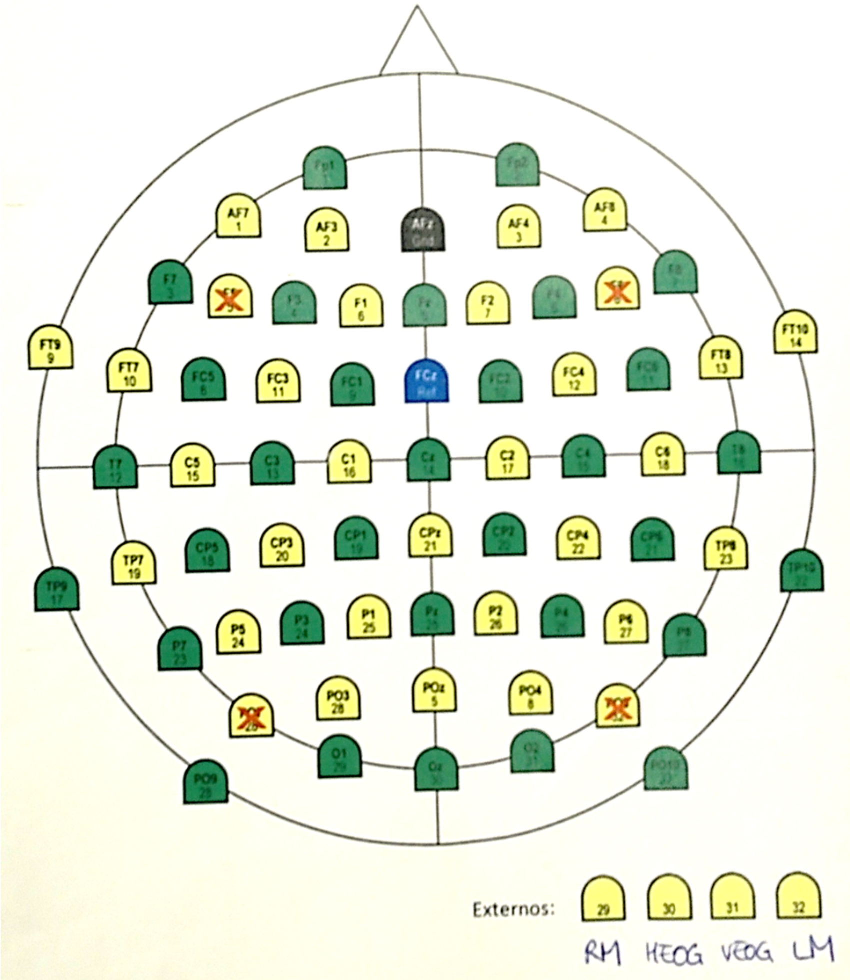

FIGURE 3.4: 60-channel EEG montage used in experiment 1. Ground was located at AFz (black) and reference at FCz (blue). The four external electrodes were used for EOG. Electrodes with a red cross were not used.

Questionnaire

After each recording session participants were asked to fill in a questionnaire which was displayed question by question on a computer screen. The questionnaire items were statements which they answered on a Likert scale ranging from -3 (corresponding to "I strongly disagree") to +3 (corresponding to "I strongly agree"). Items were presented in random order and are displayed in Table 3.1. Questions were presented in Spanish or Catalan, depending on the participant's preference.

Debriefing

At the end of each recording day we asked participants the following three questions: (1) Which of the two conditions made you more tired? (2) In which of the

TABLE 3.1: Questionnaire given to participants after each recording session. Responses were given on a 7-point Likert scale, where +3 is 'strongly agree' and –3 is 'strongly disagree'.

Item Tag	Questionnaire Item
MyBody	During the experimental session I felt as if the virtual body/stick was my body.
EmbFluct	The sensation that the virtual body/stick was my body was sometimes strong and sometimes weak.
NotConstant	During the visuotactile task it seemed as if the time between the touch and the movement of the object (cylinder) was not constant.
MovObject	During the visuotactile task it seemed as if the movements of the object (cylinder) happened sometimes before, sometimes after, and sometimes at the same time as I felt the touch.
TwoBodies	It seemed as if I had two bodies.
ObjTouchedMe	During the visuotactile task it seemed that when the object (cylinder) moved it touched my real finger.
BodyWouldMove	It felt as if the virtual body/object would move if I moved my arm.
FellAsleep	During the experimental session I had the feeling I was falling asleep.
CouldConcentrate	I was fully able to concentrate on the visuotactile task during the whole experimental session.

two conditions did you perceive the visuotactile task easier? (3) In which condition did you feel more comfortable?

3.2.4 Analysis of behavioral data

The analysis of behavioral and EEG data followed the analysis described by Monto and colleges (Monto et al., 2008).

Run length

Responses in the simultaneity task could either be Yes or No. A set of consecutive Yes (or No) responses is called a run and we calculated run lengths of consecutive responses of the same kind. Run lengths were combined into bins of 7 seconds and the probability of run length was plotted as a function of run length. For the surrogate data, we randomized the response array of the participant and thereby kept the participant's ratio between Yes and No responses. We created 200 sets of random responses and calculated run lengths and their probability for each set of surrogate data in order to obtain a distribution. For each participant, the real data was contrasted to their surrogate data.

Autocorrelation

We further computed for each participant an autocorrelation profile. The autocorrelation was performed using 4-second time lags and a total number of 80 lags. Participants' real data was contrasted against surrogate data (with a distribution created from 200 autocorrelations from randomized response arrays similar to how we created the surrogate data for the run length in the previous paragraph).

Analysis of infra-slow fluctuations

EEG-data sets were notch filtered between 48–50 Hz and then band-pass filtered between 0.01–0.1 Hz to obtain ISF (Monto et al., 2008). We used the Hilbert transform to obtain phase and amplitude of ISF. We used the values of phase, amplitude and real part at the time point of the tactile stimulus and computed for each participant 10-bin histograms, where phase, amplitude or real part defined the bins and number of Yes-responses were counted in each bin. The Yes-response probability was calculated for individual histograms and averaged over all included participants. From the cumulative binomial distribution we derived limits of 0.5%, 5%, 95%, and 95.5% for the Yes-response probability.

3.2.5 Statistics

All statistical tests were performed using RStudio (RStudio Team, 2015). Questionnaire data were analyzed with a multilevel mixed-effects ordered logistic regression (the 'clmm' function in R) with fixed-effects "Condition" and "RecordingDay", and random effects "individual subject". Because of the ordinal nature of questionnaire data, a mixed effects Gaussian linear model design would not be appropriate, and non-parametric statistical tests do not allow testing for multiple factors and their interaction effects. Differences in simultaneity threshold were analyzed with a two-factorial repeated measure analysis of variance (ANOVA) with factors "Condition" and "RecordingDay". To analyze the run length probability we took the difference in run length probability ΔRLP between real and mean surrogate data from each participant at each run length bin. We analyzed only bins in which all participants had a data point, which were the first four bins. ΔRLP was then analyzed with a two-factorial repeated measure ANOVA with factors "Condition" and "RunLength". We similarly analyzed the auto-correlation data. For each time lag we took the difference in time lag probability ΔTLP between real data and mean surrogate data. ΔTLP was then analyzed with a two-factorial repeated measure ANOVA with factors "Condition" and "TimeLag".

3.3 Experiment 2: Body ownership and pain perception

The scope of this experiment was to determine if body ownership illusions were analgesic and to better understand why previous experiments investigating this showed opposing results. When looking at the literature we found that one critical difference between the studies was the distance between real and surrogate arm (this is described in more detail in Section 1.3.4). Typically the studies used synchronous versus asynchronous VTS to induce the ownership illusion. To control for this and to add distance, the experiment had a two-by-two factorial within-subject design with one factor Distance (co-location versus 30-cm) and another factor VTS (synchronous versus asynchronous).

3.3.1 Pilot experiment

30 right-handed participants (18 females; age (in years) *Mean* = 21.8 years, *SD* = 4.9) who were naive to the research question, took part in this study. All participants had normal or corrected-to-normal vision, no history of chronic pain, no history of neurological or psychological disorders, and no medication intake during the last 24 hours. After conducting all participants we took pictures of the experimental setup and realized that our manipulation did not work in all participants (see Figure 3.5). When conducting the experiment we did not realize that during the 30-cm condition (see explanation of that condition below) participants could shift their trunk and thereby also the head mounted display which led to a colocation between virtual hand and real hand in the distance condition (see Figure 3.5 B). Therefore the collected data was useless and we needed to collect it again—this time making sure participants kept their trunk in a central position throughout the experiment.

The following sections describe the methodology used in experiment 2.

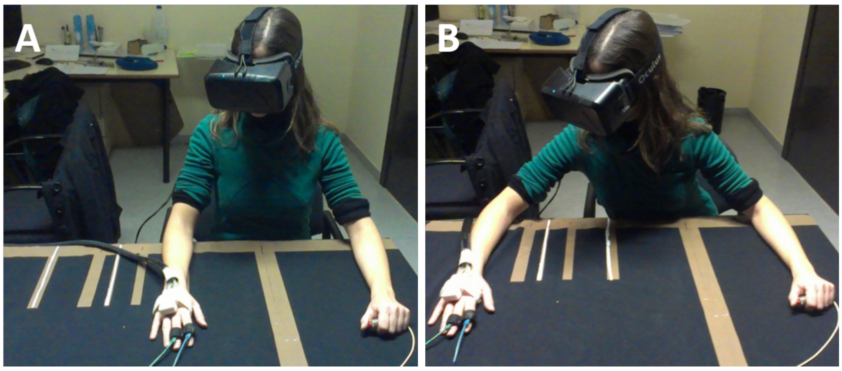

FIGURE 3.5: Experimental setup of pilot study for experiment 2. Participants were asked to look at the virtual hand in both pictures. In (A) real and virtual hand are colocated, while in (B) there should be a distance between the two. The pictures display that our manipulation in this pilot study did not work—in both cases the participant looks at the virtual but also at the real arm indicating that in (B) there was no distance between real and virtual arm. See also Figure 3.6 as comparison, where our manipulation worked.

3.3.2 Participants

24 right-handed healthy males participated in this study. We decided to include only male participants to control for sex and menstrual cycle which have been shown to contribute to variation in pain perception (Palmeira, Ashmawi, & Posso, 2011; Rhudy et al., 2013). 24 participants were recruited for this study of which 5 were removed for further analysis. Four of them were removed directly after data acquisition due to either technical problems (2 participants), extremely high (1 participant reached the maximum temperature without indicating a HTP) or extremely low (1 participant had a HTP below 38.9 °C) HPT (Yarnitsky, Sprecher, Zaslansky, & Hemli, 1995) and another participant was identified as outlier (see Section 4.2.1). This led to a final sample size of 19 participants (age (in years): *Mean* = 24.1, *SD* = 5.1; laterality quotient of the Edinburgh Handedness Inventory (Oldfield, 1971): *Mean* = 65.8, *SD* = 25.3, range = 12.5–100) who were included in subsequent analysis. Only participants who were naive to the research question, with no history of chronic pain, no neurological or psychological disorders, and no medication intake for the past 24 hours were included in this study. Participants received 5 Euros for their participation.

3.3.3 Thermal stimulation

Heat stimuli were applied with a contact heat thermode (Somedic Thermotest, Stockholm, Sweden) that was tied to the dorsum of the right hand and that had a contact area of 25 $\times$ 50 mm. The method of limits (Yarnitsky et al., 1995) was used to measure HPTs: therefore the temperature was increased from a constant baseline temperature of 32 °C at 2 °C/s and participants were asked to indicate with a button press their HPT. When pressing the button the temperature of the thermode rapidly decreased to baseline (6 °C/s). For safety reasons the maximal temperature was set to 51 °C. The temperature measures were recorded from the thermode with Matlab Simulink (The MathWorks Inc, Natick, MA) via a NI-6008 card (National Instruments Corporation, Austin, TX), which ran on a separate computer than the virtual environment.

3.3.4 Tactile stimulation

Tactile stimuli were applied via two vibrotactile stimulators described in Section 3.1.3. The stimulators were attached to the dorsal side of the second phalanx of the index and middle fingers and had a duration of 1.0 seconds.

3.3.5 Experimental procedure

Participants sat comfortably on a chair with both arms resting on a table in front of them. The thermode was attached to the dorsum of their right hand with a Velcro strap. Two vibrators were attached to the dorsal distal phalanges of their right index and middle fingers for the delivery of tactile stimuli (see Figure 3.6). Noise isolation was ensured by administration of pink noise.

Familiarization phase

Participants were first familiarized with the virtual body illusion: they donned the head-mounted display through which they saw a virtual male body located at the same place as their own body. When they looked down they saw their virtual body sitting on a chair with its arms resting on a table in front. Both virtual arms were in the same position as the real arms——the left elbow was positioned under the left shoulder and the right elbow/forearm was lying at the body midline. Like the real body, the virtual body held a button in its left hand and a virtual thermode attached to the dorsum of the right hand. Participants were instructed to look around in the virtual room, to describe what they saw and to look down at the virtual body. After this initial exploration of the virtual scenario, participants were asked to concentrate on their right virtual hand. They saw a ball tapping in random order the virtual right index and middle fingers and felt synchronous tactile feedback (vibration) on their real right index and middle fingers (synchronous VTS). They were also instructed to report out loud when they saw

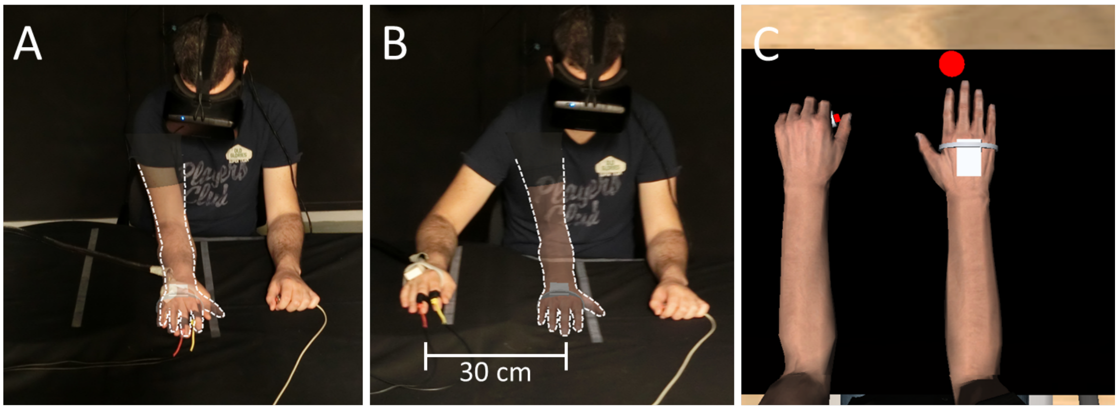

FIGURE 3.6: Experimental setup. The participant wore a head-mounted display that provided an immersive virtual environment including a virtual own body that was perceived from a first person perspective. The transparent arm outlined with a white dashed line indicates the position of the virtual arm. Position of participant during (A) colocation, where the virtual and real arm were colocated, and (B) when there was a distance of 30 cm between the real and virtual arm. (C) The virtual body from the first person perspective (participant's point of view). The red dot displays the ball that was tapping the fingers during the VTS phase at the beginning of each trial. Participants were asked to look at the right virtual arm throughout all of the experimental trials.

a letter appear on the virtual thermode. This was to ensure participants kept their attention toward the right hand. The letter appeared at the end of the 30- second stimulation period for 1 second (jittered in a time window of 5 seconds). The level of attention was defined as sufficient when participants correctly reported the displayed letter. In case the letter was not reported correctly the 30-second VTS period was repeated (including the display of another letter at the end). In the 360 trials that were presented to the 19 participants included in the analysis, we repeated the stimulation in only 4 cases (1.1% of the trials), which we consider rules out the possibility of this having affected our results. This happened a maximum of once during 1 condition, meaning that there were still 4 other trials—which happened to be equally distributed over the 4 experimental conditions—taken into account in our statistics. Then the screen went black and they were asked to answer a questionnaire. Next, participants were familiarized with the HPT measurement and the baseline for their HPT was taken. During this part they did not wear a head-mounted display. Participants were instructed to look during the whole procedure at their right hand. When the thermode heated up they had to press a button in their left hand as soon as the heat stimulation started to become painful. Seven heat stimuli were delivered during this phase, the first 2 were for the participant to become familiar with the task and the mean of the following 5 stimuli was later used as baseline. We specifically did not randomize the order of the 2 familiarization tasks because it has been shown that strength of the rubber hand illusion increases linearly with time (Fuchs, Riemer, Diers, Flor, & Trojan, 2016) and we wanted to account for possible carryover effects from the familiarization phase of the illusion to the first experimental condition.

Manipulation phase

The experiment had a 2-by-2 factorial within-participants design, with 1 factor "distance" (colocation vs 30 cm distance between the real and the virtual arm) and a second factor "VTS" (synchronous vs. asynchronous). Therefore we had 4 conditions: synchronous VTS at 0 cm distance, synchronous VTS at 30 cm distance, asynchronous VTS at 0 cm distance, and asynchronous VTS at 30 cm distance. The order of conditions was balanced among participants. We decided to use balancing instead of randomization because we wanted to have the same number of participants for each possible order of conditions. The fact that we excluded participants from the analysis did not undermine the balancing because four of the participants we had removed because of technical problems, who had extremely high, or extremely low HPTs, were already identified during the data acquisition phase and we reused their ordering of conditions for four of the other participants, maintaining the balance. Therefore we had only 1 participant who we removed from the analysis because of being an outlier. The position of the virtual body was the same for all conditions and the same as described for the familiarization period. Depending on the experimental condition, the real right arm was at the body midline, the same position as the virtual arm (colocation condition) or 30 cm to the right of the body mid-line (30 cm distance condition; Figure 3.6). To make sure that participants were able to keep their trunk straight in all conditions, we elevated the arm in the distance conditions by 4 cm. This ensured that participants with shorter arms were able to comfortably keep their forearm at the indicated position. At the beginning of each condition participants donned the head-mounted display and were asked to look around in the virtual room and to look down the virtual body. Participants were then asked to concentrate during the whole condition on their right hand only. Each condition consisted of 5 trials (1 heat stimulus per trial): Each trial started with 30 seconds of VTS during which participants had to report the name of the letter they saw, then there was a pause of 2 to 4 seconds, the thermode heated up, and participants pressed the button in their left hand when the increasing heat reached their individual HPT. The left virtual arm was occluded from sight during the heat stimulation to make sure the right arm was the only focus of participants' attention. At the end of each condition the screen turned black and participants were asked to answer the same questionnaire as mentioned previously (a description of the questionnaire can be found in the following section on response variables, and in Table 3.2), which took approximately 2 to 3 minutes.

TABLE 3.2: Questionnaire given after the familiarization phase and after each manipulation phase. Responses were given for questions 1–6 on a 7-point Likert scale, where 7 is 'strongly agree' and 1 is 'strongly disagree'. And for question 7 (OwnershipStrength) on a 10-point Likert scale, where 10 is 'strongly agree' and 1 is 'strongly disagree'.

Item Tag	**Questionnaire Item**
TappingLocation	(1) It seemed as if I were feeling the tapping in the location where my fingers were.
BallCausesTouch	(2) It seemed as if the vibration I was feeling on my fingers was caused by the ball touching the virtual fingers.
OwnershipPresence	(3) It seemed as if the virtual hand was my real hand.
MultipleHands	(4) I felt as if I had more than 1 hand.
VibrationBetweenHands	(5) It seemed as if the vibration I felt came from a place between my real hand and the virtual hand.
RealHandTurnsVirtual	(6) It seemed as if my real hand were becoming virtual.
OwnershipStrength	(7) On a scale from 1 to 10, how strong did you have the illusion that the virtual hand was your real hand?

3.3.6 HPT

It was carefully explained to participants that the HPT is the temperature at which the sensation of an increasing heat stimulus changes from a hot to a painful percept. They were further instructed to look at their real (during the baseline) or the virtual (during the experimental conditions) right hand and press a button located in their left hand as soon as they perceived the stimulus to be painful. The initial 2 stimulations allowed the experimenters and the participants to confirm whether the task had been well understood. The baseline and all 4 experimental conditions consisted each of 5 heat stimulations.

3.3.7 Questionnaire

A questionnaire (see Table 3.2) was administered after the familiarization phase and after each condition of the manipulation phase. The items are shown in Table 1 (see Appendix B.1.2 for Spanish version used in the experiment). The first 6 items were presented in random order and participants were asked to report their degree of agreement with each statement on a 7-point Likert scale (1 = absolutely disagree, 7 = absolutely agree). Question 7 was always asked at the end to obtain the participant's overall rating of the illusion. It is important to note that although question 3 is meant to assess the presence of the body ownership illusion, question 7 assesses the strength of it. Questionnaire items were adapted from Botvinick and Cohen (1998) and the additional question from Mohan et al. (2012). Participants wore the head-mounted display with the screen black while the experimenter read the items of the questionnaire out loud and they gave oral responses, during which the pink noise was turned off.

3.3.8 Data handling

All statistical tests were performed using Stata 13 (StataCorp LP, College Station, TX). Mean values of the 5 HPTs measured during each experimental condition and 5 HPTs during baseline were used for subsequent analysis. The variable of interest was ΔHPT = (HPT [manipulation phase]) – (HPT at baseline). Each participant carried out 4 different experimental conditions. This is therefore a mixed-effects design, with fixed-effects "distance" and "VTS", and random effects over the "individual subjects", and is appropriately analyzed using a multilevel mixed-effects linear regression (the 'mixed' function in Stata). Questionnaire data were analyzed with a multilevel mixed-effects ordered logistic regression (the 'meologit' function in Stata) with fixed-effects "distance" and "VTS", and random effects "individual subject". Because of the ordinal nature of questionnaire data, a mixed effects Gaussian linear model design as used for the HPT data would not be appropriate, and non-parametric statistical tests do not allow testing for multiple factors and their interaction effects. We measured the overall strength of ownership illusion in 2 ways—with the question OwnershipStrength and with a principle component analysis. The latter constructed a single variable (V) as the highest variance linear combination of the 4 original body ownership questions. A mixed effects regression using the Stata 'mixed' function, with fixed effects over the 2 factors (distance and VTS) and covariate Ownership-Strength or V, and random effects over the individuals, showed that the response variable ΔHPT is linearly associated with OwnershipStrength (or V).

3.4 Experiment 3: Body ownership and agency

In this experiment we aimed to investigate the level of illusory agency that can be induced by different BCI protocols and the involvement of motor areas in the sense of agency. In two experimental conditions participants were able to move the right arm of the virtual body (over which they felt ownership) through a BCI, which was either exploiting motor areas (SMR-based BCI, MotorImagery condition) or visual areas (SSVEP-based BCI, SSVEP condition). In a control condition participants simply observed the movement of the arm (Observe condition). We hypothesized that when participants induce the movement through motor imaginary, agency levels should be higher than when controlling the same movement through looking at a blinking light, and should be the lowest when simply observing the virtual arm movement.

3.4.1 Development of the experimental setup

Integrating the SSVEP stimuli in the virtual environment

The SSVEP based BCI method produces SSVEP at a specific frequencies in primary visual areas, which are then measured by EEG. Therefore, this method requires a stimulus in VR that is blinking constantly at a specific frequency. Developing this can be challenging because the used software and hardware is designed to create the best user experience at the cost of perfect stimulus control. Therefore, a testing procedure was necessary to ensure that the signal created in the virtual environment was exact and constant. Further, this stimulus needs to be big enough to induce SSVEPs but should at the same time be small enough in order to have the size of a virtual button. We were also limited to a frequency that could be represented by a refreshing rate of 75 Hz in the head mounted display screen. In order to make sure that the SSVEP signal produced in the head mounted display was constant and at the correct frequency, we measured it with a light diode connected to an oscilloscope. Our first recordings showed that the stimulus was not constant (3.7). Although our algorithm should have produced a 5 Hz frequency, the frequency displayed by the oscilloscope was just an approximation and was not accurate enough to produce a oscillation at the correct frequency in the brain. In order to get the signal constant, we started a testing procedure in which we first tried to get the flickering constant on the computer screen and then on the head mounted display screen. We started with a very simple environment in Unity that consisted of two white boxes on a blue background (see Figure 3.8). We started changing always one variable in the environment and

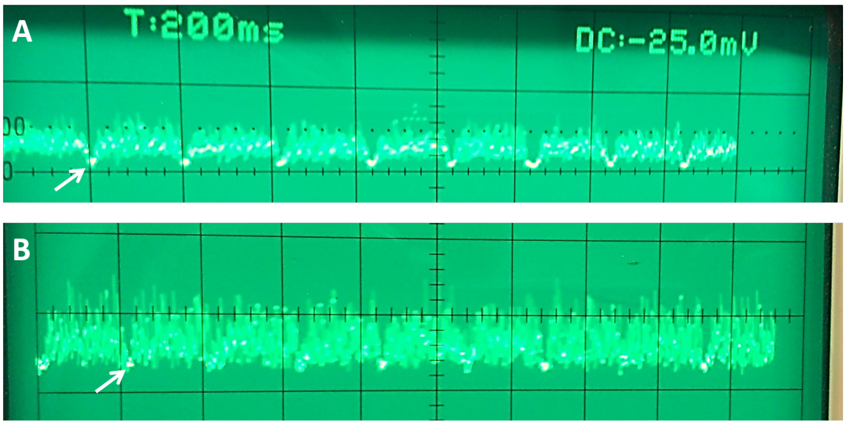

FIGURE 3.7: Recordings of SSVEP signals at the beginning of our testing phase. The blinking stimulus was recorded with a light diode connected to an oscilloscope on (A) a computer screen and (B) an Oculus DK1 screen. The signal is in neither of the two recordings precise at 5 Hz (in order to be precise each stimulus has to appear at a vertical line). Note the increase of background noise and the increased delay in the recording done with the Oculus head mounted display. The white arrows indicate a stimulus.

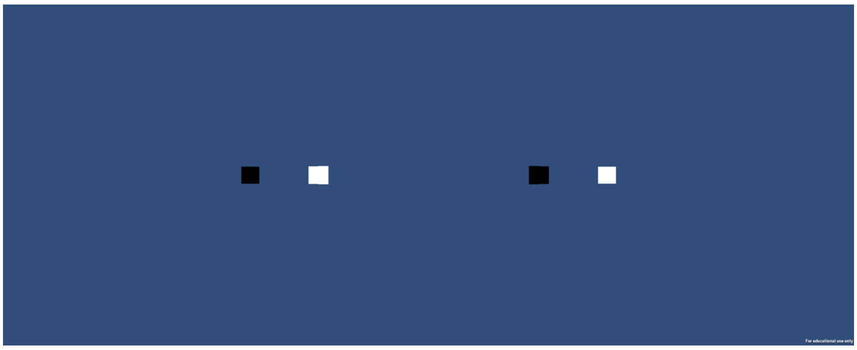

FIGURE 3.8: SSVEP stimulus used for the testing procedure to identify the settings to produce a stable flickering on the head mounted display screen. There are only two blinking boxes, the other two are due to stereoscopic imaging to produce a three dimensional perception.

checked how it affected the outcome of the flickering using an oscilloscope. The variables we changed were the algorithm that produced the flickering, the settings within the Untiy Game Engine, the size of the flickering boxes, and the frequencies of the flickering. Next we added step by step the environment, checking that the rendering of the environment and the control of other events in the virtual environment would not interfere with the frequency of the flickering during the motor initiation phase. Figure 3.9 displays a two second oscilloscope recording in the final experimental environment with the two selected final frequencies of 7.5 Hz and 9.4 Hz (the recording was done at the end of our testing procedure). Note that the stimulus is much more precise and distinct compared to the

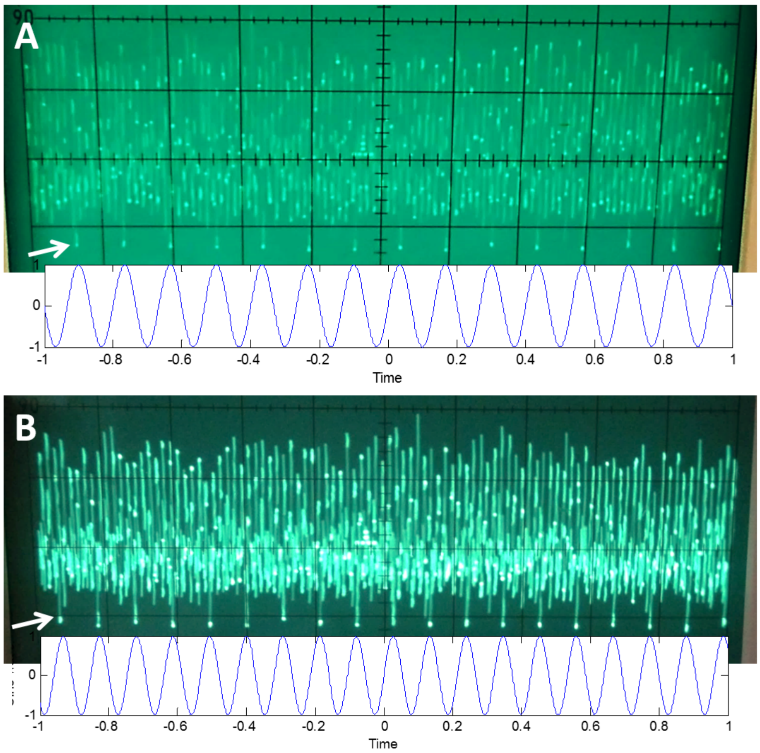

FIGURE 3.9: Recordings of SSVEP signals at the end of the test series. The blinking stimulus was recorded with a light diode connected to an oscilloscope on an Oculus DK2 screen (same screen as the one used in the experiment). (A) 7.5 Hz stimulus and (B) 9.4 Hz stimulus. Below each recording is a sine wave with the frequency of interest—note that both stimuli are now very precise.

stimulus in our first recording (Figure 3.7). We further checked if the presented frequencies can be detected by EEG. Figure 3.10 shows that there were clear peaks in the spectrum calculated over all 8 SSVEP channels (green channels in Figure 3.12) for the two frequencies 7.5 and 9.4 Hz, and their harmonics.

Selecting the number of buttons

In the first experimental setup we used only one button. Pilot experiments revealed that people do not feeling agency during the SSVEP condition when there is only one button—therefore, we introduced a second button. The two buttons were blinking at different frequencies (7.5 Hz and 9.4 Hz, as mentioned above).

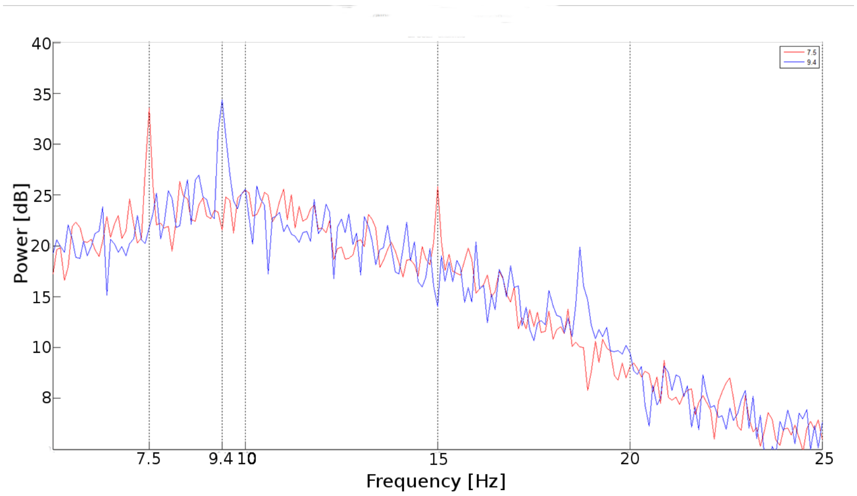

FIGURE 3.10: Spectrum of SSVEP channels while the participant is looking at an SSVEP stimulus. There were two different SSVEP stimuli, one was blinking at 7.5 Hz (red), and the other was blinking at 9.4 Hz (blue).

Adaptation of the SSVEP Simulink model

The simulink model for the SSVEP-based BCI ("SSVEP BCI", V2.14.01) was provided by g.tec (Guger Technologies OEG, Graz, Austria). It extracts the signal from 8 channels over occipital areas (PO7, PO3, POz, PO4, PO8, O1, Oz, O2, see Figure 3.12) and came in its original version with four different frequencies. In order to adjust the model to only two frequencies, we had to do several adjustments which needed to be tested in pilots. First we needed to decide which frequencies to choose. We wanted to stay with the SSVEP frequencies below the somatosensory alpha rhythm, between 10 and 12 Hz (Pfurtscheller, Brunner, Schlögl, & Lopes da Silva, 2006). Therefore we tested the frequencies 5, 6.3, 7.5, 8.3 and 9.4 Hz. We further adjusted the model to be used in combination with VR. A screen shot of the model is displayed in Figure C.1.

In first tests we identified which frequencies where the best ones to be differentiated by the BCI and found that frequencies below 6 Hz are not very well detected by the BCI and further that too close frequencies were also difficult to be differentiated. We therefore selected 7.5 and 9.4 Hz as the two frequencies to be displayed during the experiment. The BCI classifier makes its classification based on the signal to noise ratio (SNR) of the two different frequencies, which should be higher for the frequency that the participant looks at. Figure 3.11 displays the SNR for the frequencies 7.5 and 9.4 Hz and shows the selection of the classifier. Note that the classifier still selected one of the two classes when no stimulus was presented (see Figure 3.11 in the time window before the first trigger was presented). Therefore we introduced a third class to the BCI model with

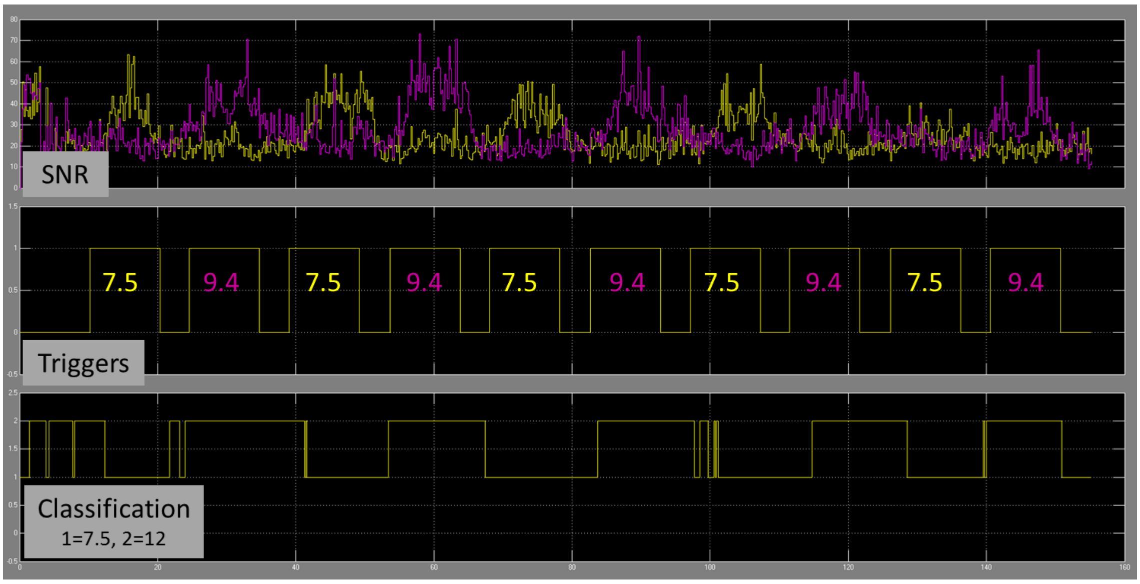

FIGURE 3.11: The BCI classifer is based on the signal to noise ratio (SNR, displayed in the top row) which should be higher for the frequency the participant is looking at than the other frequency. The second row shows the triggers that indicated the participant to look either at the light blinking at 7.4 Hz or at 9.4 Hz. The third line shows the decision of the classifier which could be either 1 (7.5 Hz) or 2 (9.4 Hz). Note that the BCI used only two frequencies, therefore when there is no frequency displayed the classifier still selects one of the two classes. For this reason a third dummy frequency was later introduced to the BCI Simulink model. X-axis displays time in seconds.

a dummy frequency set to 20 Hz (dummy frequency because the frequency was never displayed in the virtual environment, instead participants were looking at a fixation point in the virtual environment—see paragraph 3.4.7 where the SSVEP BCI is explained in detail). A sensitive classifier would select this class when the participant was not looking at one of the two frequencies.

Testing motor imagery ability

A big problem in SMR-based BCI protocols is that not all people can learn to control it, especially not in less than 1 hour (which was necessary to participate in the experiment). This problem is called BCI illiteracy and concerns 15-30% of participants (Dickhaus, Sannelli, Müller, Curio, & Blankertz, 2009). We encountered this problem in our pilots and therefore decided to pre-select our participants based on their ability to imagine a movement.

We searched the literature for a suitable questionnaire and selected the Test of Ability in Movement Imagery (Madan & Singhal, 2013) because it does not rely on the perceived vividness of an imagined movement but instead asks participants to imagine 10 series of explicit movements. After imagining each movement series participants are asked to remember the final pose and select the corresponding pose out of several images. The questionnaire gives a movement imagery score based on the correctness of the answers. We gave this questionnaire to seven pilot participants from our laboratory and found that test performance could not predict performance in the SMR-based BCI. Therefore we did not use this questionnaire in the final experiment, instead we pre-selected our participants based on the clear occurrence of the sensorimotor alpha rhythm.

Power spectral density in Laplace-transformed EEG-channels (C3 for right hand motor imagery) has been identified as predictor for SMR-based BCI performance (Dickhaus et al., 2009). Therefore we decided to pre-select participants based on the occurrence of a clear sensorimotor alpha rhythm. Participants were excluded from participating in the experiment after performing two motor imagery training runs. This happened if we did not see a clear sensorimotor alpha peak in their power spectrum or if we could not create a usable classifier.

3.4.2 Participants

Of the 62 invited participants, 22 were excluded directly after the motor imagery training before even starting the experiment due to the screening procedure explained in Section 3.4.1. 40 healthy, right-handed females (age: *Mean* = 21.8 years, *SD* = 3.0; laterality quotient (Oldfield, 1971): *Mean* = 70.3, *SD* = 22.5) with normal or corrected-to-normal vision, no neurological or psychological disorders, and no medication intake that could influence their perception, participated in the experiment. Participants were novices to BCI and those with accuracy rates lower than 75% in either one of the BCI protocols were removed from further analysis, which lead to a final sample size of 29 participants (age (in years): *Mean* = 21.5, *SD* = 2.6; laterality quotient: *Mean* = 71.0, *SD* = 23.4). Real movement was only recorded in 21 participants. Therefore all analysis related to this data was based on 18 participants (excluding participants with too low accuracy rates). Participants received 5–20 euro for their participation (participants who dropped out after the screening procedure received 5 euros).

3.4.3 Virtual environment and tracking system

The virtual room was a custom made replica of a VR laboratory and was the same during all experimental conditions. Movements of the right arm and fingers were tracked with the right arm setup of Perception Neuron (Noitom, Beijing, China), a full body tracking system.

3.4.4 EEG and EOG recordings

EEG data were recorded with a 59 active Ag/AgCl ring electrodes (g.LADYbird) mounted on a g.GAMMAcap (g.tec). All electrodes had standard positions in accordance with the 10-percent electrode system (Chatrian, Lettich, & Nelson, 1985). The ground electrode was located at AFz (see Figure 3.12 for electrode positions). The two electrooculographic (EOG) electrodes were placed next to

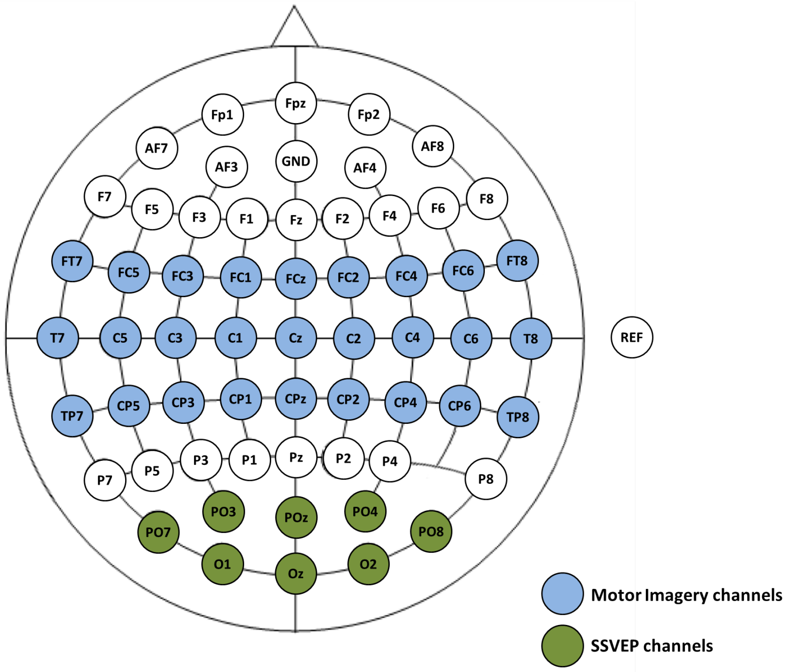

FIGURE 3.12: EEG montage. The electrode positions used in this experiment are displayed. Ground was positioned at AFz and electrodes were referenced to the right ear lobe. Colored electrodes indicate those electrodes used for online analysis—blue ones for SMR-based BCI and green ones for SSVEP-based BCI.

the outer canthus and below the right eye. EOG and EEG electrodes were referenced to the right ear. The data were recorded with a g.HIamp amplifier (g.tec) and Matlab R2013a Simulink software (The MathWorks, Inc., Natrick, USA) on a separate computer than the one generating the virtual environment. During the data acquisition EEG, EMG, and EOG signals were band-pass filtered between 0.5 and 250 Hz, notch filtered at 50 Hz, and digitized at a rate of 512 Hz. The data were analyzed offline using Matlab and the Berlin Brain-Computer Interface toolbox (https://github.com/bbci/bbci_public; Blankertz et al., 2016) and online (for BCI) using Matlab Simulink. To compensate for network latencies between the two computers, we synchronized them by using the network time protocol and time-stamped triggers with the times of the Unity and the Matlab computer. Triggers were then adapted in the analysis so that time stamps would match.

3.4.5 EMG recordings

Electromyography (EMG) data were recorded with a bipolar montage from the anterior deltoid muscle using the same amplifier and amplifier settings as described for EEG data. One electrode was located over the muscle belly and the other electrode more distal but still on the muscle. Ground was the same as for EEG data.

3.4.6 SMR-based BCI

The Simulink model for the SMR-based BCI ("Common Spatial Patterns 2-class BCI", V2.14.01) was provided to us by g.tec and extracted the signal from 27 channels over somatosensory areas (see Figure 3.12). This model uses the Common Spatial Pattern (CSP) approach (Fukunaga, 1990; Graimann & Pfurtscheller, 2006; Koles, Lind, & Soong, 1995; Müller-Gerking, Pfurtscheller, & Flyvbjerg, 1999) to extract ERD over sensorimotor areas, which is an established approach to distinguish two classes of motor imagery, in our case imagination of a right arm and a left foot movement (the movements are described below). The model was adjusted to be used in combination with VR (see Figure C.2).

Motor imagery training

Before the actual experiment, participants went through a motor imagery training that consisted of 1–4 training sessions of each 7–10 minutes. The number of training sessions depended on how quickly participants were able to change their SMR through motor imagery in a way that it could be detected by the BCI (the basics of SMR-based BCI protocols are explained in Section 1.5.1). Participants who did more than one training were doing one or two training sessions in the very beginning of the experiment and the rest directly before the motor imagery condition. This helped to recall the motor imagery and to keep their performance higher during the motor imagery condition.

Before starting the motor imagery training, we asked participants to concentrate on their breath and relax. We instructed them to first focus on the different parts of their left leg and foot and then to move their left foot five times from the tip of their toes to the heel and back. While doing this movement they had to concentrate on what they perceived in all parts of their leg and foot. Then we asked them to describe their sensation. After this they were instructed to imagine the movement eight times. The same procedure was repeated for the right arm and hand. The movement they were asked to perform with their right arm was to press a button in front of them. This was the same movement they would see later during the experimental conditions in VR. After this initial period, we started the motor imagery training. The first training was performed with a template classifier and did not give any feedback to the participant. The following training sessions were performed with the classifier obtained in the previous training and gave the participant feedback on their performance.

The motor imagery training was based on the training recommended by g.tec (Guger, Edlinger, Harkam, Niedermayer, & Pfurtscheller, 2003). It consisted in 40 trials of motor imagination—20 right arm and 20 left foot movements. The participant sat comfortably in a chair 1 meter in front of a computer screen. Participants were instructed to keep both arms and hands relaxed on the table and to look at the center of the computer screen throughout the training. The training started with a blue fixation cross at the center of the screen. After three seconds they saw a red arrow for 1.25 seconds that could point either to the right (indicating the right arm movement) or down (indicating the left foot movement). The participant had to imagine the movement indicated by the error for the next 3.75 seconds. Starting from the second training participants received feedback that was based on the classifier calculated in the previous training. During this time the EEG was classified online and the classification result was translated into a feedback stimulus in form of a blue bar that would extend in space either go to the right (to indicate right arm movement) or the left side (to indicate left foot movement) to indicate. In this feedback mode the participant's task was to keep the feedback bar on the side indicated by the arrow cue in the beginning of the trial and if possible extend the length of the bar. Participants were instructed to stop imagining the movement when the fixation cross disappeared from the screen. One trial lasted 8 seconds and the time between two trials was randomized in a range of 0.5 to 2.5 seconds to avoid adaptation.

3.4.7 SSVEP-based BCI

For SSVEP-based BCI we used an established model for online analysis and classification of SSVEP (see Section 3.4.1 on how we adapted the Matlab Simulink model).

SSVEP training

The SSVEP-training was performed while participants wore the head mounted display and was adapted from (Guger et al., 2012). As described in Section 3.4.1, the 20 Hz frequency was utilized as dummy frequency in order to get a more precise classifier. This frequency was neither displayed during the training phase nor during the experiment, instead participants were instructed to look in the middle of the two (not blinking) buttons (a fixation cross was displayed at beginning of each trial at that point). The SSVEP training had 15 trials, 5 for each frequency. In order to get a better classifier, only the frequency of interest was displayed during the training phase. Later during the experiment, both frequencies (7.5 and 9.4 Hz) were displayed.

3.4.8 Experimental procedure

On arrival participants gave informed consent to take part in the experiment and were informed that they could abort the experiment at any moment. Participants were asked to sit comfortable in a chair having their arms lying on a table in front of them. The two middle fingers had a distance of 55 cm (see Figure 3.13).

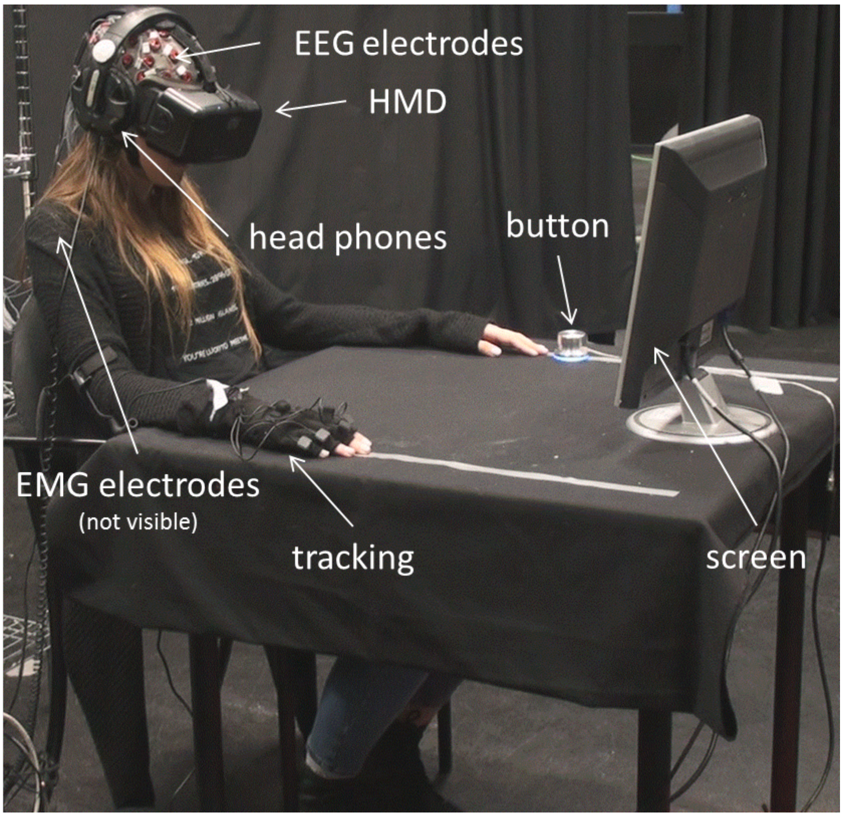

FIGURE 3.13: Position of participant throughout experiment 3. Participants were asked to move their right hand during the embodiment phase and movements were tracked and mapped onto the virtual right arm. During the other parts of the experiment they were asked not to move their hands. Instructions were given via head phones.

Preparation of EEG, EOG and EMG took about 40 minutes. All instructions were pre-recorded and given to participants through head phones. In addition the experimenter asked participants if they understood the instructions and clarified their doubts.

Calculation of BCI classifiers

Before starting the experiment participants needed to do a training session for each of the two BCI protocols in order to calculate individual classifiers (see experimental time line in Figure 3.14 A). Both classifiers were calculated using gBSanalyze (Version 5.16.00, g.tec).

Executed movement

Executed movement was only recorded in a subset of participants (N = 22). Participants were sitting comfortably in a chair with their hands resting on a table in front of them. Through head phones they heard a beep every 8 seconds with a jitter of $\pm$ 1 second. They were instructed to move their right hand and press a button in front of them whenever they heard the beep. The movement resembled the one they were seeing later in the virtual environment.

Experimental condition

Embodiment phase Each experimental condition started with an embodiment phase. When entering the virtual environment participants saw a virtual body from first person perspective that was sitting at a table with the arms lying on top of the table at the same position as their own arms. They further saw a computer screen on the table. They were instructed to look around and describe what they were seeing. They were further instructed to look at the virtual body they saw from first person perspective sitting in the same position as them. Next they were instructed to move their right hand and fingers for 1 minute. These movements were tracked and mapped onto the movements of the virtual body, so that they saw the right virtual arm moving in the same way. This procedure was carried out to boost the sense of body ownership over the virtual body. Directly after this two questions were presented in randomized order. One question asked for their feeling of control over the virtual arm and the other for their feeling of body ownership; the questions are displayed in Table 3.3. We decided to let them just move the hand and not the arm because arm movements introduced a spatial drift over time which reduced the feeling of body ownership and control.

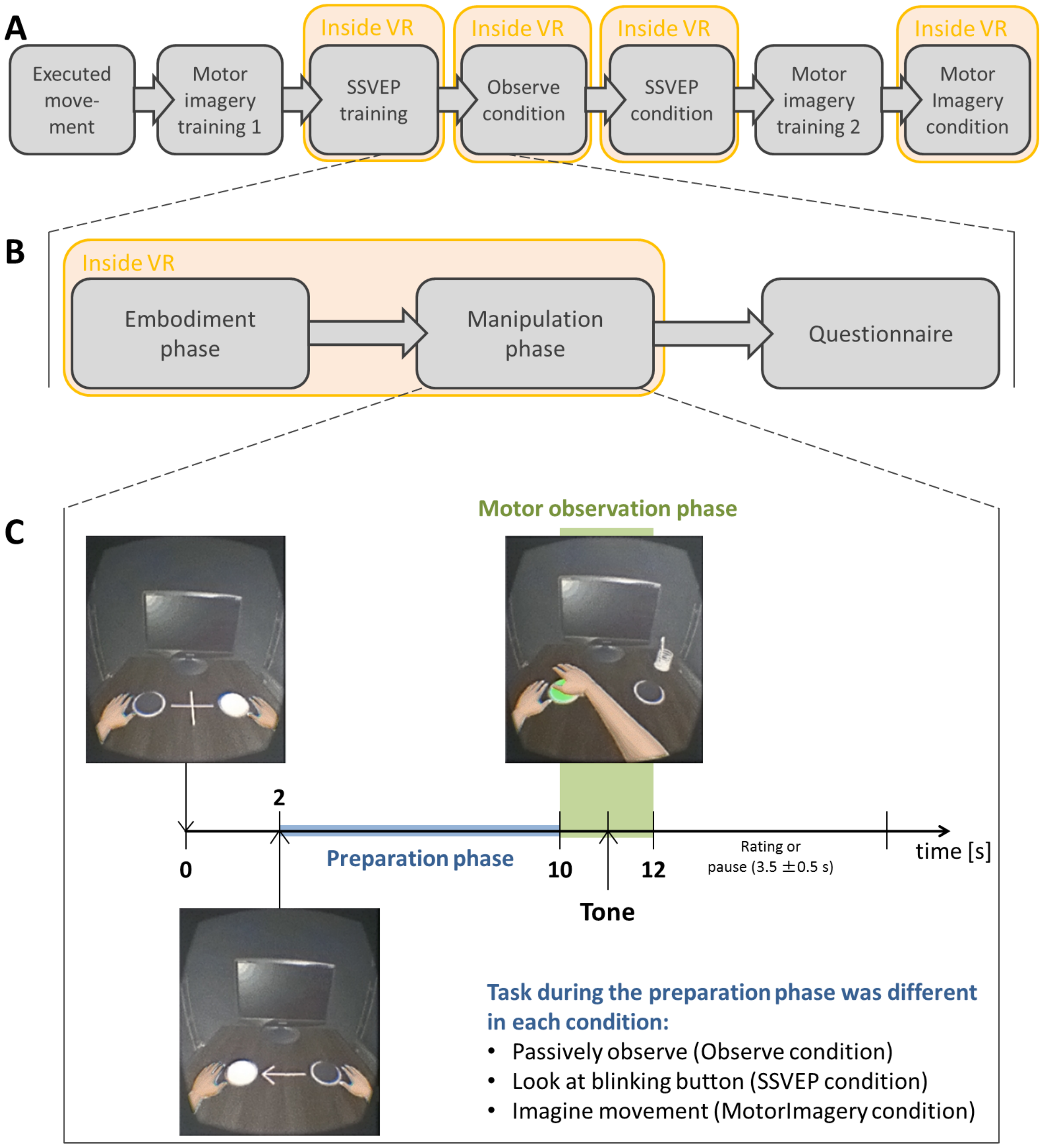

FIGURE 3.14: Time line. (A) Time line of the whole experiment. Motor imagery trainings were divided into two parts—one in the beginning and one just before the MotorImagery condition started. The order of conditions was randomized among participants. (B) Time line of one experimental condition. Each condition started with the embodiment phase followed by the manipulation phase which were both inside VR and ended with the participant filling out a questionnaire. (C) Time line of one trial. Each experimental trial started with a fixation cross followed by an arrow indicating the button the arm should move to. This was followed by a preparation phase in which participants either passively observed what was happening, looked at the indicated blinking button or imagined the arm movement to this button. This was followed by the movement of the arm (or an error tone if the BCI-classifier did not detect the movement). Every 10 trials participants had to rate their experience of control over the virtual movement.

Manipulation phase Directly after the embodiment phase participants were instructed to not move their arms throughout the rest of the experimental condition. The virtual environment was the same as during the embodiment phase, except now they saw two buttons on the table in front of them (see Figure 3.14 C). The two buttons were blinking each with one of the two SSVEP frequencies. There were three different conditions: the SSVEP condition, the motor imagery condition and the observe condition. Each of the three conditions had 40 trials. Each trial started with a fixation cross displayed between the two buttons. Two seconds later an arrow indicated the button in for this trial. In the following 6 seconds participants were either imagining the arm movement (MotorImagery condition), looked at the button (SSVEP condition) or simply observed what was happening (Observe condition). During MotorImagery and the SSVEP conditions the previously calculated BCI-classifier was classifying their signal online and if the classification was correct the virtual arm moved towards that button to press it and moved back to its initial position. If the classification was not correct they heard an error sound and the trial was repeated one more time. During the Observe condition participants were instructed to simply observe what was happening. Figure 3.14 C displays the time line of one trial.

3.4.9 Questionnaire

Table 3.3 displays all questionnaire items. Some items were asked inside VR (MyBody, Control, Responsibility) and others were asked outside VR (MyBody, MySound, ITouchedObject, MyMovement). All items were rated on a horizontal visual analogue scale (VAS) from 0 to 10 with 0 corresponding to "strongly disagree" and 10 corresponding to "strongly agree ", except for item 6 (see below). For further analysis, ratings continuous ratings were down-scaled into ordinal ratings ranging from 1 to 10.

Questionnaire items during VR experience

Questionnaire items were displayed in the virtual environment on a virtual screen. Participants gave their responses through a button (Power Mate, Griffin Technologies, Nashville, USA) under their left hand. When they turned the button right a little bar indicating their response moved to the right on the VAS (rating increased) and when they turned it left the little bar went right (rating decreased). They confirmed their rating by pressing the button. While the statement was displayed on the virtual screen a virtual board prevented them from seeing the virtual forearms.

TABLE 3.3: Questionnaire items answered by participants before, during and after each experimental condition. Responses were given on a visual analogue scale ranging from 0 to 10, where 10 is 'strongly agree' and 0 is 'strongly disagree'. Note that 7 has an inverse scale and was merged with item 6.

Item Tag	Questionnaire Item
MyBody	(1) It felt as if the right virtual arm was my arm.
Control	(2) It felt as if it was me who controlled the movement of the virtual arm.
Responsibility	(3) It felt as if it was me who broke the vase.
MySound	(4) It felt as if it was me who produced the sound (when the hand touched the button).
ITouchedObject	(5) It felt that out of inobservance I touched the objects with my hand when they fell off the table.
MyMovement	(6) It felt as if the movement of the virtual arm was my movement /the movement of another person. (7) It felt as if the virtual arm moved by itself.

MyBody. At the end of the embodiment phase participants rated how strong they felt the virtual arm was their arm (Table 3.3, item 1). They also responded to the Control statement (see next paragraph). The two items were displayed in random order.

Control. At the end of the embodiment phase and every 10 trials during each experimental condition participants rated how strongly they felt they were controlling the virtual arm (Table 3.3, item 2).

Responsibility. During each experimental condition the virtual arm accidentally threw an object off the table which resulted in a breaking sound (Figure 3.15 A and B). This happened 4 times throughout each experimental condition, once during each block of 10 trials at a random trial (not directly before or after they were answering the Control item because we didn't want participants to answer a question on 2 subsequent trials). The objects were a pencil stand, a vase, a coffee cup, and a glass and appeared in random order. Directly after breaking the object participants were asked how strongly they felt responsible for breaking it (Table 3.3, item 3). Object names were changed respectively. One of the four trials was a catch trial in which the virtual body did not touch the object and therefore did not throw it off the table, instead the object fell off the table by itself (Figure 3.15 C). This trial was included to confirm that our measure worked.

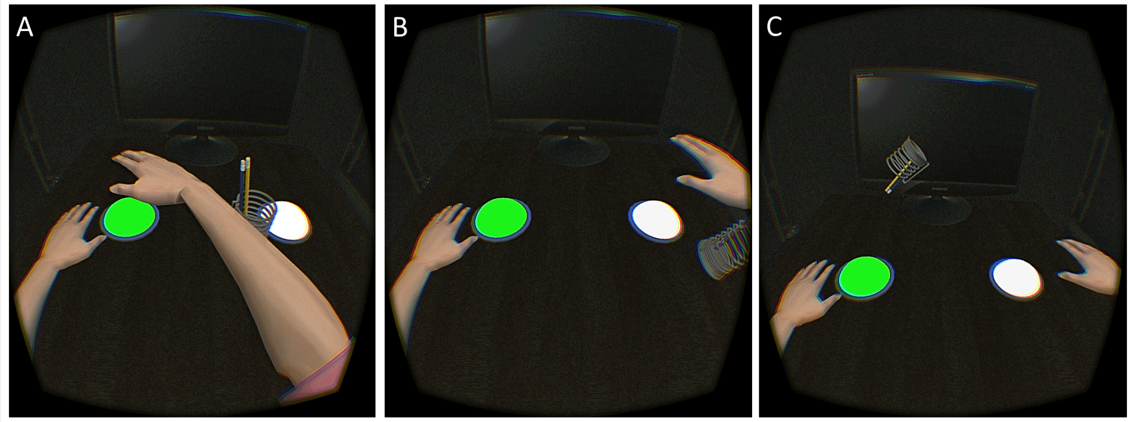

FIGURE 3.15: In four random trials of one experimental condition an object fell off the table. In three of those trials the virtual body threw the object off the table (A and B) and in one trial the object fell of the table by itself (C). The object was for all four trials different and changed between a pencil stand, a vase, a coffee cup and a glass. Participants were asked to rate the degree of perceived responsibility directly after the trial.

Questionnaire items after VR experience

A questionnaire with five items was given to participants directly after each experimental condition. Participants answered the questionnaire on a laptop using the right and left arrow button to give higher or lower ratings on the VAS and the return button to confirm their rating. Questionnaire items were displayed in random order. The questionnaire included questions on how strong the virtual arm was their arm (MyBody, Table 3.3 item 1), how strong they felt it was them producing the sound when the virtual arm touched the button (MySound, Table 3.3 item 4), whether they accidentally touched the objects when they fell of the table (ITouchedObject, Table 3.3 item 5), whether they felt the movement was their own movement or another person's movement (Table 3.3 item 6), and whether the virtual arm was moving by itself (Table 3.3 item 7, note that this item was inversely scaled). MyMovement is the median of item 6 and the inverse of item 7.

Debriefing

At the end of the experiment we asked participants to rate the three different experimental conditions according to their experience of controlling the virtual movement from strongest to weakest.

3.4.10 Processing of EEG data

We first identified artifacts in the EEG data, analyzed the amplitude modulation of spontaneous alpha oscillations, and then extracted ERP. In the following I will describe each of these steps.

Artifact identification

Very noisy EEG channels were visually identified and removed from further analysis (this affected 1–2 channels in 5 participants). During the data collection phase electrode F5 broke and we continued data collection without this electrode (this affected 12 participants). For artifact detection the signal was filtered between 0.5 Hz and 40 Hz.

ERP For ERP analysis eye blink artifacts were identified and projected from EEG data with Independent Component Analysis (ICA) performed on concatenated epoched data (FastICA; (Hyvärinen & Oja, 2000)). The epochs were generated around the onset of the tone and consisted of 1000 ms pre-stimulus and 1000 ms of post-stimulus interval. The epochs were visually inspected for the presence of muscular and mechanical artifacts, indicated by the variance of the maximal activity and by the Mahalanobis distance (Nikulin et al., 2008). Within different participants we rejected between 0% and 8% of epochs.

Executed movement Artifacts in the executed movement data were visually identified in epochs ranging from –1000 to 3000 ms around the tone indicating the participant to start moving. Epochs containing them were removed at a later step in the analysis (0%–25% of epochs).

Amplitude modulation of spontaneous alpha oscillations

We were interested in alpha oscillations because they have the largest amplitude among spontaneous oscillations and therefore allow a reliable estimation of ERD (Nierula, Hohlefeld, Curio, & Nikulin, 2013; Nikouline et al., 2000; Pfurtscheller & Lopes da Silva, 1999), which is important for obtaining clear spatial patterns on which the performed source localization is based.

Identifying individual sensorimotor alpha range The individual sensorimotor alpha peak frequencies were identified in the pre-stimulus spectrum of Laplace transformed channels (Graimann & Pfurtscheller, 2006; Hjorth, 1975). The signal of all conditions and the executed movement was then filtered in a range of 4 Hz around the individual peak frequency.

Identifying individual ERD peak-latencies in executed movement data The peak latency of ERD was identified in Laplace transformed channel C3 of the executed movement data using the following procedure. The signal, which was filtered in the individual alpha range, was Laplace transformed and the amplitude envelope was obtained with the Hilbert transform (Clochon, Fontbonne, Lebrun, & Etevenon, 1996; Graimann & Pfurtscheller, 2006; Rosenblum & Kurths, 1998). The signal was next cut into epochs from —1000 to 3000 ms around the tone and previously identified epochs containing artifacts were removed from further analysis. ERD% was calculated using the following equation, where AMP (amplitude) refers to the activity at each time point t of the averaged epochs and PRE is the mean amplitude in the pre-stimulus interval (from –500 to 0 ms): ERD%(t) = (AMP(t) – PRE) / PRE · 100. Time points with lowest ERD% were identified in the first 1500 ms after movement onset in the Laplace-transformed channel C3 (*N* = 18, latency: *Mean* = 808 ms, *SD* = 228 ms).

Extracting CSP in executed movement data The filtered, epoched and cleaned executed movement signal was used for CSP analysis. No ICA was applied because prior application of another spatial filtering could lead to possible deterioration in the performance of CSP (Blankertz, Tomioka, Lemm, Kawanabe, & Müller, 2008; Nierula et al., 2013). For CSP, pre-stimulus epochs were merged from executed movement and all three experimental conditions and the mean was subtracted from single epochs in the post-stimulus interval. The CSP algorithm is commonly used to separate two classes of data by determining the spatial filters W that maximize the variance of one class while simultaneously minimizing the variance of another class. In case of our data one class contained the data of the pre-stimulus interval (from —500 to 0) and the other class contained data of the post-stimulus interval (±250 ms around the ERD peak previously identified in Laplace transformed C3 channel). In the case of bandpass-filtered EEG-signals variance is equivalent to power in a given frequency range (Blankertz, Dornhege, Krauledat, Müller, & Curio, 2005; Dornhege, Blankertz, & Curio, 2003; Nierula et al., 2013; Nikulin et al., 2008) which means that CSP can be also used to optimize ERD (Lemm, Müller, & Curio, 2009). CSP has been successfully used to classify single EEG epochs (Blankertz et al., 2005; Dornhege et al., 2003; Koles et al., 1995; Nikulin et al., 2008). The inverse of the filter matrix W is the Common Spatial Pattern. W-1 contains components/patterns that are sorted by the size of their eigenvalue from high to low. Within the first four patterns we selected the pattern with the strongest Eigenvalue that showed the strongest activity in sensorimotor areas. Patterns were validated by splitting the epochs into two sets (epochs with even numbers were in one set and those with odd numbers in the other). Only patterns that appeared in both sets were considered for further analysis.

Source reconstruction of CSP patterns Source reconstruction of CSP patterns was performed using Brainstorm (Tadel, Baillet, Mosher, Pantazis, & Leahy, 2011). The forward model was generated with OpenMEEG using the symmetric Boundary Element Method (Gramfort, Papadopoulo, Olivi, & Clerc, 2010; Kybic et al., 2005) on the cortical surface of a template Montreal Neurological Institute (MNI) brain (non-linear MNI-ICBM152 atlas, Fonov et al., 2011) with a resolution of 1 mm. Cortical sources were then estimated using the Tikhonov-regularized minimum-norm (Baillet, Mosher, & Leahy, 2001) with a Tikhonov parameter of λ = 10% of maximum singular value of the lead field, and mapped to a distributed source model consisting of 15000 current dipoles. Sources of CSP patterns were visually inspected for their origin in sensorimotor areas.

ERD The extracted spatial filter W from the CSP pattern used for source analysis (see previous paragraph) was used to project the data X from the three experimental conditions (Observe, SSVEP, and Motor Imagery) using the following formula: Z = WX. To obtain ERD% we extracted the amplitude envelope of the analytic signal with the Hilbert transform and then calculated ERD% using the formula above (see Section 3.4.10, "Identifying individual ERD peak-latencies"). PRE referred to the averaged activity in the pre-stimulus interval from –500 to 0 ms. The minimum value of ERD% during the preparation phase and during the motor observation phase was later used for statistical comparisons.

ERP components

Artifact-free epochs were averaged and baseline-corrected (baseline interval was before stimulus onset from –50 to 0 ms). The signals from electrodes F3, Fz, F4, FC3, FCz, FC4, C3, Cz, and C4 were averaged and N100 (minimum between 70–140 ms), P200 (maximum between 135–205 ms), and P300 peaks (maximum between 250–350 ms) were identified. To obtain the N100–P200 peak-to-peak amplitude we subtracted the N100 from the P200 amplitude. P300 amplitudes and N100–P200 peak-to-peak amplitudes were used for further statistical analysis.

EMG and EOG

The EMG recordings were high-pass filtered at 10 Hz and EOG recordings were low-pass filtered at 50 Hz. Both, filtered EMG and EOG recordings were then segmented into epochs from –2000 to 8000 ms with respect to the arrow indicating one of the two buttons. The root-mean square values were calculated in two intervals to obtain measures for motor activation (MA) and eye movement (EM)—during the preparation phase (from 0–6000 ms; resulting in the variables MAp and EMp) and during the motor observation phase (from 6000–8000 ms; resulting in the variables MAo and EMo).

EMG and EOG recordings served as covariates in order to control for feelings of agency based on possible attributions of eye or arm movements to the virtual movement. Therefore, before fitting a statistical model we checked if EMG or EOG could explain some of the variance.

3.4.11 Statistics

All statistical tests were performed using Stata 13 (StataCorp LP, College Station, TX). Residuals were tested for normal distribution when necessary using the Shapiro-Wilk test. Violations of the sphericity assumption were tested with Mauchly's sphericity test and Greenhouse-Gaisser corrections were applied where necessary. BCI-accuracy between SSVEP and MotorImagery conditions were analyzed with Student's paired t-test. Relationships between variables were assessed with mixed effects regression (the 'mixed' function in Stata). Questionnaire reports were analyzed with a multilevel mixed-effects ordered logistic regression (the 'meologit' function in Stata) with fixed-effects "condition" and random effects "individual subject". For agency-related questionnaire items, Likelihood ratio tests were used to identify if the variables MAp, MAo, EMp, or EMo should be added as covariates to the model. For post hoc analyses we used the Scheffé post hoc criterion for significance. ERD% and ERP components were analyzed using repeated measure ANOVA with factor condition and post hoc comparisons were performed using the Scheffé criterion.

Chapter 4

Results

4.1 Experiment 1

The motivation of this experiment was to investigate whether the experience of body ownership is fluctuating and if so, whether these fluctuations are linked to spontaneous ISF. In order to test this we asked participants to perform a visuotactile simultaneity task in two experimental conditions and on two different days. In one condition participants saw a virtual body colocated with their real body from fist person perspective, and in another condition there was no body and instead a wooden stick at the position of their hand. The final sample size consisted of 13 participants, both conditions were presented in counterbalanced order on the two recording days. In the following we will show the results obtained from the first experiment.

4.1.1 Questionnaire reports

Questionnaire reports are displayed separately for the two recording days in Figure 4.1 and Table 4.1. The following paragraphs show the findings for the different questionnaire items.

MyBody. An ordinal regression revealed an effect for Condition (z = –4.76, P < .001, 95% confidence interval: –5.728– –2.388) but not for RecordingDay (z = 0.26, not significant (n.s.)). Participants gave higher ratings in the Body (*Median* = 2, *IQR* = 1–2) compared to the Object (*Median* = –2, *IQR* = –3– –1) condition.

EmbFluct. An ordinal regression revealed an effect for Condition (z = –2.51, P = .012, 95% CI: –2.344– –.2868) but not for RecordingDay (z = –0.13, n.s.). Participants gave higher ratings in the Body (*Median* = 1, *IQR* = 0–2) compared to the Object (*Median* = –1, *IQR* = –2–1) condition.

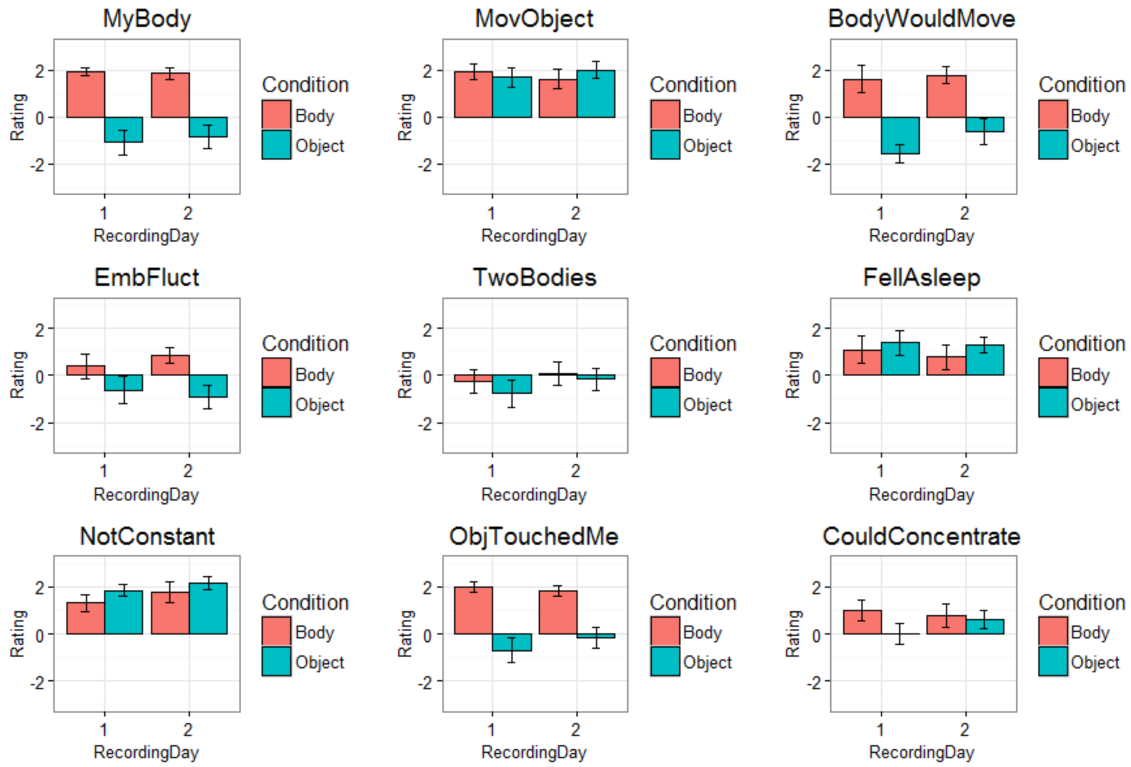

FIGURE 4.1: Box plots of the different questionnaire items in the two different conditions separated by the two recording days.

NotConstant. An ordinal regression revealed an effect for RecordingDay (z = 2.23, P = .026, 95% CI: 0.158–2.461) but not for Condition (z = 1.35, n.s.). Participants gave higher ratings on day 2 (*Median* = 2, *IQR* = 2–3) compared to day 1 (*Median* = 2, *IQR* = 1–2).

MovObject. An ordinal regression showed no effect for neither Condition (z = 1.04, n.s.) nor RecordingDay (z = –0.21, n.s.).

TwoBodies. An ordinal regression showed no effect for neither Condition (z = –0.91, n.s.) nor RecordingDay (z = 0.87, n.s.).

ObjTouchedMe. An ordinal regression revealed an effect for Condition (z = –4.47, P < .001, 95% CI: –4.681– –1.826) but not for RecordingDay (z = 0.17, n.s.). Participants gave higher ratings in the Body (*Median* = 2, *IQR* = 1–2) compared to the Object (*Median* = –1, *IQR* = –2–1) condition.

BodyWouldMove. An ordinal regression revealed an effect for Condition (z = –4.63, P < .001, 95% CI: –5.192– –2.103) but not for RecordingDay (z = 0.59, n.s.). Participants gave higher ratings in the Body (*Median* = 2, *IQR* = 2–3) compared to the Object (*Median* = –1.5, *IQR* = –3–0) condition.

FellAsleep. An ordinal regression showed no effect for neither Condition (z = 0.87, n.s.) nor RecordingDay (z = -1.08, n.s.).

CouldConcentrate. An ordinal regression revealed a trend for Condition (z =

TABLE 4.1: Median values and interquartile ranges (IQR) of responses to questionnaire items.

Item	Condition	Day 1		Day 2	
		Median	*IQR*	*Median*	*IQR*
MyBody	Body	2	2–2	2	1–2
	Object	–2	–3–1	–2	–2–1
EmbFluct	Body	1	–2–2	1	0–2
	Object	–2	–2–2	–1	–2–0
NotConstant	Body	1	1–2	2	2–3
	Object	2	1–2	2	2–3
MovObject	Body	2	2–3	2	2–2
	Object	2	2–2	2	2–3
TwoBodies	Body	0	–2–1	1	–1–1
	Object	–1	–3–1	0	–2–1
ObjTouchedMe	Body	2	2–2	2	1–2
	Object	–1	–2–1	0	–2–1
BodyWouldMove	Body	2	2–3	2	2–2
	Object	–2	–3–0	–1	–2–1
FellAsleep	Body	2	1–2	1	–1–2
	Object	2	1–3	1	1–2
CouldConcentrate	Body	2	1–2	2	–1–2
	Object	-1	–1–1	1	–1–2

–1.89, P = .059, 95% CI: –2.210–0.0411) but not for RecordingDay (z = 0.84, n.s.). Participants gave higher ratings in the Body (*Median* = 2, *IQR* = –1–2) compared to the Object (*Median* = 1, *IQR* = –1–2) condition.

4.1.2 Debriefing

Figure 4.2 displays histograms of participant's (N = 13) answers to the three different debriefing questions. Most participants felt the task to be easier during the Body condition than during the Object condition. Furthermore, participants felt the Body condition to be more comfortable than the Object condition. Interestingly, when asking in which condition they found the task to be more tiring a majority of participants found the object condition on the first recording day more tiring while on the second recording day the numbers of participants were almost the same for the two conditions.

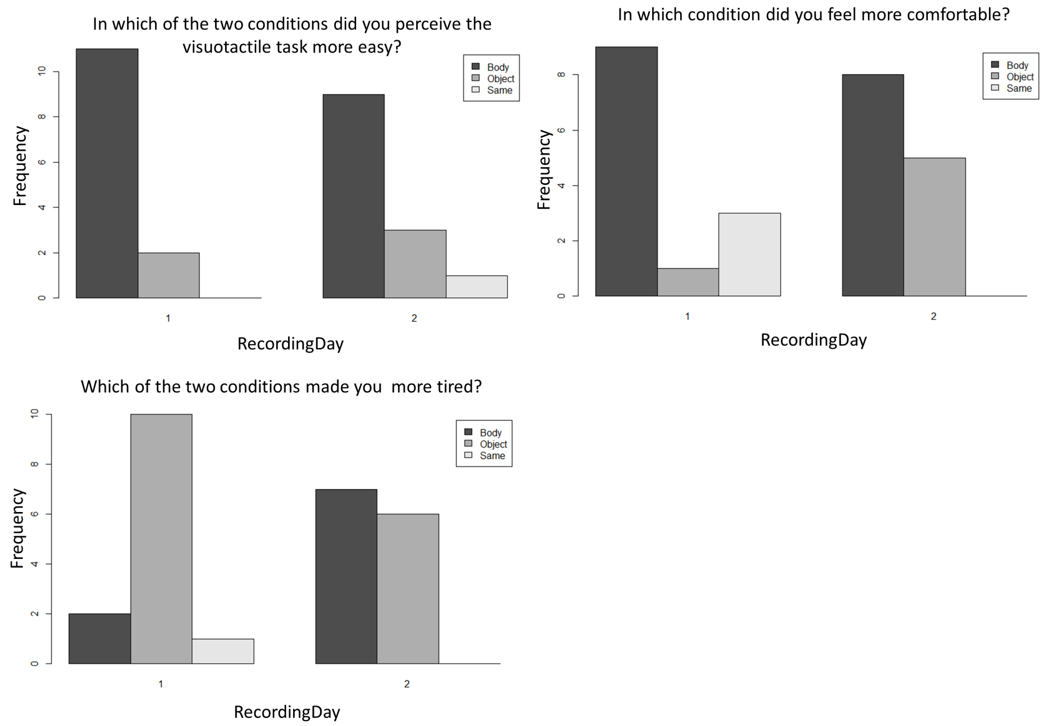

FIGURE 4.2: Histograms of the three debriefing questions separated by recording day.

4.1.3 Simultaneity threshold

A two factorial repeated measures ANOVA with factors Condition and RecordingDay revealed that simultaneity thresholds were on average higher during Body (*Mean* = 567.3 ms, *SEM* = 32.9) than during Object conditions (*Mean* = 527.9 ms, *SEM* = 27.4; $F(1,12)$ = 7.47, P = .019, η_p^2 = 0.384; see Figure 4.3). Further, simultaneity thresholds were lower on the first recording day (*Mean* = 512.5 ms, *SEM* = 31.1) compared to the second one (*Mean* = 582.7 ms, *SEM* = 28.2; $F(1,12)$ = 5.55, P = .036, η_p^2 = 0.316). There was no significant interaction ($F(1,12)$ = 0.01, n.s.).

4.1.4 Yes/No responses

One big challenge in this experiment was the setting of the simultaneity threshold. Since the threshold setting procedure was performed in VR, we needed to set the threshold within 5–7 minutes in order to not expose participants for too long to the virtual environment. It was important that the threshold would be set

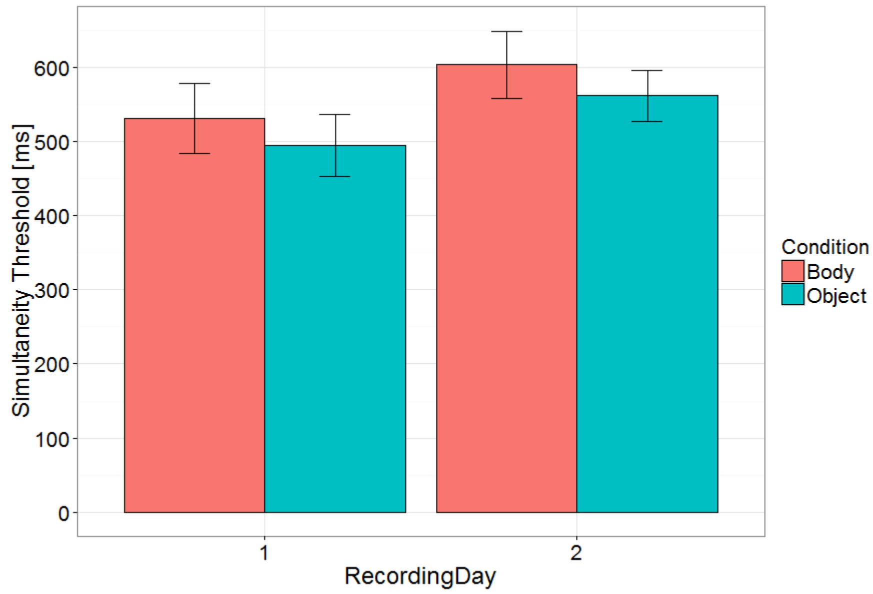

FIGURE 4.3: The Effect of Condition and RecordingDay on simultaneity threshold. The graph displays the mean simultaneity threshold in the two different conditions separated by the two recording days. Error bars indicate the standard error of the mean.

in the beginning of each experimental condition and that participants started directly with the experimental condition without removing the head mounted display. In some cases the threshold ended up being too high or too low (Table 4.2). We decided to include only participants with a Yes response rate between 35%–65% to keep the threshold close to 50%. This was the case for 9 participants, most of them on only 1 recording day. We therefore included only one recording day into the analysis.

When looking at a single subject level, run length probability curves differed in all participants that are within the selected Yes response rate range from the computed surrogate distribution. Figure 4.4 displays the data from one representative participant.

A repeated measure ANOVA with the factors Condition (two levels: Body or Object), RunLength (20 levels: from 3.5 to 136.5 s) and Data (two levels: Real or Surrogate) and their interactions on RunLengthProbability revealed an effect of RunLength ($F(19,152)$ = 2069, $P < .001$, $\eta_p^2 = 0.996$), but not of Data ($F(1,5)$ = 0.132, n.s.) or of Condition ($F(1,5)$ = 0.164, n.s.). There was a two-way interaction of RunLength × Data ($F(19,152)$ = 372.5, $P < .001$, $\eta_p^2 = 0.979$) but not of Condition × RunLength ($F(19,152)$ = 0.064, n.s.) or of Condition × Data ($F(1,8)$ = 0.132, n.s.). The three-way interaction of Condition × RunLength × Data was also not significant ($F(19,152)$ = 0.067, $P = .077$).

Next, we looked again at the questionnaire reports of the item MyBody, which

TABLE 4.2: Percentage of Yes responses in the visuomotor simultaneity task. Responses are in %.

	Day 1		**Day 2**	
Participant Number	*Body*	*Object*	*Body*	*Object*
2	65	63	57	50
3	78	74	73	74
4	60	52	53	67
5	42	52	50	76
6	11	42	49	64
7	65	45	54	45
8	72	53	77	74
9	70	79	70	41
10	58	85	79	29
11	52	46	18	67
12	58	67	63	61
13	58	74	49	45
14	49	64	64	63

represented whether our manipulation worked or not. Although questionnaire reports for item MyBody were significant between conditions on a group level, some participants reported no difference between experimental conditions (e.g. participants 7 and 10, see Appendix A.6) or very small differences (e.g. participant 14). To understand if there is anything in our data, we selected participants with MyBody ratings above 1 in the Body condition and below -1 in the Object condition for further analysis. Of the nine participants that had a Yes-rate between 35% and 65%, five participants met this selection criteria, all of them only on one recording day. We therefore included recording day 1 from participants 4, 5, and 11 and recording day 2 from participant 2 and 13. Box plots displaying the questionnaire responses from the selected participants can be found in Appendix A.7. A repeated measure ANOVA with the factors Condition (two levels: Body or Object), RunLength (20 levels: from 3.5 to 136.5 s) and Data (two levels: Real or Surrogate) and their interactions on RunLengthProbability revealed an effect of RunLength ($F(19,95)$ = 539.3, $P < .001$, η_p^2 = 0.991) and of Data ($F(1,5)$ = 8.315, P = 0.034, η_p^2 = 0.624), but not of Condition ($F(1,5)$ = 2.394, n.s.). There was a two-way interaction of RunLength $\times$ Data ($F(19,95)$ = 114, $P < .001$, η_p^2 = 0.958) but not of Condition x RunLength ($F(19,95)$ = 0.738, n.s.) or of Condition $\times$ Data ($F(11,5)$ =

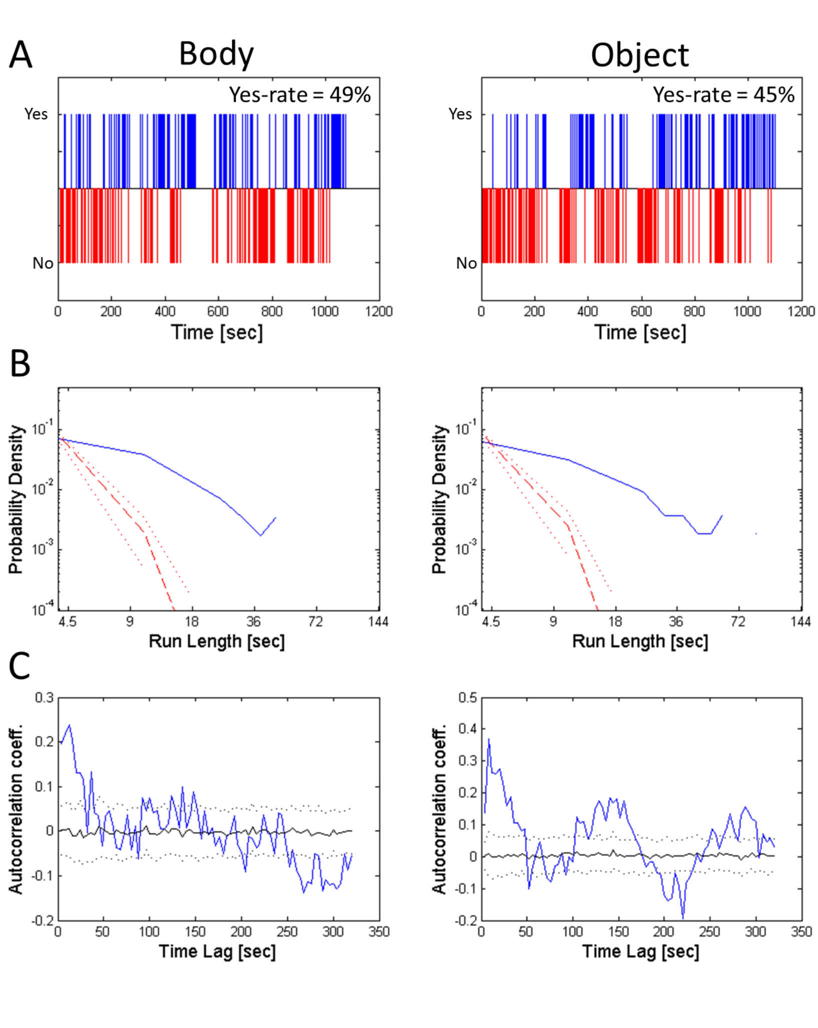

FIGURE 4.4: Behavioral data from one representative participant (S11) during one recording day. The left column displays the body condition and the right column the Object condition. (A) displays the single responses given by the participant over the whole recording (blue indicates Yes- and red indicates No-responses). (B) probability density function, blue indicates the participant's data and red the surrogate data. (C) autocorrelation, blue indicates the participant's data and black the surrogate data. Dotted lines indicate the 95% CI.

1.947, n.s.). The three-way interaction of Condition × RunLength × Data showed a trend but was not significant (*F(19,95)* = 1.581, P = .077, η_p^2 = 0.240). Figure 4.5 displays bar plots of RunLengthProbability for real (A) and surrogate data (B).

There was further no effect of condition in the auto-correlations. A repeated measure ANOVA with the factors Condition (two levels: Body or Object), Time-Lag (80 levels: 4 to 320 s), and Data (two levels: Real or Surrogate) and their interaction on the autocorrelation coefficient revealed only a main effect of Time-Lag (*F(79,395)* = 5.217, P < .001, η_p^2 = 0.511) and a trend of Data (*F(1,5)* = 5.262,

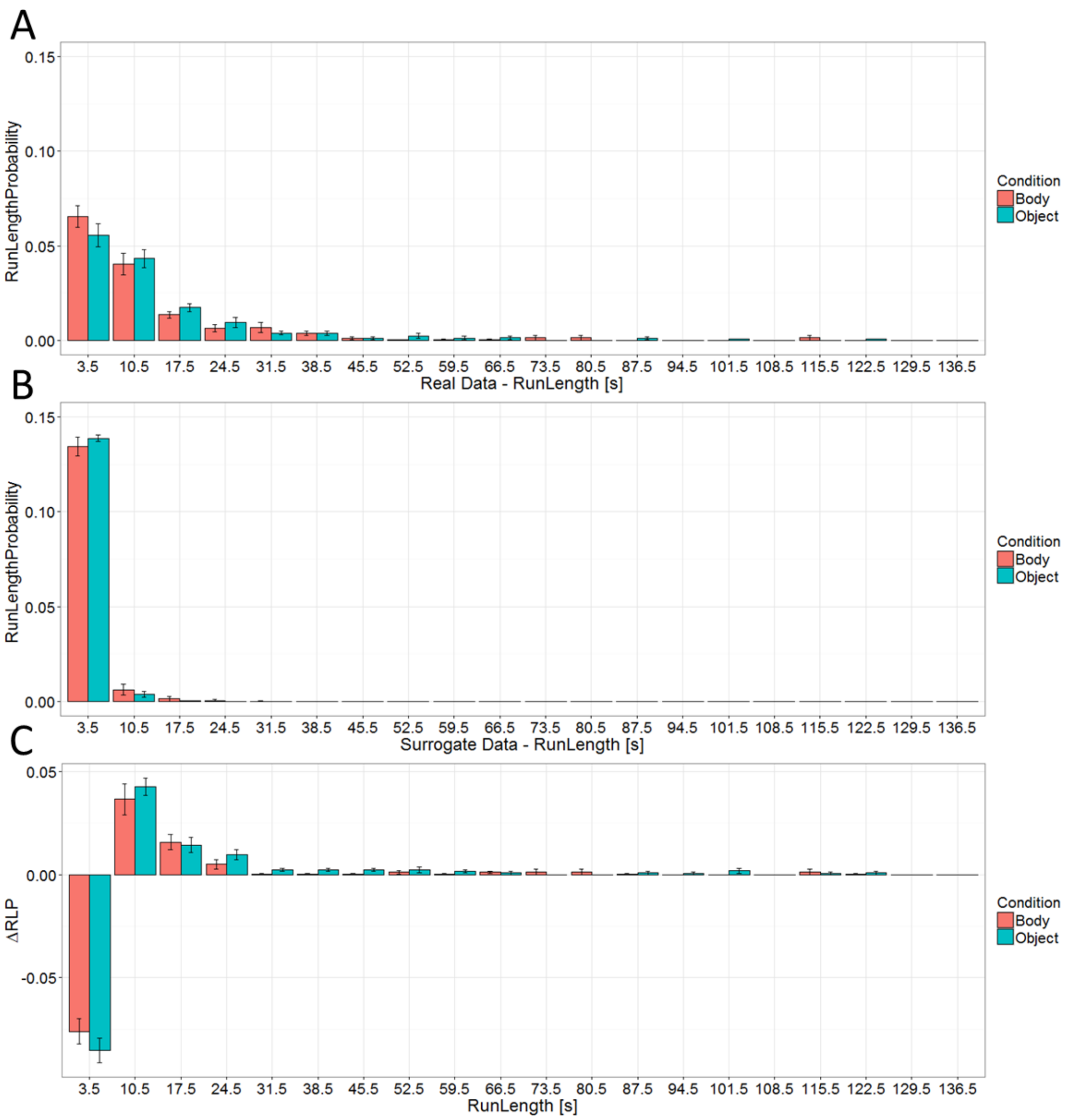

FIGURE 4.5: The Effect of Condition and RunLength on RunLength-Probability in (A) real data and (B) surrogate data. (C) Displays the difference in runLengthProbability ΔRLP of real and surrogate data. Error bars indicate standard error of mean.

P = 0.070, η_p^2 = 0.512), but not of Condition (*F(1,5)* = 0.45, n.s.). The two-way interaction TimeLag × Data was significant (*F(79,395)* = 3.979, P < .001, η_p^2 = 0.443) but not the two-way interactions Condition × TimeLag (*F(79,395)* = 0.851, n.s.) or Condition × Data (*F(1,5)* = 0.04, n.s.). There was also no significant three-way interaction Condition × TimeLag × Data (*F(79,395)* = 1.061, n.s.). Figure 4.6 displays bar plots of the autocorrelation coefficient for all 80 TimeLag bins for real and surrogate data.

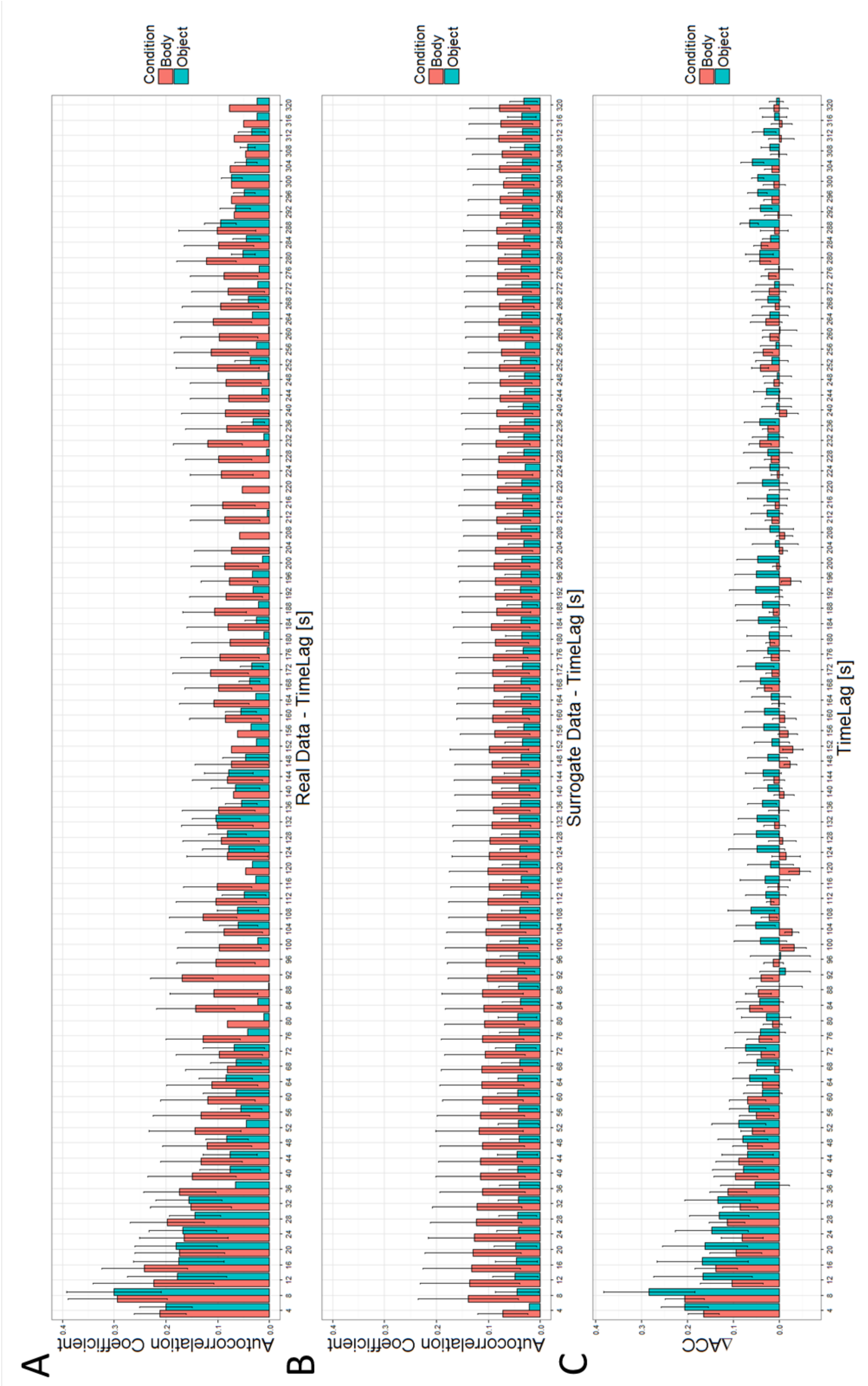

FIGURE 4.6: The Effect of Condition and Time Lag on the autocorrelation coefficient in (A) real data and (B) surrogate data. (C) Displays the difference in autocorrelation coefficient ΔACC between real and surrogate data. Error bars indicate standard error of mean.

4.1.5 Correlation of Infra-Slow Fluctuations with Behavior

We further analyzed ISO following the analysis of Monto et al. (2008). Figure 4.7 displays the change in Yes-response probability as a function of the ISF phase, amplitude, and real part for the Body and the Object condition at electrode C3 (see also Appendix A Figures A.8–A.14 for the same Figure at electrodes FC3, FC1, C4, CP6, P5, POz, and PO4). Although on an individual level some participants showed Yes-response probabilities below .05 or above .95 this effect none of the Wilcoxon signed rank tests showed significant differences on a group level.

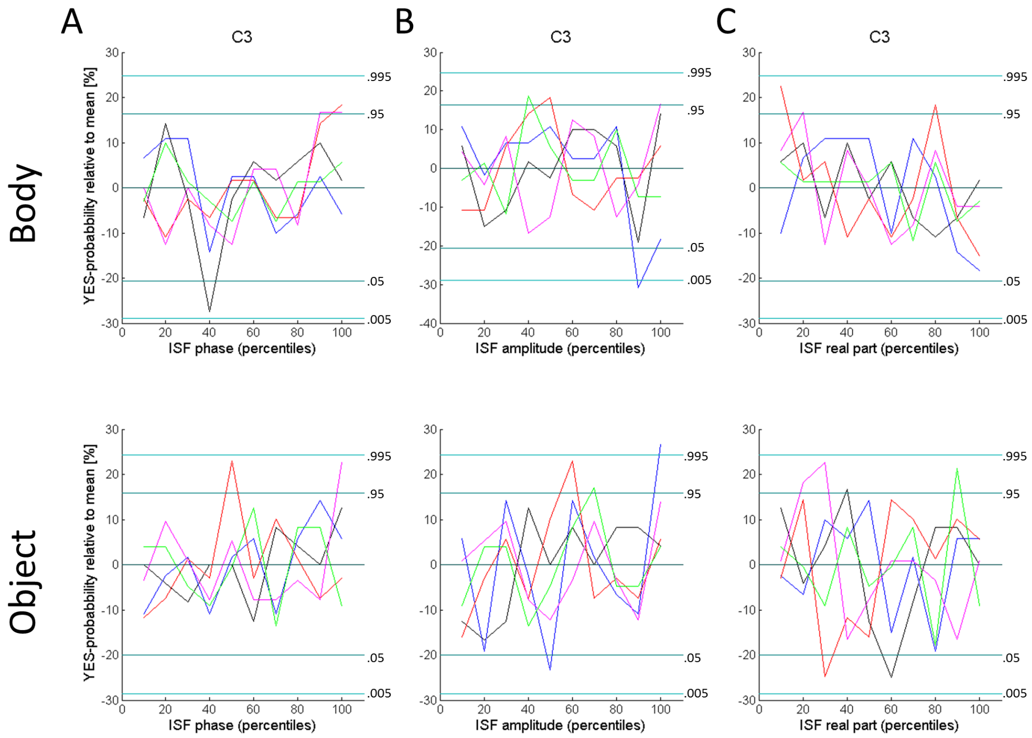

FIGURE 4.7: Change in Yes-response probability as a function of phase (A), amplitude (B), and real part (C) of the ISF recorded at electrode C3. Y-axis indicates the change in Yes-probability relative to the mean. The top row displays the Body and the bottom row the Object condition. Each line color indicates the changes in Yes-response probability of one participant. The statistical significance of hit probability was estimated for each bin using the cumulative binominal distribution. 0.005, 0.05, 0.95, and 0.995 values are indicated by horizontal lines. The axis range from -π to π (A), from 0 to maximum amplitude (B), and from minimum to maximum of the ISF EEG (C).

4.2 Experiment 2

The motivation of this experiment was to investigate whether looking at an embodied surrogate virtual hand is analgesic and to better understand why there are controversial findings in the literature. We identified that one difference between previously performed studies, which led to opposing results, is the distance between real and surrogate arm. To test whether distance could explain previous findings, we performed an experiment, in which we manipulated in a two factorial design the factors distance between real and virtual arm (which could be colocated or at a 30-cm distance) and synchrony of VTS (which could be synchronous or asynchronous), and measured participants HPT and their level of body ownership. We had four experimental conditions: Colocation + SynchronousVTS, Colocation + AsynchronousVTS, 30cmDistance + SynchronousVTS, 30cmDistance + AsynchronousVTS. Five heat pain stimuli were applied in each condition. Our final sample size was 19 male participants. In the following we will show the results obtained from our second experiment.

4.2.1 HPT Analysis

Figure 4.8 shows the means and standard errors of ΔHPT according to distance and VTS. There is an apparent large effect of distance, with the HPT lower for the 30-cm distance. The mixed effects analysis of variance shows that this difference is significant, with main effect of distance ($z = -2.24$, $P = .025$, 95% CI: –0.7977671––0.0527321; see Appendix B.2 for the analysis of normal distribution of residuals). The analgesic effect of seeing the virtual arm was therefore lower when the virtual hand was located at 30 cm from the real hand than when colocated. Table 2 shows means and standard errors of the mean of the raw HPT. A likelihood ratio test comparing the full model including the interaction term (distance + VTS + [distance × VTS]) with the model that only includes distance shows no difference at all between these (e.g., $P > .9$, *Akaike Information Criterion* = 232 for the full model and 236 for the reduced model). Hence there is clearly no effect of VTS. One extreme outlier was removed from all analyses described previously on the basis of visual inspection of HPT during baseline plotted against HPT during the experimental conditions.

4.2.2 Analysis of questionnaire responses

Questionnaire responses are displayed in Figure 4.9 and Table 4.3.

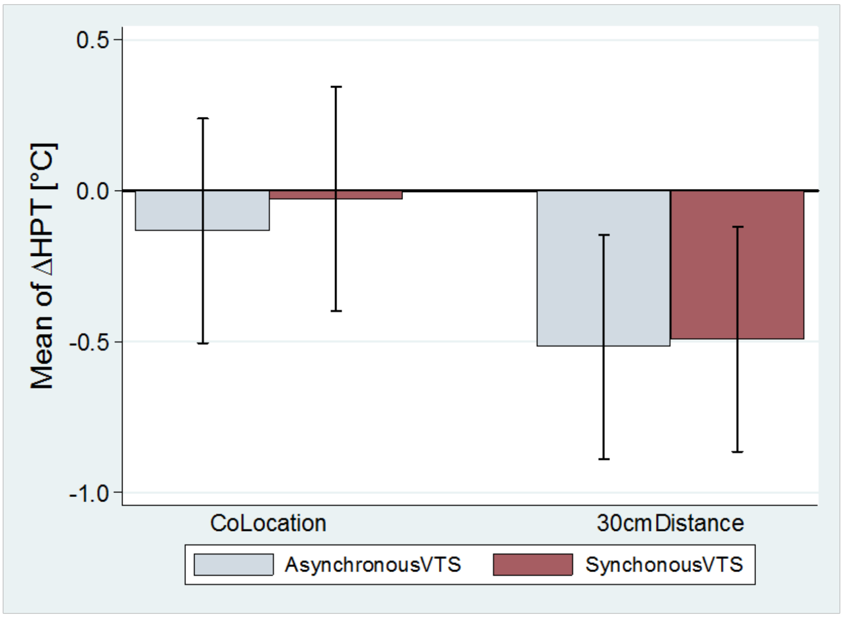

FIGURE 4.8: The mean of ΔHPT in the four different experimental conditions with respect to the baseline. Error bars indicate the confidence interval of the coefficient for the factor distance.

Ownership-related questions Regarding the ownership related questions, OwnershipPresence, OwnershipStrength, and RealHandTurnsVirtual showed similar response patterns. They were all negatively influenced by distance, meaning that for colocation ratings were significantly higher than for the 30-cm distance (OwnershipPresence: $z = -3.98$, $P < .001$, 95% CI: –4.058– –1.378; OwnershipStrength: $z = -3.96$, $P < .001$, 95% CI: –4.108– –1.388; RealHandTurnsVirtual: $z = -3.64$, $P < .001$, 95% CI: –3.869– –1.161). Further, both were positively influenced by synchrony of VTS, meaning that during synchronous VTS ratings were higher than during asynchronous VTS (OwnershipPresence: $z = 3.03$, $P = .002$, 95% CI: 0.710–3.312; OwnershipStrength: $z = 4.10$, $P < .001$, 95% CI: 1.542–4.363; RealHandTurnsVirtual: $z = 3.66$, $P < .001$, 95% CI: 1.370–4.532). Moreover, all three showed no significant interaction between distance and synchrony of VTS (OwnershipPresence: $z = -.06$, not significant (n.s.); OwnershipStrength: $z = -.88$, n.s.; RealHandTurnsVirtual: $z = 1.33$, n.s.).

Illusion induction-related questions The two questions related to illusion induction, TappingLocation and BallCausesTouch, showed a similar response pattern. Both were positively influenced by synchrony of VTS—synchronous VTS led to higher ratings than asynchronous VTS (TappingLocation: $z = 5.02$, $P < .001$, 95% CI: 2.447–5.582; BallCausesTouch: $z = 5.94$, $P < .001$, 95% CI: 3.847–7.635).

TABLE 4.3: Upper Part: Raw HPT Values at Baseline and at the 4 Different Experimental Conditions; Lower Part: Questionnaire Ratings. Ratings could range in the first 6 questions from 1 to 7 and in the last question from 1 to 10 (IQR = interquartile range, SEM = standard error of the mean).

			Synchronous VTS				**Asynchronous VTS**			
			Colocation		**30-cm distance**		**Colocation**		**30-cm distance**	
Response variable	*Mean*	*SEM*	*Mean*	*SEM*	*Mean*	*SEM*	*Mean*	*SEM*	*Mean*	*SEM*
HPT, °C	45.0	0.4	45.2	0.4	44.7	0.4	45.1	0.5	44.7	0.5
			Median	*IQR*	*Median*	*IQR*	*Median*	*IQR*	*Median*	*IQR*
Ownership										
OwnershipPresence (Q3)			6	5–7	5	2–6	5	4–6	3	2–4
OwnershipStrength (Q7)			8	7–9	5	4–7	6	5–8	4	2–5
RealHandTurningVirtual (Q6)			6	6–6	4	3–6	5	4–6	3	2–5
Illusion induction										
TappingLocation (Q1)			7	6–7	5	4–6	4	1–6	3	2–5
BallCausesTouch (Q2)			7	6–7	6	5–6	2	1–3	2	1–4
Illusion perception										
MultipleHands (Q4)			1	1–2	3	2–4	2	1–3	4	2–5
VibrationBetweenHands (Q5)			3	2–5	4	2–5	3	2–5	3	2–6

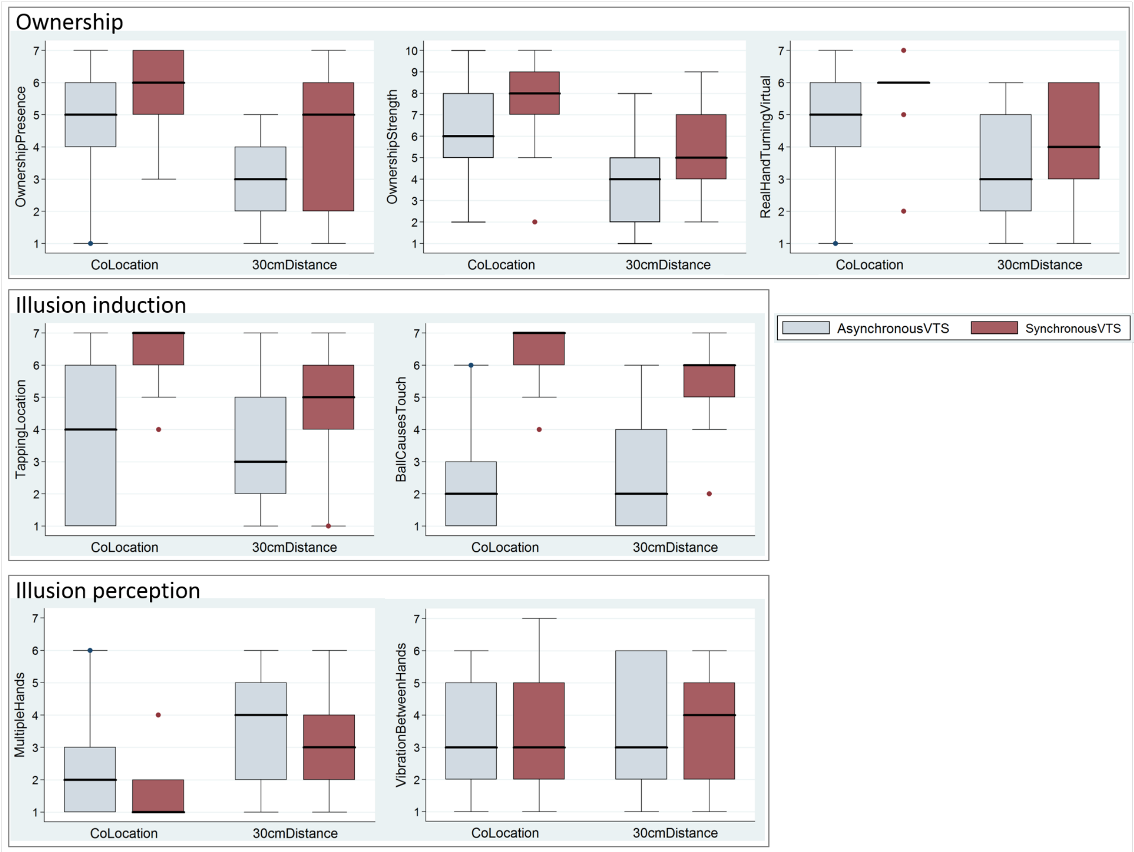

FIGURE 4.9: Box plots of questionnaire ratings after each experimental condition separated by questions aiming at ownership, illusion induction, and illusion perception. Note that ratings could change in all questions from 1 to 7 except for question OwnershipStrength where they could change from 1 to 10.

Distance had no influence on either of them (TappingLocation: $z = -.73$, n.s.; BallCausesTouch: $z = -.78$, n.s.), but in both was a significant interaction between distance and VTS (TappingLocation: $z = -2.09$, $P = .037$, 95% CI: –3.625– –0.113; BallCausesTouch: $z = -2.04$, $P = .041$, 95% CI: –3.806– –0.078). During colocation there was a greater difference between synchronous and asynchronous VTS than during 30-cm distance conditions.

Illusion perception-related questions MultipleHands was positively influenced by distance; during 30-cm distance ratings were significantly higher than during colocation ($z = 2.22$, $P < .026$, 95% CI: 0.175–2.733); further, MultipleHands was negatively influenced by synchrony of VTS, meaning during asynchronous VTS ratings were higher than during synchronous VTS ($z = -2.12$, $P = .034$, 95% CI: –2.906– –0.111); there was no significant interaction between synchrony of VTS and distance on MultipleHands ($z = 1.19$, n.s). VibrationBetweenHands was not influenced by distance ($z = -.10$, n.s.) or by synchrony of VTS ($z = -.14$, n.s.); there was no significant interaction between synchrony of VTS and distance (z = .10, n.s.).

4.2.3 Relationship between body ownership and HPT

The OwnershipStrength score is an overall indication of ownership. A mixed effects regression of ΔHPT on OwnershipStrength reveals a significant positive relationship (z = 2.52, P = .012). The coefficient of OwnershipStrength in the linear model has a 95% CI of .03 to .22. In contrast, if we take the scores of the same question for the baseline, then there is no relationship at all (z = .10, P > .90). If we take all of the questions indicating a relationship (TappingLocation, BallCausesTouch, OwnershipPresence, OwnershipStrength), then a principal components factor analysis yields one variable accounting for 72% of the variance giving almost equal weight to all four scores. We refer to this variable as OwnershipPCA. The mixed effects regression of HPT on OwnershipPCA similarly shows a positive association (z = 2.2, P = .028). In the baseline condition, z = .68, P = .5. Hence, greater levels of ownership are associated with higher ΔHPT. This is independent of VTS or distance. It could be that because distance, as we have seen, is also associated with ownership, that this relationship reflects the effect of distance rather than ownership. Indeed, this is likely to be the case because when these regressions are run for each level of distance separately, then the relationship between ownership and ΔHPT is not found. However, this does suggest that ownership modulates the effect of distance on ΔHPT, that it is not 'distance' in itself responsible for the effect but the effect of distance via ownership.

4.3 Experiment 3

The motivation of this experiment was to investigate the level of illusory agency that can be induced by different BCI protocols and the involvement of motor areas in the sense of agency. In two experimental conditions participants were able to move the right arm of the virtual body (over which they felt ownership) through a BCI, which was either exploiting motor areas (SMR-based BCI, referred to as MotorImagery condition) or visual areas (SSVEP-based BCI, referred to as SSVEP condition). In a control condition participants simply observed the movement of the arm (Observe condition). We excluded participants with BCI-accuracy rates below 75% which led to a final sample size of 29 participants. In 18 of these participants we also recorded their activity during real movement. Below we show the results obtained in our third experiment.

4.3.1 BCI-accuracy

Accuracy has been shown to influence the perceived level of control over a BCI (Fard & Grosse-Wentrup, n.d.). Therefore we first checked if accuracy differed between the two BCI conditions and if it had an influence on ERD%, control, or responsibility measures.

Figure 4.10 displays accuracy in the two BCI conditions MotorImagery and SSVEP. Accuracies were higher during SSVEP (Mean = 90.9%) than during MotorImagery condition (Mean = 87.4%; paired t-test, $t(28) = 2.03$, $P = .052$, 95% CI: –.032–6.998).

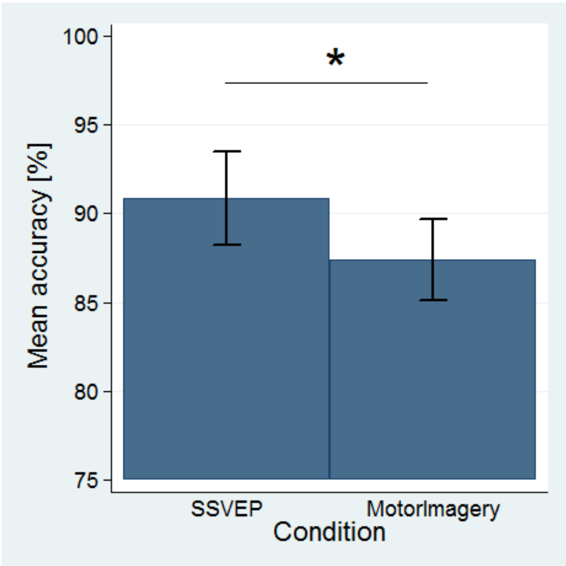

FIGURE 4.10: Bar plot of mean accuracies during MotorImagery and SSVEP conditions. Only participants with an accuracy higher than 75% were included (N = 29). Error bars indicate the Standard Error of the Mean, stars indicate level of P-values: $*$: $P \leq .05$, $**$: $P \leq .01$, $***$: $P \leq .001$

In the preparation phase, there was no relation between ERD% and accuracy—neither in the SSVEP (mixed effects regression; z = –0.75, n.s.) nor in the MotorImagery condition (z = –0.02, n.s.; see also Figure 4.11).

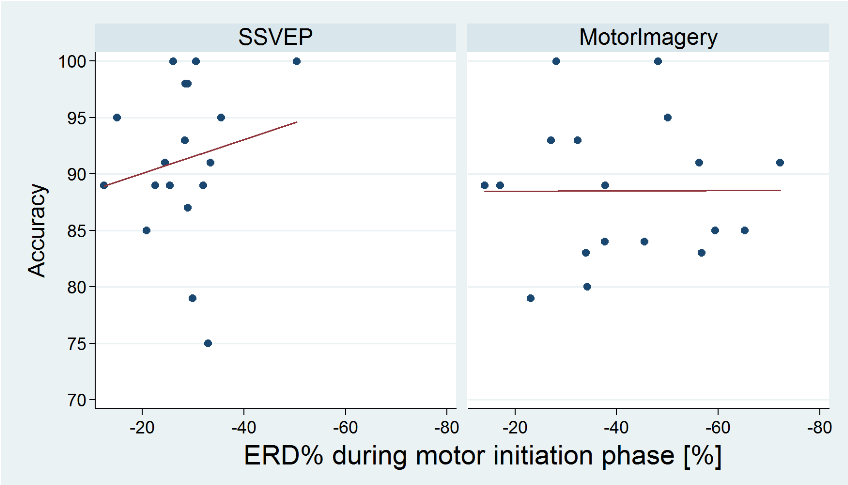

FIGURE 4.11: Accuracy plotted against ERD%. Note that the x-axis is inverted. Lower ERD% indicate stronger sensorimotor cortex activity.

There was a significant positive relationship between accuracy and Control in the MotorImagery condition ($z = 3.72$, $P < 0.001$), but not in the SSVEP condition ($z = -1.16$, n.s.). In none of the two BCI conditions was a significant relationship between accuracy and Responsibility (SSVEP: $z = -0.64$, n.s.; MotorImagery: $z = 0.96$, n.s.; see also Figures 4.12 A and B).

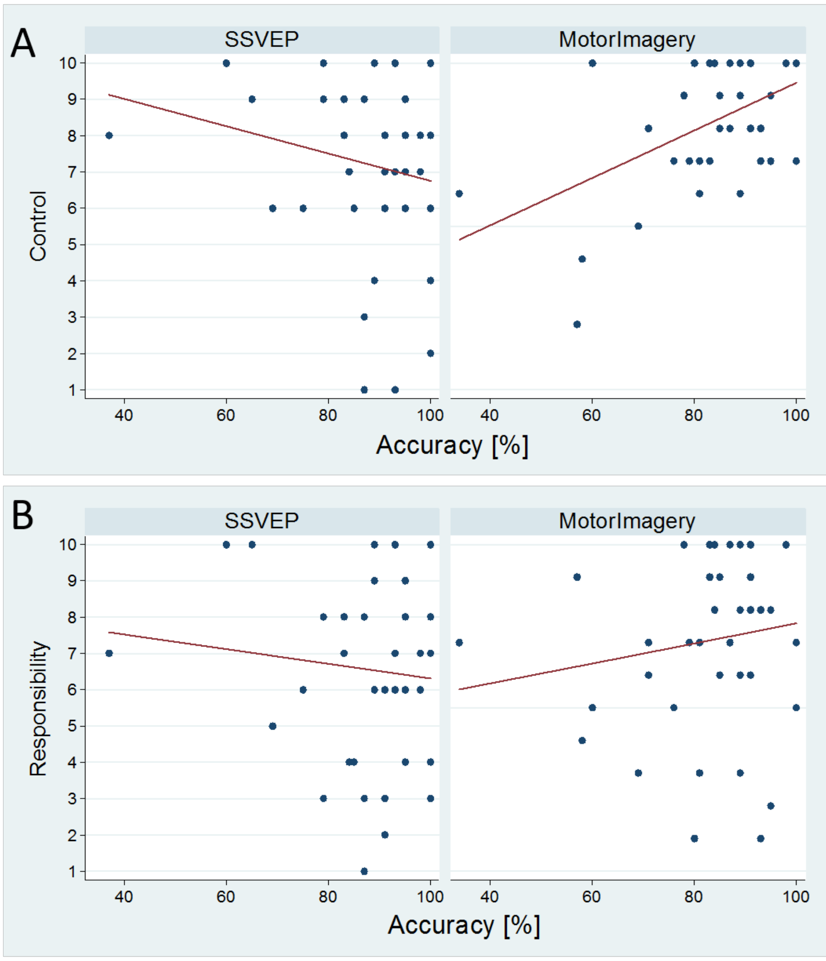

FIGURE 4.12: Accuracy in % plotted against (A) Control and (B) Responsibility ratings.

4.3.2 Embodiment phase

The embodiment phase served to boost the feeling of body ownership over the virtual body. Participants reported high MyBody and Control ratings at the end of this phase, indicating that it induced high feelings of body ownership and control over the virtual body as intended by our experimental design (see Figures 4.13 A and B). Neither control ratings (ordered logistic regression, z = 1.01, n.s.) nor embodiment ratings (z = -0.41, n.s.) differed between experimental conditions during the embodiment phase.

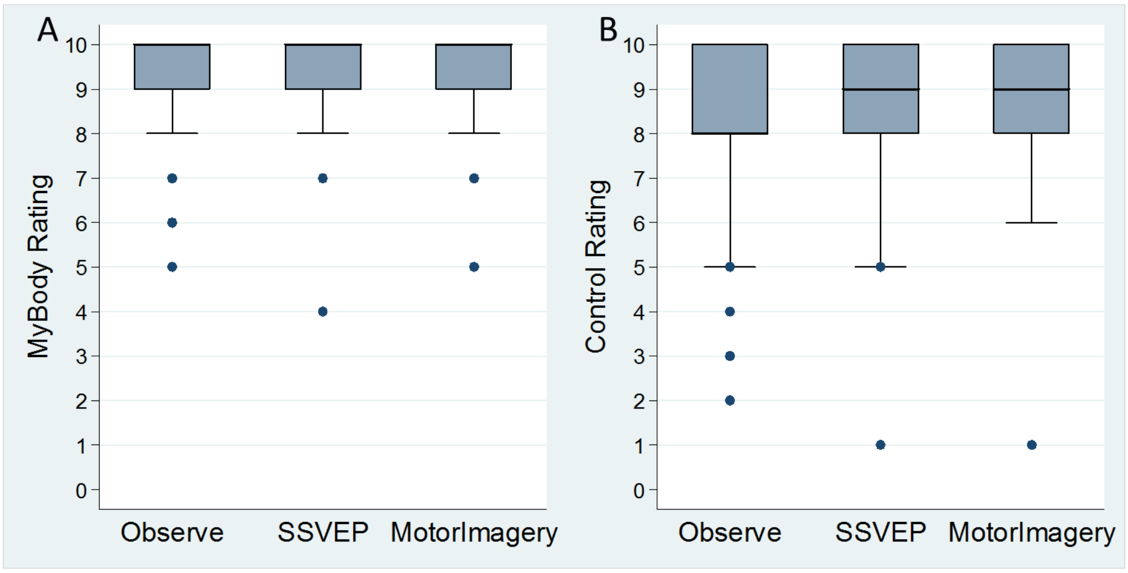

FIGURE 4.13: Boxplots of ratings given at the end of the embodiment phase.

4.3.3 Covariates

To control for possible misattribution of actually performed movements or muscle activity to the virtual movement we introduced the following covariates: muscle activity (MA) in the right shoulder and eye movements (EM). We measured them during the preparation phase (MAp and EMp) and during the motor observation phase (MAo and EMo) and added them as covariates to our statistical model in all agency related measures. We kept them in the model if they improved the fit of the model to the data.

MA and EM differed in the three experimental conditions in the preparation phase (MAp: $F(2,52)$ = 3.81, P = .029, η_p^2 = 0.128; EMp: $F(2,56)$ = 3.54, P = .036, η_p^2 = 0.112), and the motor observation phase (MAo: $F(2,52)$ = 2.78, P = . 071, η_p^2 = 0.096; EMo: $F(2,56)$ = 4.59, P = .014, η_p^2 = 0.141).

4.3.4 Control and Responsibility ratings

Control and Responsibility ratings are displayed in Figure 4.14, and Median values and IQR are in Table 4.4.

Control

An ordinal regression revealed an effect of condition on the Control ratings (z = 5.14, P < .001; for information on model selection see Appendix C.3.1; Figure 4.14 displays the boxplots). Pairwise comparisons indicated differences between

TABLE 4.4: Median values and interquartile ranges (IQR) of responses to questionnaire items during the embodiment phase, during the experimental condition, and after the experimental condition.

	Observe		**SSVEP**		**MotorImagery**	
	Median	*IQR*	*Median*	*IQR*	*Median*	*IQR*
Embodiment phase						
MyBody	10	2	10	1	10	1
Control	8	1	9	2	9	2
During exp. condition						
Control	5	6	8	4	9	3
Responsibility	5	5	6	4	8	4
Responsibility-NoTouch	2	4	2	3	4	6
After exp. condition						
Embodiment	6	6	7	3	8	3
MySound	3	5	7	3	8	4
ITouchedObject	5	4	6	5	8	5
MyMovement	4	4	8	4	9	2
	Mean	*SEM*	*Mean*	*SEM*	*Mean*	*SEM*
ERD% (in %)						
preparation phase	-21.653	2.290	-28.146	1.939	-41.060	3.919
motor observ. phase	-24.880	2.603	-30.938	2.266	-31.319	3.430
Covariates (in μA)						
MAp	0.754	0.078	0.686	0.056	1.266	0.257
MAo	0.724	0.069	0.699	0.067	1.042	0.162
EMp	3.353	0.319	2.466	0.224	3.347	0.612
EMo	4.759	0.812	5.357	0.604	7.555	0.985

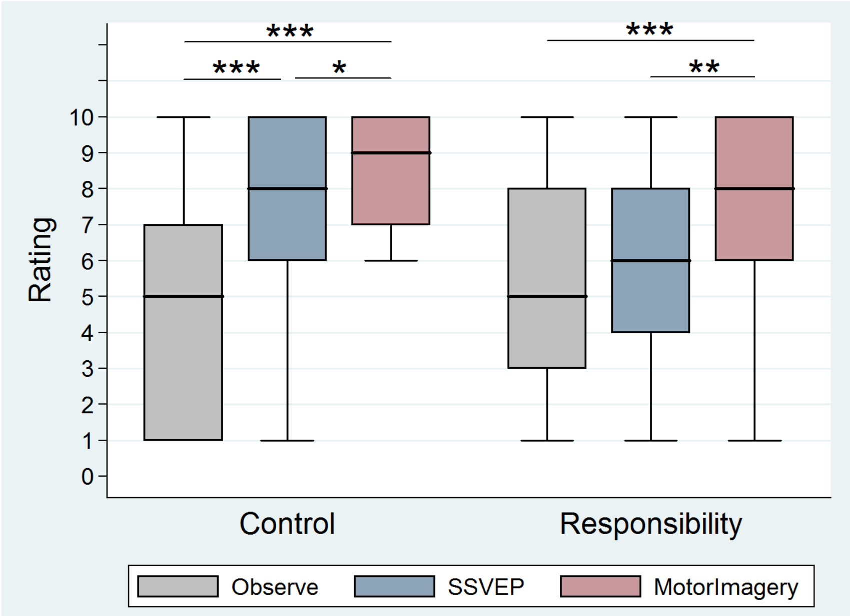

FIGURE 4.14: Boxplot of Control and Responsibility ratings during the three different experimental conditions. Stars indicate level of P-values: $*$: $P \leq .05$, $**$: $P \leq .01$, $***$: $P \leq .001$

all three experimental groups. During MotorImagery participants gave higher ratings than during Observe (*Scheffé* z = 5.14, P < .001, 95% CI 1.989–4.442) and during SSVEP (*Scheffé* z = 2.29, P = .022, 95% CI 0.169–2.196). During SSVEP participants gave higher ratings than during Observe (*Scheffé* z = 3.68, P < .001, 95% CI 0.950–3.115).

Responsibility

One of the four responsibility trials was used to check if this question really captured responsibility. In this trial the object fell off the table by itself without the arm touching it. In the other four responsibility trials the virtual arm touched the object and caused it falling off the table. Figure 4.15 displays a boxplot of the four responsibility ratings and shows that ratings were significantly lower during the NoTouch-trial. This was confirmed a multilevel mixed-effects ordered logistic regression with fixed factor condition and EMp as covariate (for information on model selection see Appendix C.3.1) revealed a significant effect of question (z = 7.12, P < .001). Post-hoc paired comparisons showed that in the NoTouch-trial ratings were significantly lower than in the first (*Scheffé* z = 6.28, P < .001, 95% CI 1.181–2.688), the second (*Scheffé* z = 6.41, P < .001, 95% CI 1.212–2.710), or the third responsibility trial (*Scheffé* z = 7.12, P < .001, 95% CI 1.432–2.934). There was no difference between second and first (*Scheffé* z = 0.10, n.s), third and first (*Scheffé* z = 0.91, n.s), or third and second responsibility questions (*Scheffé* z = 0.82, n.s).

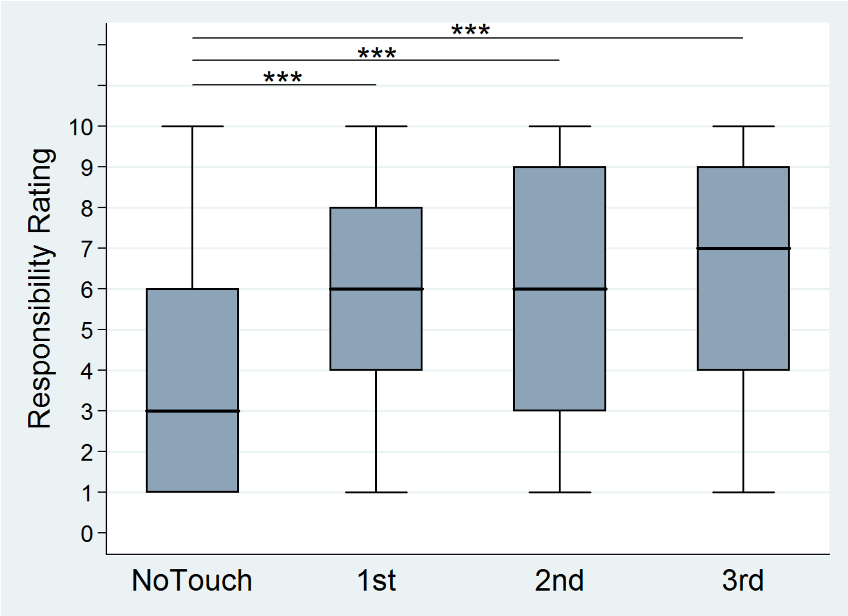

FIGURE 4.15: Boxplots of the four Responsibility ratings independent from condition. The x-axis displays the three ratings when the virtual hand touched the object (1st, 2nd, and 3rd) in temporal order and the rating when the object just fell off the table without being touched (NoTouch). Note that NoTouch was presented at a random position within the four trials and is therefore not in temporal order. Stars indicate level of P-values: $*$: $P \leq .05$, $**$: $P \leq .01$, $***$: $P \leq .001$

Regarding the Median responsibility ratings from the three trials where the virtual hand actually touched the object, an ordinal regression with factor condition and covariate EMp fitted our data best and revealed an effect of condition on the Responsibility ratings ($z = 3.62$, $P < .001$; for information on model selection see Appendix C.3.1; Figure 4.14 displays the boxplots). Pairwise comparisons indicated that during Motor Imagery participants gave higher ratings than during Observe (*Scheffé* $z = 3.62$, P < .001, 95% CI 0.931–3.127) and during SSVEP (*Scheffé* $z = 2.99$, $P = .003$, 95% CI 0.566–2.716). There was no statistical difference between SSVEP and Observe conditions (*Scheffé* $z = 0.73$, n.s.).

4.3.5 Post-condition questionnaire responses

Figure 4.16 displays the questionnaire results for the items MyBody, MySound, ITouchedObject, and MyMovement and Table 4.4 shows their Median values and IQR.

MyBody

The MyBody questionnaire item measured the level of body ownership participants experienced during the experimental condition. A mixed-effects ordered logistic regression revealed an influence of condition on MyBody (z = 3.40, P = .001; see also Figure 4.16). Post-hoc pairwise comparisons showed that ratings were highest during Motor Imagery compared to Observe (*Scheffé* z = 3.40, P = .001, 95% CI 0.710–2.643) and compared to SSVEP (*Scheffé* z = 2.22, P = .026, 95% CI 0.120–1.915), while Observe and SSVEP conditions were not significantly different (*Scheffé* z = 1.37, n.s).

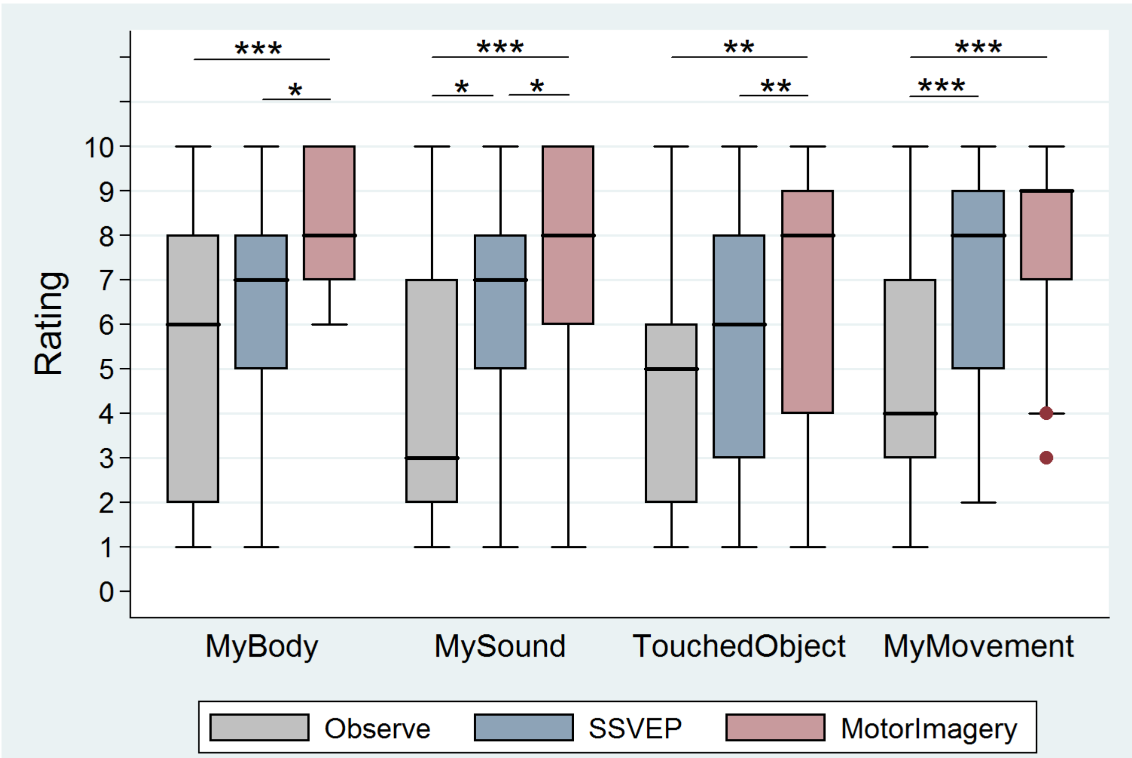

FIGURE 4.16: Boxplots of the questionnaire items given after the experimental condition. Participants filled in this questionnaire on a computer screen outside VR, however the appearance of the questions on the computer screen resembled the one of the questions inside VR. Stars indicate level of P-values: $*$: $P \leq .05$, $**$: $P \leq .01$, $***$: $P \leq .001$

MySound

The MySound questionnaire item measured how strong participants perceived it was they who produced the sound when the virtual arm touched the button. A mixed-effects ordered logistic regression revealed an influence of condition on MySound (z = 3.65, P < .001; for information on model selection see Appendix

C.3.1; Figure 4.16 displays the boxplots). Post-hoc pairwise comparisons showed that ratings were higher during Motor Imagery compared to Observe (*Scheffé* z = 3.65, P < .001, 95% CI 0.980–3.247) and compared to SSVEP (*Scheffé* z = 2.00, P = .045, 95% CI 0.021–1.982). Further, ratings were higher during SSVEP than during Observe conditions (*Scheffé* z = 2.13, P = .033, 95% CI 0.087–2.137).

ITouchedObject

The ITouchedObject item measured how strong participants felt they accidentally touching the object before it fell off the table. A mixed-effects ordered logistic regression using EMp as covariate revealed an influence of condition on ITouchedObject (z = 3.06, P = .002; for information on model selection see Appendix C.3.1; Figure 4.16 displays the boxplots). Post-hoc pairwise comparisons showed that ratings were higher during Motor Imagery compared to Observe (*Scheffé* z = 3.06, P = .002, 95% CI 0.602–2.754) and compared to SSVEP (*Scheffé* z = 2.59, P = .010, 95% CI 0.336–2.421), while Observe and SSVEP conditions were not significantly different (*Scheffé* z = 0.55, n.s).

MyMovement

The MyMovement item measured how strong participants perceived that the virtual movement they saw was their movement. A mixed-effects ordered Regression revealed an influence of condition on MyMovement (z = 4.39, P < .001; for information on model selection see Appendix C.3.1; Figure 4.16 displays the boxplots). Post-hoc pairwise comparisons showed that ratings were higher during Motor Imagery compared to Observe (*Scheffé* z = 4.39, P < .001, 95% CI 1.325–3.464), but not significantly different compared to SSVEP (*Scheffé* z = 1.56, n.s). Ratings were higher during SSVEP than during Observe conditions (*Scheffé* z = 3.21, P = 0.001, 95% CI 0.651–2.685).

4.3.6 Activity in sensorimotor areas

Sources of CSP patterns generated from Executed Movement data

18 participants out of the 22, in which we recorded the Executed Movement, had an accuracy higher than 75% in both BCI protocols. The mean activity over these 18 participants was strongest at coordinates X = -52.5, Y = -7.5 and Z = 52.9 in the MNI space. As displayed in Figure 4.17 the mean sources were located in the precentral gyrus.

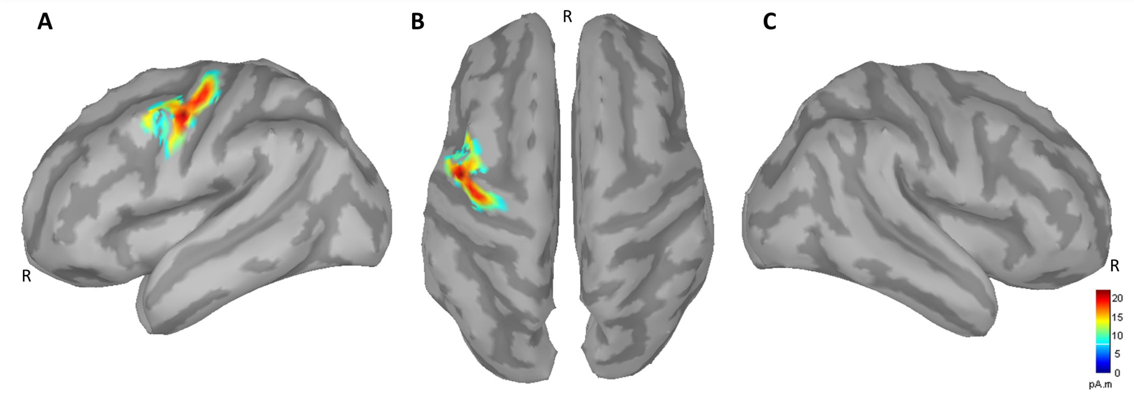

FIGURE 4.17: Average sources of Executed Movement from 18 participants. The graph on the left displays the left hemisphere and the one on the right the right hemisphere. The graph in the middle displays both hemispheres from a top view. R = rostral.

Strength of ERD in the three experimental conditions

The spatial filters obtained from CSP analysis in real movement were used to project the data of the three experimental conditions. Figure 4.18 displays the projected signal. We analyzed the strength of ERD% during both the preparation

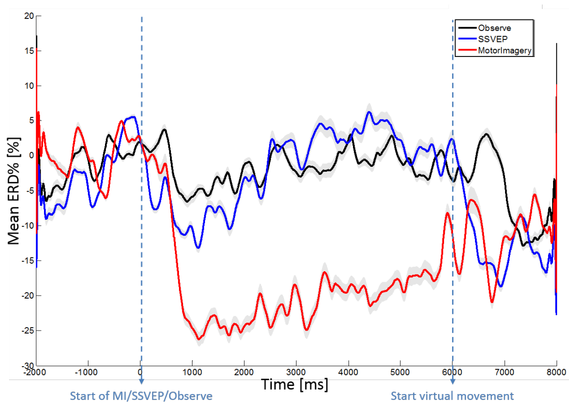

FIGURE 4.18: The signal from the three experimental conditions projected through the spatial filters obtained with the CSP applied on real movement data.

phase that is when participants were either imagining the movement, looking at the blinking light, or simply observing, and the motor observation phase, that is when participants saw the virtual arm move.

Preparation phase The statistical analysis of ERD% in the preparation phase showed that our experimental manipulation was working. A repeated measure ANOVA with fixed effect condition revealed differences in sensorimotor activity between the three experimental conditions ($F(2,34)$ = 12.70, P < .001, η_p^2 =

0.428; for information on model selection see Appendix C.3.1). Pairwise comparisons revealed that ERD% was highest during Motor Imagery compared to SSVEP (*Scheffé t* = -3.29, *P* = .009) and Observe (*Scheffé t* = -4.95, *P* < .001). There was no statistically significant difference between SSVEP and Observe (*Scheffé t* = -1.66, n.s.). Mean values and SEM are displayed in Table 4.4.

Movement observation phase A repeated measure ANOVA with fixed effect condition revealed a trend in sensorimotor activity between the three experimental conditions (*F(2,34)* = 2.96, *P* = .065, η_p^2 = 0.148; for information on model selection see Appendix C.3.1). Pairwise comparisons did not show any differences between experimental conditions (Motor Imagery compared to SSVEP: *Scheffé t* = -0.13, n.s.; Motor Imagery compared to Observe: *Scheffé t* = -2.17, *P* = .111; SSVEP compared to Observe: *Scheffé t* = -2.04, *P* = .140). Mean values and SEM are displayed in Table 4.4.

4.3.7 Relationship between agency related questionnaire items and sensorimotor activity

We performed a principle components factor analysis on the questions indicating responsibility (Responsibility ITouchedObject) which resulted in one variable accounting for 95 % of the variance giving almost equal weight to both scores. We refer to this variable as ResponsibilityPCA.

Preparation phase

Mixed effects regressions of ERD% on the different questionnaire responses on agency were used to reveal significant relationships between those variables during the preparation phase (Bonferroni corrections were applied for multiple comparisons).

ResponsibilityPCA There was a negative relationship between ERD% and ResponsibilityPCA in the MotorImagery condition (*z* = –2.76, *P* = .006; see also Figure 4.19). Note that the stronger the sensorimotor activity the lower ERD%, meaning that participants with stronger sensorimotor activity gave higher Responsibility ratings. There was no relationship in the two other conditions between the two variables (Observe: *z* = –1.14, n.s.; SSVEP: *z* = 1.59, n.s.).

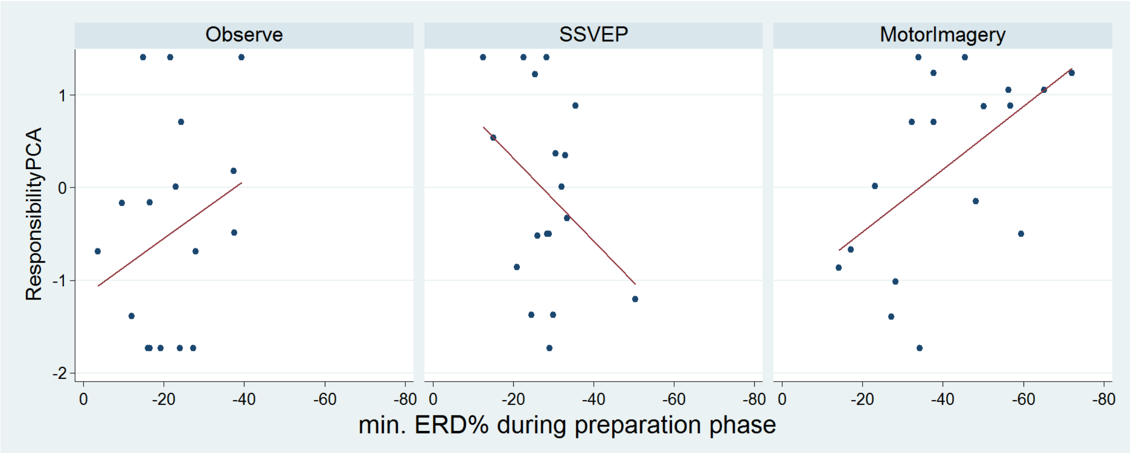

FIGURE 4.19: ERD% responses during preparation phase plotted against ResponsibilityPCA. Note that the x-axis is inverted. Lower ERD% ratings indicate higher sensorimotor cortex activity.

Control There was no relationship between ERD% and Control in none of the three experimental conditions (Observe: z = –0.58, n.s.; SSVEP: z = –0.05, n.s.; MotorImagery: z = –0.88, n.s.)

MySound There was a positive relationship between ERD% and MySound in the SSVEP condition (z = 3.01, P = .003; see also Figure 4.20). There was no relationship in the two other conditions between the two variables (Observe: z = –0.02, n.s.; MotorImagery: z = 0.41, n.s.).

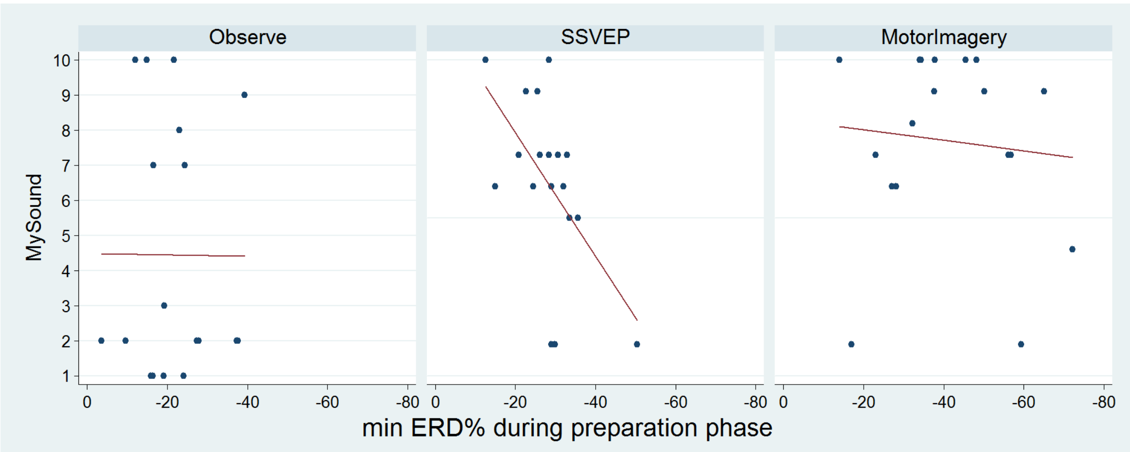

FIGURE 4.20: ERD% responses during preparation phase plotted against MySound. Note that the x-axis is inverted. Lower ERD% ratings indicate higher sensorimotor cortex activity.

MyMovement There was no relationship between ERD% and MyMovement in none of the three experimental conditions (Observe: z = –0.80, n.s.; SSVEP: z = –0.30, n.s.; MotorImagery: z = –0.03, n.s.)

Motor observation phase

In the motor observation phase we also used mixed effects regressions of ERD% on agency related questionnaire responses to reveal significant relationships between those variables and applied Bonferroni corrections for multiple comparisons. There were no relationships between ERD% and ResponsibilityPCA (Observe: z = –1.55, n.s.; SSVEP: z = –0.26, n.s.; MotorImagery: z = 0.13, n.s), Control (Observe: z = –0.51, n.s.; SSVEP: z = –0.32, n.s.; MotorImagery: z = –0.62, n.s), MySound (Observe: z = 0.23, n.s.; SSVEP: z = –0.31, n.s.; MotorImagery: z = 0.15, n.s), or MyMovement (Observe: z = 0.28, n.s.; SSVEP: z = 0.05, n.s.; MotorImagery: z = –1.41, n.s).

4.3.8 ERPs to tone

When the virtual hand pressed the button participants heard a tone. We measured event-related auditory N100–P200 peak-to-peak amplitudes and P300 components to the onset of this tone. Figure 4.21 displays the averaged epochs for each experimental condition.

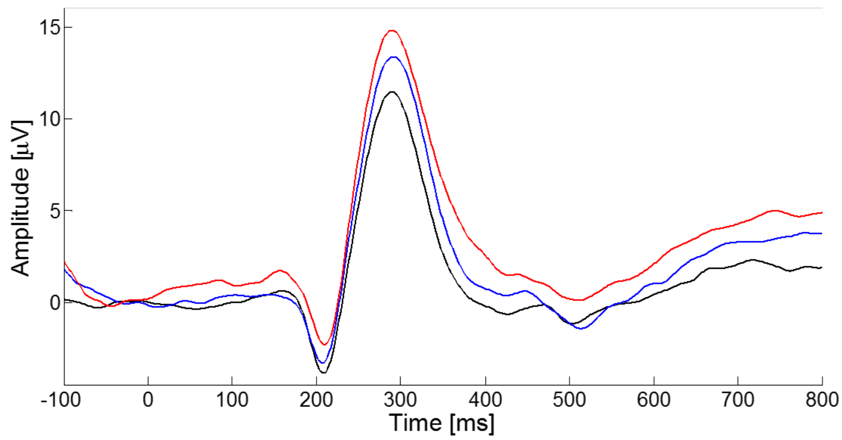

FIGURE 4.21: EEG signal averaged over 29 participants with BCI accuracies above 75 %. Amplitudes are averaged over electrodes (F3, Fz, F4, FC3, FCz, FC4, C3, Cz, and C4).

N100–P200 peak-to-peak amplitudes

Attenuation effects to self-generated tones are typically observed in the auditory N100-P200 ERP complex. We measured the mean N100–P200 peak-to-peak amplitudes over all participants in averaged frontocentral electrodes (F3, Fz, F4, FC3, FCz, FC4, C3, Cz, and C4). A repeated-measure ANOVA with factor Condition showed no effect ($F(2,56) = 0.38$, n.s.). Figure 4.22 displays the N100–N200 peak-to-peak amplitudes in the three different conditions.

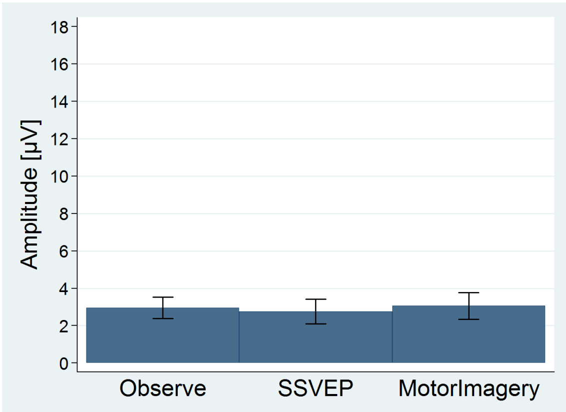

FIGURE 4.22: Bar plot of mean N100–P200 peak-to-peak amplitudes. Error bars indicate SEM.

Relationship between N100–P200 and agency related questionnaire responses
We next looked whether there was any relationship between agency related questionnaire responses and the N100-P200 peak-to-peak amplitudes. Mixed effects regressions showed no significant relationships between N100–P200 peak-to-peak amplitudes and ResponsibilityPCA (Observe: $z = 0.30$, n.s.; SSVEP: $z = 0.46$, n.s.; MotorImagery: $z = -0.23$, n.s.), Control (Observe: $z = 0.79$, n.s.; SSVEP: $z = -0.38$, n.s.; MotorImagery: $z = 0.03$, n.s.), MySound (Observe: $z = 1.68$, n.s.; SSVEP: $z = 0.96$, n.s.; MotorImagery: $z = -0.31$, n.s.), or MyMovement (Observe: $z = 1.37$, n.s.; SSVEP: $z = 0.25$, n.s.; MotorImagery: $z = 1.10$, n.s.). Bonferroni correction were applied for multiple comparisons.

P300 amplitudes

Repeated-measure ANOVAs with factor Condition on the mean P300 amplitude over central electrodes (F3, Fz, F4, FC3, FCz, FC4, C3, Cz, and C4) revealed an effect of Condition ($F(2,56) = 11.75$, $P < .001$, $\eta_p^2 = 0.296$). P300 amplitude following the tone in the MotorImagery condition ($Mean = 15.603$ μV) was larger than in the

Observe condition (*Mean* = 12.422 μV; *Scheffés t(28)* = 4.81, *P* < .001). P300 amplitudes were also larger in the SSVEP (*Mean* = 14.364 μV) compared to the Observe condition (*Scheffés t(28)* = 2.94, *P* = .018). There was no difference between MotorImagery and SSVEP conditions (*Scheffés t(28)* = 1.87, n.s.). Mean amplitudes of the P300 component over all participants are displayed in Figure 4.23.

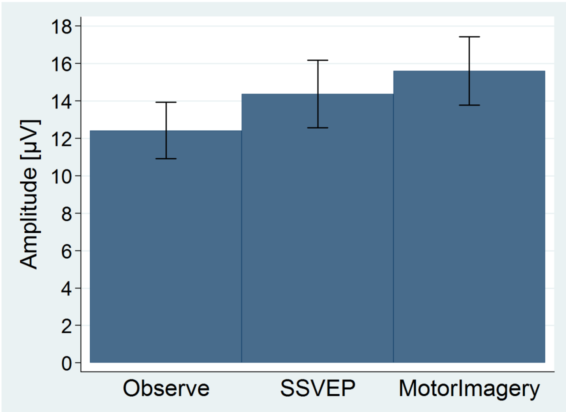

FIGURE 4.23: Bar plot of mean P300 amplitudes at electrode Cz. Error bars indicate SEM.

Relationship between P300 and agency related questionnaire reports A mixed effects regression of P300 amplitudes on agency related questionnaire reports revealed no relationship for none of the items (Bonferroni corrections were applied for multiple comparisons): ResponsibilityPCA (Observe: z = –0.67, n.s.; SSVEP: z = 1.34, n.s.; MotorImagery: z = –0.09, n.s.), Control (Observe: z = –0.49, n.s.; SSVEP: z = 2.48, n.s.; MotorImagery: z = 2.42, n.s.), MySound (Observe: z = –0.77, n.s.; SSVEP: z = 2.90, n.s.; MotorImagery: z = 0.64, n.s.), and MyMovement (Observe: z = –1.01, n.s.; SSVEP: z = 2.86, n.s.; MotorImagery: z = –0.05, n.s.).

4.3.9 Debriefing

When participants were asked at the end of the experiment to order the three conditions regarding their perceived sense of control, most reported that they had the strongest feeling of control during the MotorImagery condition, SSVEP came for most participants second, and Observe third. Figure 4.24 displays a histogram of participants' reports of high, medium or low feelings of control in the three conditions.

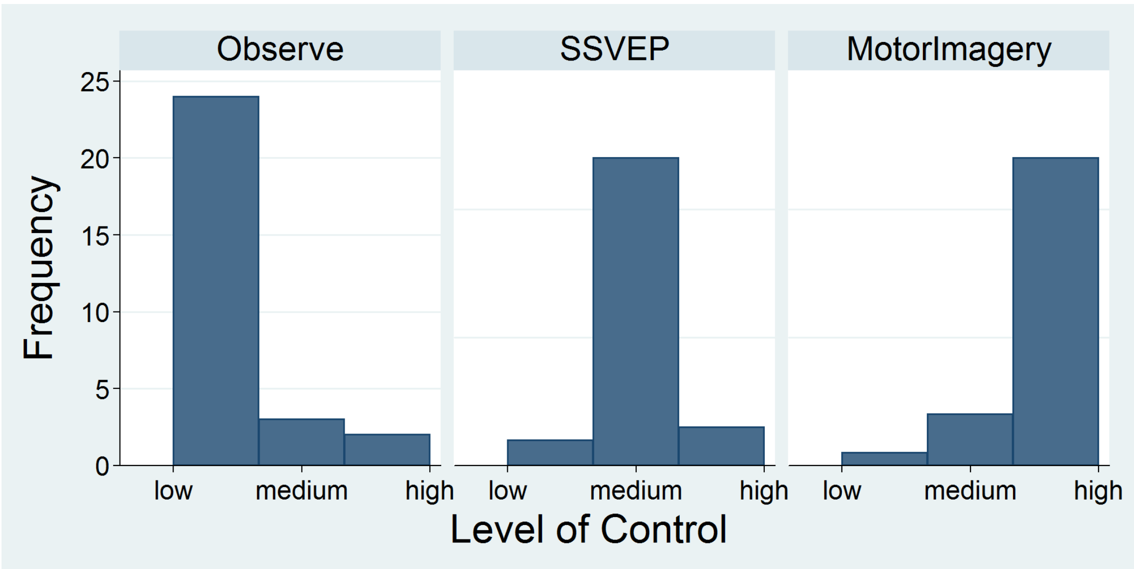

FIGURE 4.24: Histogram of reports from participants after the experiment. Participants were asked to order the three different conditions from high to low regarding their perceived sense of control.

Chapter 5

Discussion

In this chapter I will discuss the obtained results in the light of the current literature for each experiment separately. I will end the chapter with a section on how the conducted experiments bring some further understanding to the use of VR for therapeutic applications.

5.1 Experiment 1: Perceptual fluctuations in embodiment

In this experiment we investigated whether the experience of body ownership fluctuates over time and if so, whether such fluctuations can be predicted by spontaneous neuronal activity measured with EEG. Body ownership relaxes temporal constraints between tactile and visual stimuli, when these stimuli are applied to the virtual body (Maselli et al., 2016), meaning that the visual and tactile sensory inputs of an object touching the virtual body can be presented with a bigger temporal offset and will still be perceived by the participant as simultaneous, compared to the same object is touching a wooden stick. Changes in body ownership should therefore be reflected in a visuotactile simultaneity task. The temporal offset of visual and tactile stimulus was set at a detection threshold at which participants would perceive the two stimuli as being simultaneous in 50 % of times. The simultaneity responses were measured in two conditions, a Body and an Object condition. We found that simultaneity thresholds were significantly higher during the Body condition. Fluctuations of the response compared to random data were observed but did not differ between experimental conditions. The spontaneous neuronal activity between 0.01 and 0.1 Hz could further not predict the observed fluctuations. In the following we will discuss the obtained results and why we think we cannot yet rule out a relation between spontaneous neuronal activity and fluctuations of body ownership.

5.1.1 Manipulation of body ownership

The rubber hand illusion has been shown to be stronger when seeing a human shaped hand in an anatomically correct position than when seeing a non-corporeal object (Haans, IJsselsteijn, & de Kort, 2008; Tsakiris et al., 2010) meaning that the surrogate body needs to fit with structural information about one's body or body parts (Lenggenhager et al., 2007; Tsakiris, 2008). This is in line with our findings that show that participants felt stronger body ownership (MyBody questionnaire item, see Figure 4.1) in the Body compared to the Object condition. Further they had a stronger feeling that the virtual body would move if they moved in the Body compared to the Object condition (BodyWouldMove item) and they felt stronger that the virtual cylinder touched their real hand in the Body compared to the Object condition (ObjTouchedMe item). However, when looking at the individual level we saw that not all participants felt differences between the two conditions. Six out of 13 included participants reported on at least one recording day very small or no differences between Body and Object condition in the MyBody questionnaire item (see Figure A.6) indicating that our manipulation did not work in all participants on both recording days. This fits with reports in the literature that show that participants can even incorporate a table through simultaneous VTS (Armel & Ramachandran, 2003). We coped with this problem by including only participants that reported at least ratings higher than 1 (maximum rating was 3) in the Body condition or lower than –1 (minimum rating was –3) in the Object condition.

5.1.2 Simultaneity threshold

It has been shown that body ownership relaxes temporal constraints of multisensory integration meaning that when feeling body ownership over a surrogate body the temporal window for visuotactile integration (that is the integration of the touch felt on the real body with the touch seen on the surrogate body) increases compared to stimuli seen close but separated from the surrogate body (Maselli et al., 2016). Our results on the simultaneity threshold support this finding. We show that simultaneity thresholds were higher in the Body compared to the Object condition (see also Figure 4.3) meaning that ownership could be seen as binding factor between visual and tactile stimulus. However, simultaneity thresholds came also with two limitations. First, the simultaneity thresholds were influenced by adaptation effects meaning that although the threshold was set to 40–60% Yes-response rate in the beginning, we saw in some participants a change of this threshold during the experimental condition. Second, when adjusting the threshold using an adopted staircase procedure we were limited in time because we couldn't expose the participant for too long to the virtual environment. The experimental task was very demanding and performing this task in a virtual environment is even more demanding due to the limitation of the technology regarding refresh rate (Montegut, Bridgeman, & Sykes, 1997) and resolution (Ziefle, 1998). Therefore we limited the time of VR-exposure per experimental condition to a maximum of 30 minutes on each recording day. This however influenced the time we could spend for the threshold procedure. We coped with these limitations by including only participants into the analysis that had a final Yes-response rate between 35–65%. Although participants reported that they were feeling as if they were falling asleep, they also reported that they were able to concentrate throughout the session, meaning that although the experimental conditions were demanding, they were not too long.

5.1.3 Real data is different from surrogate data

Psychophysical performance often fluctuates in time scales larger than 10 seconds (Gilden, Thornton, & Mallon, 1995; Monto et al., 2008; Verplanck, Collier, & Cotton, 1952). Such fluctuations can be seen in form of clustering of the psychophysical performance or in form of trial-by-trial correlations. In our data the dynamics in psychophysical performance were different between real and surrogate data. Note that the Yes-response rate cannot explain this difference because we kept the individual response rate in the surrogate data the same as in the real data. We show that psychophysical performance is clustered. Surrogate data had a higher probability for very short run lengths (up to 7 seconds) and a lower probability for larger run lengths than real data. We further show that responses are stronger auto-correlated for lower time lags in real data than in surrogate data. However, these findings are based on a very low sample size (N = 6) based on high number of participants we had to exclude from analysis.

5.1.4 Condition might have an effect on clustering of responses

There was a trend for very short clustering, i.e. run lengths between 0–7 seconds. Such short clustering seem to occur more often in the Body condition than in the Object condition. This relation might be reversed for longer clustering, i.e. run lengths between 7–14 seconds and between 21–28 seconds, in the sense that they seem to occur more likely in the Object than in the Body condition. However, based on our data we cannot draw such conclusions because the three-way interaction just showed a trend and none of the post-hoc t-tests survived corrections for multiple comparison. This might be due to the reduced sample size since we used only one recording day from each participant and had to exclude more than half of the original sample.

5.1.5 No relation between psychophysical performance and ISF

A relation between psychophysical performance and spontaneous slow brain activity fluctuations has been shown in several studies (Boly et al., 2007; Kleinschmidt, Büchel, Zeki, & Frackowiak, 1998; Linkenkaer-Hansen, Nikulin, Palva, Ilmoniemi, & Palva, 2004; Monto et al., 2008; Sadaghiani et al., 2009, 2015). In this study we aimed at a possible connection between ISF and fluctuations of the sense of body ownership. Our data however did not show such a relationship. Although some participants might have shown different Yes-response rates compared to surrogate data, such relationships in Yes-response and phase of the spontaneous slow fluctuation was not significant for the population.

The limitations of experiment 1 are discussed in Section 5.6.

5.2 Experiment 2: Embodiment and pain perception

In this study we investigated whether the distance between a real and a virtual arm had an effect on pain perception (Longo et al., 2009, 2012; Mancini et al., 2013, 2011), thus explaining disputed findings in the literature (Gilpin, Bellan, Gallace, & Moseley, 2014; Giummarra et al., 2015; Hegedüs et al., 2014; Martini et al., 2014; Martini, Perez-Marcos, & Sanchez-Vives, 2015; Mohan et al., 2012; Siedlecka et al., 2014). Our analysis confirmed that the threshold to perceive a heat pain stimulus as painful is modulated by seeing a virtual embodied arm and that the HPT is higher when the virtual arm is colocated with the real arm than when the virtual arm is 30 cm away from the real arm. The latter 30-cm distant condition is an arrangement similar to the one in a rubber arm illusion experiment. We further found that participants who report stronger ownership illusion over the virtual arm tend to have higher HPT. In the following sections we discuss possible interpretations of the obtained results.

5.2.1 Introducing a distance eliminates the analgesic effect of colocation

Our data show similar HPTs when looking at the colocated virtual body compared with looking at the real hand during the baseline measurement (Figure 4.8), which was conducted outside VR. This is consistent with the body of literature showing an analgesic effect of looking at one's own hand (Longo et al., 2009, 2012; Mancini et al., 2013, 2011). Specifically, in an earlier experiment we showed that looking at a virtual hand that is perceived as one's own hand is analgesic compared with looking at a virtual noncorporeal object or compared with not seeing one's limbs (Martini et al., 2014). Building on this finding, the responses during colocation conditions could be interpreted as analgesic.
However, when introducing a distance between a real and a virtual hand, our data show significant differences between the baseline and the distance condition and between the colocation and the distance condition. In other words, our results show that looking at a surrogate virtual hand that is attributed to the self when a surrogate and a real hand are colocated has analgesic effects similar to looking at one's real hand. This effect diminishes when introducing a distance between a real and a surrogate virtual hand.
Baseline levels were always taken before the conditions in VR, thus, the effect of habituation would not affect the baseline values. For the 4 conditions the potential effect of habituation should have been removed by balancing their order. However, it is interesting to note that, without the potential effect of habituation, the vision of the real hand brought about the highest average HPT, equalized only by the synchronous colocated VR condition.
A significant body of literature shows an analgesic effect of looking at one's own body (Longo et al., 2009, 2012; Mancini et al., 2013) (for a review see (Martini, 2016)). However, in the present study we did not manipulate the vision of the embodied virtual body versus, for example, a noncorporeal object, which would have allowed us to replicate the analgesic effect of looking at one's embodied virtual arm (Martini et al., 2014). Therefore, we cannot show that this effect is in our data, however we postulate that we can build on this known effect.

5.2.2 Distance alters multisensory remapping into a common reference frame

The analgesic effect of seeing one's own body has been explained by two mechanisms: 1) an increase in intracortical inhibition, and 2) reorganization of somatotopic maps in terms of sharpening receptive fields in primary somatosensory areas. Several pieces of evidence support this view: for instance, it has been shown that the vision of one's own hand increases intracortical inhibition compared with seeing an object (Cardini, Longo, & Haggard, 2011). Furthermore, several forms of chronic pain are associated with reduced inhibition in sensorimotor cortex (Eisenberg et al., 2005; M. Lenz et al., 2011; Schwenkreis et al., 2003) and treatments that foster this inhibition, such as gamma-aminobutyric acid-agonistic (GABA) drugs or transcranial magnetic stimulation, are used as effective treatments for chronic pain (Canavero & Bonicalzi, 1998; Kalckert & Ehrsson, 2014a). These findings can be related to the effect of GABAergic inhibition sharpening the size of tactile receptive fields in primary somatosensory areas (Dykes, R. W., Landry, Metherate, & Hicks, T. P., 1984). Studies of chronic pain typically report reduced tactile sensitivity on the painful body part (Moriwaki & Yuge, 1999; Moseley, 2008; Pleger et al., 2006) and disorganization of somatotopic maps (Flor et al., 1995; Knecht et al., 1995; Maihofner, Handwerker, Neundorfer, & Birklein, 2003; Pleger et al., 2006; Tecchio, Padua, Aprile, & Rossini, 2002; Tsao, Danneels, & Hodges, 2011). Studies on chronic pain show further that the relationship between chronic pain and body representation seems to be more complex. Chronic pain is connected to changes in the central nervous system and reorganization processes in the brain are assumed to contribute to its chronification (Flor et al., 1995; Montero-Homs, 2009; Moseley & Flor, 2012). Pain has a multifactorial nature (Butler & Moseley, 2013) and the conscious perception of pain is even more disconnected from the actual tissue damage in chronic pain than in acute pain (Moseley & Flor, 2012; Wall & McMahon, 1986). Further cognitive, affective, and behavioral factors play an important role in the development and maintenance of chronic pain (Turk & Meichenbaum, 1999). Body representation has been shown to be distorted in chronic pain (Birklein & Schlereth, 2015; Eisenberg et al., 2005; Flor, Braun, Elbert, & Birbaumer, 1997; Grüsser et al., 2001; Moseley, 2005, 2008; Tecchio et al., 2002; Trojan, Diers, Valenzuela-Moguillansky, & Torta, 2014) but the extent of this distortion seems to vary in different chronic pain syndromes (Catley, O'Connell, Berryman, Ayhan, & Moseley, 2014). When surrogate limbs are used to modify such distorted body representations, the ability of the patient to accept the surrogate limb as his/her own limb seems to play an important role. A recent study by Foell and colleagues in chronic phantom limb pain patients showed that perceived colocation of a phantom as well as a surrogate arm plays a crucial role in facilitating analgesic effects in mirror therapy (Foell, Bekrater-Bodmann, Diers, & Flor, 2014). In this study two groups of chronic phantom limb pain patients were compared: one group had the telescopic phenomenon in which the phantom arm is perceived as if it was pulled into the stump whereas the other group did not have this phenomenon. Importantly, they showed that only the group without telescopic phantom phenomenon gained from the mirror therapy (i.e., showed the analgesic effect) indicating that colocation of a phantom arm and a surrogate arm is an important factor. In line with these findings our results show that colocation of a real and a surrogate arm is also important in acute pain.

5.2.3 Reduced embodiment mediated through distance reduces predictability of heat stimulus

The perception of our own body is a flexible, multisensory construction (Kilteni, Maselli, Kording, & Slater, 2015). This construction is the basis of the principles of multisensory integration (Blanke et al., 2015), which, in the case of conflicting sensory information, results in a compromise. Such conflicting information is, for example, present during asynchronous VTS of a real and a surrogate body part, or, for example, when there is a distance between the two. Asynchronous stimulation (Botvinick & Cohen, 1998; Kilteni et al., 2015; Slater et al., 2008) and distance (Kalckert & Ehrsson, 2014b; Lloyd, 2007) have both been shown to reduce the feeling of body ownership over the surrogate body, a finding that we replicate in the present study (see questionnaire results, Figures 4.9 A and B). Interestingly, although asynchronous stimulation is associated with reduced body ownership, the analgesic effect of looking at one's embodied surrogate arm persists in the asynchronous condition under colocation. This is probably because, in VR, the colocation of the virtual arm together with being immersed in the first person perspective are strong enough input to induce ownership. This induces a large tolerance toward the asynchronous stimuli (Slater et al., 2010), which can still induce ownership and analgesia albeit to a (nonsignificant) lesser extent than synchronous stimuli. Indeed, nonsignificant differences in analgesia between synchronous and asynchronous conditions has already been reported in previous studies (Martini, Perez-Marcos, & Sanchez-Vives, 2013; Martini et al., 2014). Non-colocation (i.e. distance) as opposed to asynchronous VTS could be potentially perceived as a stronger multisensory inconsistency. Such mismatching multisensory information might lead to blurry receptive fields and body boundaries. The predictability of potential harm would be decreased when body boundaries are blurry. To cope with this uncertainty, the brain might lower the general HPT to strengthen the body's protective mechanisms. A recent study showed, which showed that perceiving strong ownership over a transparent body (ie, a body with blurry body boundaries) results in lower HPT (Martini, Kilteni, Maselli, &

Sanchez-Vives, 2015) is another example of how a decreased visualization of the body, and larger uncertainty, decreases HPT.

5.2.4 Ownership and viewpoint of the virtual body affect pain processing

Pain perception is highly subjective and it can be modulated by different bodily representations. This relation between body representations and the processing of painful stimuli was recently investigated by Romano and colleagues (Romano, Llobera, & Blanke, 2016). In their study they used changes in skin conductance as an indirect physiological measure of pain and reported lower physiological responses when the virtual body was colocated with the real body compared with when the virtual body was spatially misaligned. Our results are in line with the physiological results of this study, and we further provide evidence that can be directly linked to pain perception (Figure 4.8). Furthermore, we find that people who perceive stronger ownership over the virtual arm have also higher HPT, in other words, the more people perceive the illusion that the virtual hand is theirs the more analgesic is the effect of looking at it. This goes in line with a previous finding that looking at a virtual body reduces the skin conductance response to painful stimuli compared with looking at a virtual object. Similar to our findings, this study found a negative correlation between reported body ownership and skin conductance response.

5.2.5 Synchrony of visuotactile stimulation does not affect HPT

Body ownership over a surrogate body can be induced in different ways: Through visuotactile (Botvinick & Cohen, 1998; Slater et al., 2008), a combination of visuomotor and visuoproprioceptive (Dummer et al., 2009; Kalckert & Ehrsson, 2014a; Sanchez-Vives et al., 2010), or as in the case of colocation through visuoproprioceptive contingencies (Maselli & Slater, 2013, 2014). Whereas the rubber hand illusion is limited to visuotactile or visuomotor contingencies, all three induction methods can be executed in a virtual environment. Our findings confirm that visuotactile as well as visuoproprioceptive contingencies induce feelings of body ownership, reflected in high ratings of body ownership-related statements in the questionnaire (Figures 4.9 A and B). Synchronous VTS versus asynchronous did not result in different HPTs; however, there was an effect of virtual body ownership on HPT. Therefore, the relevant aspect is the ownership developed over the virtual body, which does not necessarily require exogenous stimulation but which can be induced by a first person perspective together with colocation

(Maselli & Slater, 2013). A similar finding has been reported by Hänsel and colleagues (Hänsel, Lenggenhager, von Känel, Curatolo, & Blanke, 2011), who studied the perception of pressure pain during an out-of-body experience.

The limitations of experiment 1 are discussed in Section 5.6.

5.3 Experiment 3: Embodiment and agency

In this study we investigated experiences of agency over the movements of an embodied virtual body induced by either two different BCI protocols or by observation of the movement. We were interested on whether BCI-induced movements lead to stronger levels of agency than mere observation of the same movement and further, whether BCI methods employing activity in sensorimotor areas would induce higher levels of agency than those employing activity in visual areas. We used questionnaires to capture several aspects of agency over the virtual movement—the sense of control, the sense of having produced a sound by pressing the button, and the sense of seeing one's own movement. We further implemented an indirect measure, in which the virtual arm threw accidentally an object off the table, and asked participants how responsible they felt for breaking the object. Additionally we measured brain responses with EEG. We hypothesized that virtual movements induced through BCI should lead to higher levels of agency than observing the movement, and that movements induced through activity in sensorimotor areas should lead to highest levels of agency, movements induced through activity in visual areas to second highest levels of agency, and simply observing a movement should lead to lowest experiences of agency. Our analysis confirmed that BCI induces higher levels of agency than movement observation. It further confirmed that SMR-based BCI protocols induce in all aspects the highest experiences of agency and movement observation the lowest. The SSVEP-based BCI protocol, however, showed an interesting pattern—while it induced elevated levels of control, it did not elevate the feeling of responsibility over the effects of the virtual body's movement compared to just observing it. Our analysis revealed further a relation between sensorimotor activity and agency. In the following we discuss possible interpretations of the obtained results.

5.3.1 Some agency related questionnaire items reflect the BCI's capacity to induce intention and others not

Voluntary actions can be described by an intention–action–outcome chain (Roskies, 2010). de Vignemont and Fourneret (2004) proposed a model for agency based on the comparator model by Frith et al. (2000). The model postulates that the sense of agency is composed by two comparator mechanisms—a matching between intended and predicted feedback creating a sense of initiation and a matching between actual and predicted sensory feedback creating a sense of one's own movement. Other studies support that when the link between intention and action is broken (through dysfrequency of action selection), participants report lower feelings of control (Chambon, Sidarus, & Haggard, 2014; Chambon, Wenke, Fleming, Prinz, & Haggard, 2013; Wenke et al., 2010). One difference between BCI and Observe conditions is that in the Observe condition participants do not have an intention, while to operate a BCI it is necessary to have an intention. Our data follows the predictions of this model in some questionnaire items, but not in others. In the questionnaire items measuring the level of control over the movement, the feeling whether they produced the sound or whether they felt it was their movement, participants constantly rated the two BCI conditions higher than the Observe condition (see Figures 4.14 and 4.16, items Control, MySound, and MyMovement). In two of these items participants gave higher ratings when inducing the movement through motor imagery compared to when looking at a blinking light (Control and MySound). Interestingly when asked whether the virtual movement they saw was their movement (MyMovement item) participants gave similar ratings to MotorImagery and SSVEP conditions. One explanation for this could be that the feeling of initiating a movement is sufficient for experiencing this movement as one's own. This is however only a speculation. On the other hand the questionnaire items Responsibility and TouchedObject, which both aimed at measuring participant's feelings of responsibility over breaking the object in the virtual scenario, showed only during MotorImagery high ratings—SSVEP and Observe had similar low ratings. One possible interpretation could be that not the intention but the body ownership is the important factor when feeling responsibility over one's actions. We will discuss this in the next paragraph.

5.3.2 Only MotorImagery induces additional body ownership

It is possible to induce body ownership over a virtual arm through MotorImagery using an SMR-based BCI (Perez-Marcos et al., 2009). It has further been shown that body ownership is a necessary condition to induce illusory agency (Banakou

& Slater, 2014; Kokkinara et al., 2016). The model for self-attribution of action by de Vignemont and Fourneret (2004) postulates that self attribution of an action is based on agency and body ownership. When the attribution of an action to the self is only based on visual feedback ("I see my arm raising"), a self-identification with that action is necessary to attribute it to the self. For example when the feedback is only proprioceptive ("I feel my arm raising") such a self-identification is not necessary. Body ownership is crucial for such self-identification processes. Our findings are in line with the literature. Participants reported highest feelings of body ownership only during the MotorImagery condition while SSVEP and Observe had similarly low levels of body ownership (see Figures 4.15 and 4.16). Further participants reported in all agency related questionnaire items highest levels in the MotorImagery condition. Since in the present study self-attribution of the virtual body's movement was only based on visual feedback, the role of body ownership is crucial for attributing an action to the self (Banakou & Slater, 2014; Kokkinara et al., 2016).

Motor imagery and motor execution of the same movement are believed to activate similar neural networks (Ehrsson, Kuhtz-Buschbeck, & Forssberg, 2002; Gerardin et al., 2000; Pfurtscheller, Scherer, Muller-Putz, & Lopes da Silva, 2008). So maybe predictions of sensory feedback as proposed by the comparator model are not only made for real movement but also for imagined movement. The brain might not only predict the feedback of a planned motor action but also that of an imagined one. If this holds true, it could be an alternative explanation why all agency related questionnaire items have highest ratings in the MotorImagery condition.

5.3.3 MotorImagery but not SSVEP induces feeling of responsibility

Agency is the experience of controlling one's movements and therefore events in the outside world (Haggard & Tsakiris, 2009). Therefore when one is aware of one's actions one should also have a feeling of responsibility for events in the outside world caused by those actions. Based on this we captured different aspects of agency with our questionnaire items—some focused on control over the movement (Control), the feeling whether this movement was one's own movement (MyMovement), or whether participants felt they produced a sound (MySound), while others focused on responsibility for having broken a virtual object (TouchedObject and Responsibility; see also Table 3.3). We expected these items to reflect similar patterns, that is both SSVEP and MotorImagery should have higher ratings than Observe because participants can control the arm movement through the BCI, and MotorImagery should have higher ratings than SSVEP because imagining the movement before seeing it being performed should lead to a prediction of the expected sensory feedback which influences agency ratings (Frith et al., 2000). We found this pattern for Control, MySound, and MyMovement ratings but not for responsibility related ratings. When it comes to responsibility only MotorImagery led to high responsibility ratings—SSVEP did not differ from Observation. Further during the MotorImagery condition the desynchronization of the sensorimotor rhythm was related to reports of responsibility. The more desynchronized sensorimotor areas were (i.e. more activated), the more participants felt responsible for breaking the virtual object. Interestingly in the SSVEP condition there was a reverse relationship between desynchronization of sensorimotor rhythm and having produced the sound related to the button press. The less desynchronized the sensorimotor rhythm was during the SSVEP condition (i.e. less activated), the more participants felt they produced the sound.

One explanation for this could be that feeling responsible over an action's consequences is a "higher concept" of agency than feeling control over the action or its outcome. Maybe higher levels of body ownership are necessary to induce feelings of responsibility, meaning that high levels of body ownership would drive the perceived levels of agency. Indeed, a close connection between agency and body ownership has been proposed by several authors (de Vignemont & Fourneret, 2004; Haggard, 2017; Hara et al., 2016; Tsakiris, Prabhu, & Haggard, 2006), however it is not clear whether this relationship is additive or whether the two concepts are independent (Tsakiris, 2015).

Another explanation could be that the SMR-based BCI protocol itself allows participants to focus more on their body than the SSVEP-based BCI. Therefore we kept the preparation phase of the experiment as similar as possible between the three experimental conditions. Participants were instructed in all three conditions to look at the button to which the virtual arm was supposed to move. During motor imagery they additionally imagined the movement, during SSVEP they concentrated on the flickering light of the button, and during Observe they just looked at that button. Hence, when imagining the arm movement the attention is already at the body while in the SSVEP condition it is at the flickering light. However, participants could not trigger a light by just looking there they had to concentrate on the flickering light and therefore wanted to make the virtual arm move.

The difference between responsibility ratings in the MotorImagery and the SSVEP condition have implications on questions of responsibility over devices controlled through BCI. Our data showed that in order to have high levels of responsibility, one needs to have an intention and a motor plan. Further research needs to resolve whether prolonged use of BCI protocols that do not create a motor plan, as the SSVEP-based BCI, can induce feelings of responsibility.

5.3.4 Accuracy and attribution of other movements to the observed one cannot explain agency ratings

BCI methods depend on accuracy in order to produce agency. For this reason we included only participants in the analysis that achieved an accuracy rate of 75% or higher in both BCI methods. Indeed a simulation study on how BCI accuracy influences the subjective feeling of control showed that for accuracies between 50% and 75% there is a strong linear relationship between the two variables—the higher the accuracy the more control participants experienced. Above 75% they observed a saturation effect meaning that higher levels of accuracy result in only minor improvements of control (Fard & Grosse-Wentrup, n.d.). Our data showed a relationship between accuracy and subjective feeling of control for the MotorImagery condition but not for the SSVEP condition (see Figure 4.12 A). Our data showed further, higher accuracy ratings during the SSVEP compared to the MotorImagery condition (see Figure 4.10). Thus, BCI accuracy alone cannot explain the agency ratings. One explanation for the relationship between accuracy and feeling of control during the MotorImagery condition could be, that when body ownership is involved as in our case, the relationship between accuracy and control only holds true when body ownership is high. Indeed, body ownership was higher during MotorImagery than during SSVEP conditions, the latter were not distinguishable from Observation regarding body ownership (see Figure 4.16).

Our analysis further shows that the attribution of eye movement and subconscious arm activity could not explain the obtained reports of agency.

5.3.5 No modulations of ERP components previously associated with agency

ERP components have been previously studied in VR (Gonzalez-Franco et al., 2014; Padrao, Gonzalez-Franco, Sanchez-Vives, Slater, & Rodriguez-Fornells, 2015). In the auditory domain the N100 ERP is an electrophysiological marker for sensory attenuation (Baess, Horvath, Jacobsen, & Schroger, 2011; Baess et al., 2008;

Hazemann, Audin, & Lille, 1975; Martikainen, Kaneko, & Hari, 2005; McCarthy & Donchin, 1976; Schafer & Marcus, 1973). N100 deflections to self-produced tones are attenuated compared to externally produced tones. These deflections occur independent of the perception of agency (Timm et al., 2016). Agency however has been related to the auditory N100-P200 complex or the P300a. Voluntary produced tones lead to attenuations of the auditory N100-P200 peak-to-peak amplitude compared to similar involuntary produced tones (Timm et al., 2014). Further, subjective reports of agency have been related to attenuation of the auditory P200 (Timm et al., 2016) or P300a (Kühn et al., 2011). We looked at both, N100–P200 peak-to-peak amplitudes and the P300 in order to see if illusory agency over a movement that produces a tone leads to similar attenuation effects. We did not find such attenuation effects neither in the N100–P200 peak-to-peak amplitude nor in the P300 amplitude. It is although not so straight forward to conclude that these attenuation processes do not happen in case of illusory agency. There are several reasons why we might not have captured this effect. One of them might be that the Observe condition itself already induced some level of agency. This might be due to expectation effects since participants knew in each Observe trial that the arm would move and to which button it would move. This together with the feeling of body ownership over the virtual body might have induced some degree of uncertainty whether participants did the virtual movement or not (see Figures 4.15 and 4.16). If illusory agency affects these ERP components this might have also influenced the amplitude during the Observe condition leading to already reduced amplitudes in this condition and therefore no significant differences between conditions. Indeed, when looking at the ERP-plot in Figure 4.21 the deflections of N100 and P200 are really small compared to previous studies (Timm et al., 2014, 2016).

We further looked at deflections of the P300a component. Participants did not show an attenuation effect in conditions with higher levels of agency. Instead we found amplified P300 amplitudes for both BCI conditions. In an oddball task a P300 is elicited to a deviant stimulus (Polich, 2007; Polich & Kok, 1995). Since BCI accuracy rates were at 91 % in the SSVEP and 87 % in the MotorImagery condition, one could understand these conditions also as oddball paradigms, which could explain why they elicited higher P300 amplitudes.

The limitations of experiment 1 are discussed in Section 5.6.

5.4 Use of virtual reality for therapeutic applications

VR has been investigated and evaluated as assessment tool in neuropsychological practice (see Laver, George, Thomas, Deutsch, & Crotty, 2012), in sensorimotor rehabilitation after stroke (Fluet & Deutsch, 2013; Henderson, Korner-Bitensky, & Levin, 2007; Lalor et al., 2005; Laver et al., 2012; Merians et al., 2002), and in pain management (Hoffman et al., 2011; Rutter, Dahlquist, & Weiss, 2009). The following section discusses how the knowledge obtained from the studies in this thesis could contribute to therapeutic applications in VR.

5.4.1 Virtual reality in pain treatment

In pain management VR has been effectively used for its power to draw attention away from pain (for example Hoffman et al., 2008 or Rutter et al., 2009). However, in the second experiment of this thesis we show that the usefulness of VR in pain management goes beyond mere distraction processes. We showed in this study that looking at an embodied virtual arm in VR can be analgesic when real and virtual arm are colocated (Nierula et al., 2017). Other studies investigating the analgesic effect of virtual body ownership show that the color of a virtual body that is attributed to oneself influences this effect; pain stimuli on a red-colored virtual arm are perceived as more painful than on a normal- or bluish-colored arm (Martini et al., 2013). VR has significant potential to take advantage of such body-related top-down modulations on pain perception. Further, in a virtual environment it is relatively easy to change the properties of a virtual body, so it is simple to combine different factores that influence pain perception. For example, one could imagine that for high levels of acute pain the focus might be more on distraction, while for certain chronic pain patients body-related modulations on pain perception could be more helpful. On the other hand out-of-body illusions have been shown to have analgesic effects in chronic pain patients (Pamment & Aspell, 2017). The relation between body representation and chronic pain is very complex and needs further investigation. One problem is that in many states of chronic pain the body representation is disrupted (Trojan et al., 2014), including complex regional pain syndrome (Birklein & Schlereth, 2015; Moseley, 2005), chronic phantom limb pain (Grüsser et al., 2001), and chronic back pain (Flor et al., 1997; Moseley, 2008). Therefore, treatments such as mirror therapy lose their analgesic effect in patients with strong distortions of the body representation as for example in the telescopic phenomenon (Foell et al., 2014).

5.4.2 Motor imagery and motor observation in virtual environments

There are several ways in which VR could support motor rehabilitation; here we will focus on two: motor observation and motor imagery. The following section will give a brief overview on the state of research in these fields and will finish with the contributions of experiment 3 to the therapeutic use of motor imagery and motor observation in VR.

Human actions are assumed to have an overt and a covert state (Jeannerod, 2001). These two states differ in their behavioral outcome, that is whether the action is performed or not. In this sense, motor execution is an overt state, while motor observation and motor imagery are covert states.

Motor observation. Overt and covert states are assumed to engage similar neuronal circuits—this was first demonstrated in the macaque monkey for *motor observation* and motor execution. A specific set of neurons in area F5 was activated when the monkey performed a goal directed action with its hand and when it observed another monkey (or a human) performing a similar action (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). This set of neurons was later named the mirror neuron system (MNS; Rizzolatti & Craighero, 2004). A similar system was later found in humans (Hari et al., 1998; Rizzolatti & Craighero, 2004; Tremblay et al., 2004). The human MNS is active during motor observation, motor imagery, contributes to imitation (Iacoboni et al., 1999) and has been assumed to be involved in skill acquisition (Buccino, Solodkin, & Small, 2006).

Motor imagery. Similarities between motor imagery and motor execution indicate also that our action system is not only engaged in overt but also in covert actions. For example, it has been demonstrated that imagining a movement takes the same time as actually performing that movement (Decety, Jeannerod, & Prablanc, 1989; Parsons, 1994, 2001). It is therefore assumed that imagining a movement simulates performing that movement (Jeannerod, 2001). Strong evidence comes also from neuroimaging studies using fMRI, which show that motor execution and motor imagery of the same movement activate overlapping neural networks (Ehrsson et al., 2002; Gerardin et al., 2000; Pfurtscheller et al., 2008).

But how could covert states of actions be useful for motor rehabilitation? Several studies show that covert states have a positive impact on motor learning. As before described, during motor observation the MNS may directly match the observed action onto an internal motor representation of that action. This mechanism has been proposed to be the underlying mechanism for human imitation (Iacoboni et al., 1999), which has a central role in learning new motor skills (Iacoboni et al., 1999; Piaget, 1952). Motor imagery plays also an important role in motor learning. Several studies demonstrate that motor imagery training improves motor learning compared to no training (Feltz & Landers, 1983; Mulder, Zijlstra, Zijlstra, & Hochstenbach, 2004; Pascual-Leone et al., 1995) and increases muscle strength (Reiser, Büsch, & Munzert, 2011; Yue & Cole, 1992). However, in order to be effective, representations of a movement must exist during motor imagery (Mulder et al., 2004), meaning it is important imagining the movement's kinesthetic aspects rather than the visual ones. Comparing action observation with motor imagery Gatti et al. (2013) found that action observation is a better strategy for learning a novel complex motor task in the early phase of motor learning. However, the relationship between observational learning and imitation performance might be moderated by the imagery abilities of the person (Lawrence, Callow, & Roberts, 2013).

Taken together both, motor imagery and action observation, seem to have an important role in motor learning and both have been suggested as promising interventions for neurological rehabilitation (Buccino et al., 2006). Many existing rehabilitation concepts focus on educating compensation, that is, bypassing the affected brain areas in order to achieve the intended action, because it is believed to be the most effective way to achieve functional outcome. Action observation and motor imagery may instead have the capacity to cure the motor deficits (Buccino et al., 2006), at least to some degree; this process is also called remediation. If, for example, a stroke patient wants to learn to write again, the compensation approach would show him/her to use the other hand, while the remediation approach would teach him/her to write with his/her affected hand. Remediation processes are believed to add to existing therapy approaches. For example, a study with stroke patients demonstrated that action observation combined with traditional physiotherapy seems to improve motor function compared to a control group that received only physiotherapy (Ertelt et al., 2007). The study further investigated the effects of action observation by comparing pre- and post-intervention fMRI. They showed that the reorganization of motor areas in those patients was linked to recruiting a frontoparietal network similar to the MNS.

Experiment 3 in this thesis investigated the use of motor observation and motor imagery in VR. Our data showed that when controlling a movement of one's virtual body through motor imagery, people experience higher levels of body ownership and agency compared to observing the same movement, or controlling it through activity in visual areas. Our data further showed a direct relationship between the level of activity in motor areas and the feeling of responsibility for the virtual body's actions. This experiments gives first insights on how the previously introduced remediation approach (through motor imagery and motor observation) could be applied in a virtual environment in healthy humans. Motor imagery and body ownership have been shown to have overlapping brain mechanisms (Evans & Blanke, 2013) and VR-embodiment has the capacity to combine body ownership with motor imagery and imagery-related movement feedback of the body. In fact, in experiment 3 we showed that in the MotorImagery condition participants perceived higher levels of ownership over the virtual body. However, more research is needed to understand how body ownership and motor imagery influence each other. It has, for example, been demonstrated that a combination of motor imagery and motor observation leads to enhanced cortical activity compared to motor observation alone (Berends, Wolkorte, Ijzerman, & van Putten, 2013; Macuga & Frey, 2012; Nedelko, Hassa, Hamzei, Schoenfeld, & Dettmers, 2012; Villiger et al., 2013; for review see Vogt, Di Rienzo, Collet, Collins, & Guillot, 2013). Maybe body ownership could even enhance this effect. Body ownership over a virtual body that can perform movements the patient cannot perform due to injuries has a big potential in rehabilitation applications, however the mechanisms through which it can operate need to be better understood.

5.4.3 Motivational factors of virtual environments and BCI

Substantial practice in VR has been shown to result in neural reorganization and regaining of motor function (Merians et al., 2002). When combined with BCI, VR-treatments can provide direct feedback to the participant. Such feedback mediated exercises have been shown to increase patient motivation (Popović, Kostić, Rodić, & Konstantinović, 2014). The dopaminergic reward system, a system closely related to motivation, has been proposed to play a role in positive feedback (Marco-Pallarés, Müller, & Münte, 2007). However, not all participants profit from positive feedback in the context of BCI (Barbero & Grosse-Wentrup, 2010). When feedback is biased to be more positive, only participants with accuracy rates around chance level profit from this change in feedback, not those that are already capable of operating a BCI. Further studies are necessary to understand the influence of feedback on patient motivation in combined VR and BCI treatments.

5.5 Ethical questions

Besides following ethical norms when conducting experiments in VR, it is also important to be aware of further ethical issues, such as the dual use problem, the problem of giving false hope to patients, and the unclear effects of long-term immersion (Madary & Metzinger, 2016).

A problem especially in the field of rehabilitation might be that new technologies could induce expectations in patients they are not capable to meet. It is therefore important to investigate the effects of such interventions well and to communicate them with patients. It is further important to understand when a VR treatment is beneficial to the patient, when it can be a stand-alone treatment, and when it is an additional treatment to traditional therapy approaches. This is especially important to communicate with institutions paying the treatment.

immersive VR applications that make use of body ownership are mostly developed and investigated for their ability meet with the virtual representation of another person over distance, or for their therapeutic potential (Slater & Sanchez-Vives, 2016). However, these tools have also a potential use in military applications. For example they could allow interrogation procedures and torture over distance. Further, applying the techniques of embodiment to robots could be used in teleoperated weapon systems. Although researchers and engineers have normally no influence on how discoveries are used later on, it is important to be aware of them.

5.6 Limitations

5.6.1 Limitations of experiment 1

Sample size and number of stimuli Since this experiment had a rather exploratory nature and a power estimation was not possible due to lack of knowledge about effect size, we followed the sample size that is typical in this field, which is between 8–16 participants. The experiment was planned to have two recording days for each participant, however due to exclusion criteria described above only one of the two recording days could be included into analysis which had an effect on the number of stimuli given to one participant. Both the sample size included in the analysis and the number of stimuli given to each participant could explain the rather weak results of this study.

Problems in the experimental design One problem of the experimental design was that the Object condition did not work in all participants. To overcome this problem, one could present instead of the wooden stick a hand in an anatomically incorrect position—for example rotated by 180° so that the fingers are directed towards the participant's body. In addition one could introduce a distance between object and real arm which has been shown to reduce the feeling of body ownership (Kalckert & Ehrsson, 2014b; Lloyd, 2007; Nierula et al., 2017).

Further analysis steps Regarding the EEG analysis one could analyze additional bands and see if their phase is correlated with the psychophysical performance. Besides the 0.01–0.1 Hz range, ongoing oscillations have been connected to behavior in the delta (Wyart et al., 2012), alpha (Baumgarten et al., 2015, 2016; Callaway & Yeager, 1960; Drewes & VanRullen, 2011; van Erp et al., 2014), and beta band (Baumgarten et al., 2015; Drewes & VanRullen, 2011). While alpha and beta ranges seem to be more connected to cross-modal integration (van Erp et al., 2014), temporal discrimination (Baumgarten et al., 2015, 2016), and reaction times (Callaway & Yeager, 1960; Drewes & VanRullen, 2011), ongoing oscillations in the delta range have been shown to predict decision making (Wyart et al., 2012).

5.6.2 Limitations of experiment 2

Further control condition One limitation of experiment 2 could be that we did not include a condition in which participants looked at an object. One could argue that only if we included such a condition we can conclude that an hypoanalgesic effect of looking at one's own hand occurred in this experiment. In some studies it is necessary to replace the body by for instance a non-corporeal object which allows extracting the expected hypoalgesic effect of seeing the virtual "own" body. We think we can, however, rely on the literature (presented in the introduction chapter) that reports such analgesic effect. Importantly, in a previous experiment, conducted in our laboratory it has already been shown that the vision of the avatar's body can be analgesic when the virtual body is felt as own (Martini et al., 2014). The present study, however, aimed at shedding light to an ongoing dispute in the literature as explained in the introduction of this thesis. This dispute is regarding whether the analgesic effect of looking at one's own hand is also present when looking at an illusory owned hand during the rubber hand illusion. Some studies found an analgesic effect during the rubber hand illusion while others did not (explained in detail in the introduction). In the present experiment we compared seeing the real arm to seeing the virtual arm in two different conditions and show in Figure 4.8 that confidence intervals in the colocation conditions clearly include the baseline (that is, when participants look at their real hand, resembled by the 0-line). Therefore we think our experimental design allows us to conclude that seeing the virtual co-located arm is the same as seeing the real colocated arm. The whole point of our experimental design is to see if seeing the virtual colocated arm is the same as seeing the real arm, and to explain the effect that the rubber hand illusion has been found by some not to be analgesic.

Multiple measures of HPT Another limitation of experiment 2 is that when taking multiple measures of HPT, these measures could be influenced by temporal effects. However, the advantage of taking multiple measures instead of only one single measure is that the mean of multiple measures will be more accurate than any of the single measures. This approach combined with randomizing or balancing the order of conditions allowed us to overcome this limitation; we further stick with the standards applied in other relevant studies in using this approach (for example, Cardini et al., 2011; Diers, Löffler, Zieglgansberger, & Trojan, 2016; Diers et al., 2013; Mancini et al., 2011; Osumi, Imai, Ueta, Nobusako, & Morioka, 2014; Romano, Pfeiffer, Maravita, & Blanke, 2014). Figure B.5 displays the individual responses of the 19 participants in each experimental condition, including the baseline. The mean values do not follow a linear trend of time, thus showing that the measure of heat pain threshold was not affected by the number of repetitions. Thus, any effect of time between conditions was canceled out by counterbalancing the order of conditions across participants.

5.6.3 Limitations of experiment 3

One limitation of experiment 3 is, that the ERP response to the tone, that participants heard when the virtual body pressed the button, might have been disturbed by other processes. Several studies showed diminished ERP responses in conditions with agency compared to conditions with no agency (Kühn et al., 2011; Timm et al., 2014, 2016). One difference that might have influenced the ERP response in our study could be, that we investigated illusory agency. It has been shown, that illusory agency can be induced over an action of a surrogate body, when people perceive strong body ownership over that body (Banakou & Slater, 2014; Kokkinara et al., 2016). So in comparison to other experiments, participants did not move in our study. It is not clear, how this could have influenced the the ERP response. Further, when looking at the BCI-feedback as a stimulus, the series of feedback in one condition could be seen as an oddball paradigm, in which the typical stimulus is seeing the arm movement and the deviant stimulus is not seeing the arm movement and instead hearing an error sound. Such oddball paradigms typically produce a P300 ERP-response (Polich, 2007; Polich & Kok, 1995), which we also saw in our data. It is, however, not clear how the production of a P300 response influences the typical ERP response to a tone. Therefore, more studies are necessary to investigate the connection between ERP responses and illusory agency.

5.7 Future directions

Motor imagery, motor observation, body ownership, and agency have a lot of potential in rehabilitation. However, how their underlying mechanisms influence each other when combining them has not been studied much, especially when combining body ownership or agency with motor imagery, motor observation, or both. Understanding under which conditions body ownership and agency could contribute to the remediating effects of motor observation and motor imagery is an important future direction in VR-embodiment.

Chapter 6

Conclusions

1. When feeling **body ownership** over a virtual body, one can apply a visual and a tactile stimulus at corresponding locations on the virtual and the real body. Our data shows, that when visual and tactile stimulus are applied with a temporal offset, body ownership fosters the binding of the two stimuli in time.

2. Some participants who experienced virtual body ownership often reported fluctuations over time in their feeling of body ownership. Our experiment results suggest that body ownership fluctuates over time, which might reflect fluctuations in multisensory integration.

3. With our sample size we have not been able to detect a direct relationship between spontaneous infra-slow fluctuations in the range of 0.01–0.1 Hz and body ownership fluctuations. Further studies are needed.

4. Looking at a colocated embodied virtual hand has similar analgesic effects as looking at one's real hand.

5. When introducing a distance of 30 cm between real and surrogate arm, the analgesic effect induced by looking at one's own hand, disappears.

6. There have been contradictory findings in the literature regarding whether looking at an "owned" rubber hand is analgesic. Our data attributes these discrepancies to the distance between the real and the rubber hand, demonstrating that colocation of real and surrogate hand is important to obtain analgesia.

7. Our results conclude that when using virtual reality tools for pain management it is important to colocate real and surrogate limb in such applications.

8. **Agency** over our own movements gives us a sense of control and responsibility of our own actions. An embodied virtual body can be moved by

means of a brain-computer interface (BCI). The sense of control or agency over such BCI-induced movements is higher compared to observing the same movements.

9. The level of agency over BCI-induced movements of an embodied virtual arm depends on the BCI paradigm. SMR-based methods, in which the participant has to imagine the movement, lead to higher levels of agency than SSVEP-based methods, in which the participant needs to focus at a blinking light.

10. In our experimental design, some actions performed by the virtual body led to unintended effects in the environment, in this case breaking a virtual object. Only SMR-based BCI paradigms produced a high sense of responsibility over such unintended actions while observation or SSVEP did not.

11. In VR it is possible to feel body ownership over a virtual body, thorough colocation between virtual and real body. Only SMR-based BCI paradigms can enhance this body ownership, not SSVEP-based ones.

12. Our results conclude that SMR-based BCI methods have a potential in VR-rehabilitation because of their ability to induce higher feelings of body ownership and agency.

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Appendix A

Supplementary material of experiment 1

A.1 Consent form and questionnaire

A.1.1 Consent form

The following figures A.1 and A.2 display the consent form, which was read and signed by each participant before participating in the experiment. The original size of each page was DIN A4.

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Appendix 2

INFORMACIÓN PARA LOS PARTICIPANTES

Este experimento forma parte de una larga serie de estudios para comprender las respuestas de la gente dentro de un entorno virtual. Este estudio ha sido aprobado por el Comité Ético de Investigación Clínica de la Corporación Sanitaria Hospital Clínic de Barcelona.

Por favor lea esta información y siéntase libre de preguntar cualquier duda a los experimentadores. Sin embargo los aspectos específicos que buscamos con este estudio no podrán ser comentados con usted antes de terminar la sesión. Intentaremos que el conjunto del estudio nos lleve el menor tiempo posible.

Por razones de seguridad, mujeres embarazadas, pacientes con epilepsia y personas que vayan a conducir coches/motos/bicicletas o a trabajar con maquinaria compleja o peligrosa inmediatamente después del experimento, no pueden participar en este estudio. También personas que han tomado medicamentes psicoactivos, no pueden participar en este estudio.

Usted va a usar un sistema de Realidad Virtual (RV) compuesto por un sistema de posicionamiento y unas gafas o casco de RV. El equipo de visión puede ser usado sobre sus propias gafas. Además del equipo usado para navegar por el entorno virtual, y dependiendo de la prueba específica que le sea asignada, es posible que le coloquemos un equipo fisiológico diseñado para medir su actividad muscular, cerebral, cardiaca, o corriente galvánica de la piel, todas ellas respuestas que usted tendrá al navegar en un entorno virtual. Estos valores fisiológicos están medidos por medio de electrodos que solo captan la actividad fisiológica y por tanto nunca procuran algún tipo de estimulación.

Usted podrá también recibir una serie de estímulos de tacto (por ej. de vibración) durante algunas fases del estudio. Los estímulos son inocuos y solo tienen la función de dar un feedback táctil.

IMPORTANTE

Cuando la gente usa un sistema de RV, algunas personas podrían experimentar cierta sensación de mareo o estrés. Algunos tipos de video podrían llegar a generar un episodio epiléptico, como se ha informado que ocurre en algunos videojuegos.

La información que hemos reunido nunca será mostrada de forma que pueda usted ser identificado individualmente. La información será transmitida de forma agrupada y estadística. Si se escribe un artículo de investigación, podría emplearse algún comentario verbal que usted haya hecho, aunque siempre de forma anónima.

FIGURE A.1: Consent form page 1 of experiment 1.

Por favor tenga en cuenta que si en algún momento usted no desea continuar participando en el experimento, recuerde que es libre de salir sin tener que dar explicaciones.

Procedimientos que cada participante deberá comprender y aceptar:

- Se le pide que lea, comprenda y firme su consentimiento informado. Si usted lo firma, el estudio contará con su participación. Recuerde que usted puede abandonar dicho estudio en cualquier momento sin tener que dar razón alguna para ello.
- Apague el móvil antes de usar el equipo.
- Durante la prueba se le puede pedir que responda a un número de preguntas de manera verbal o sobre papel.
- A usted se le podrán colocar una serie de sensores para medir su actividad muscular, cerebral, cardiaca, respiratoria y corriente galvánica de la piel.
- Usted se moverá en un entorno virtual usando un casco de realidad virtual o unas gafas estereoscópicas para ver en 3D en una pantalla.
- En la pantalla verá un cuerpo virtual. Es posible que se le pida concentrar su atención en alguna parte durante unos minutos o realizar una tarea sencilla (por ejemplo, mirar hacia un punto del campo visivo, o pensar con mover el brazo, etc.).
- Al acabar el experimento tendrá una conversación con el experimentador sobre su experiencia, mientras se revisa la grabación realizada. Durante todo este tiempo, usted puede ser grabado en video y audio.
- Finalmente deberá contestar a un breve formulario.
- Por favor, no comente el estudio con otros durante los próximos 3 meses.
- Se pagarán de 5 a 40 euros por su participación dependiendo de la prueba específica que le sea asignada.

Si tiene alguna cuestión relacionada con el estudio, por favor contacte con nosotros:

- Dr. Antonella Maselli (antinulla@gmail.com)
- Birgit Nierula (bnierula@gmail.com)
- Dr. Maria V. Sánchez-Vives (msanche3@clinic.ub.es)
- Dr. Mel Slater (melslater@ub.edu)

FIGURE A.2: Consent form page 2 of experiment 1.

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CONSENTIMIENTO INFORMADO DEL PARTICIPANTE

El voluntario deberá leer y contestar cuidadosamente las siguientes preguntas:

¿Ha leído toda la información sobre este estudio?	**SI**	**NO**
¿Ha tenido la oportunidad de preguntar y comentar cuestiones sobre el estudio?	**SI**	**NO**
¿Ha recibido respuestas satisfactorias a todas las cuestiones?	**SI**	**NO**
¿Ha recibido la suficiente información sobre este estudio?	**SI**	**NO**
¿Ha comprendido que usted es libre de abandonar este estudio…		
• … en cualquier momento?	**SI**	**NO**
• … sin dar ninguna razón?	**SI**	**NO**
¿Ha comprendido y aceptado los riesgos asociados con el uso de la Realidad Virtual?	**SI**	**NO**
¿Está de acuerdo en tomar parte en este estudio?	**SI**	**NO**
¿Está de acuerdo en ser grabado en video?	**SI**	**NO**
¿Está de acuerdo en ser grabado en audio?	**SI**	**NO**
¿Está de acuerdo en ser monitorizado fisiológicamente?	**SI**	**NO**

Nombre y apellidos del investigador que le ha informado sobre el estudio (escriba siempre en MAYÚSCULAS): ………………………………………………..

Yo certifico que no tengo epilepsia y que no conduciré ni coches, ni motos, ni bicicletas, ni usaré maquinaria compleja que pueda ser peligrosa inmediatamente después de acabado el estudio.

Firma del participante: **Firma Investigador:**

Fecha: …………………… **Fecha: ……………………**

La información obtenida de su experimento nunca será publicada individualmente. Los datos serán analizados en grupos y aquellos comentarios verbales, en el caso que se publiquen, serán presentados de forma anónima.

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FIGURE A.3: Consent form page 3 of experiment 1.

A.1.2 Questionnaire

The following questions were presented to the participant in random order. The questions displayed were given after the Body condition. The questions in the Object conditions said instead of virtual body (cuerpo virtual) stick on the table (palo sobre la mesa). All questions were displayed similar to the one seen in Figure A.4. If participants answered question two with a rating higher than 0 they were also asked to rate the question displayed in Figure A.4.

1. Durante toda la sesión experimental, sentí que el cuerpo virtual era mi propio cuerpo.

2. La sensación de que el cuerpo virtual era mi propio cuerpo, era a veces fuerte y otras veces débil.

3. Durante la tarea visuo-táctil me pareció que el tiempo entre el tacto y el movimiento del objeto (cilindro) no fuera constante.

4. Durante la tarea visuo-táctil parecía que los movimientos del objeto (cilindro) sucederían a veces antes, a veces después y a veces al mismo tiempo que la sensación de tacto.

5. Parecía como si tuviera dos cuerpos.

6. Durante la tarea visuo-táctil parecía que cuando el objeto (el cilindro) se movía tocaba mi dedo réal.

7. Tenía la sensación de que el cuerpo virtual se movería si yo movía mi propio brazo.

8. Durante la sesión experimental tenía la sensación de que me estaba quedando dormida.

9. Fui totalmente capaz de concentrarme en la tarea visuo-táctil durante toda la sesión experimental.

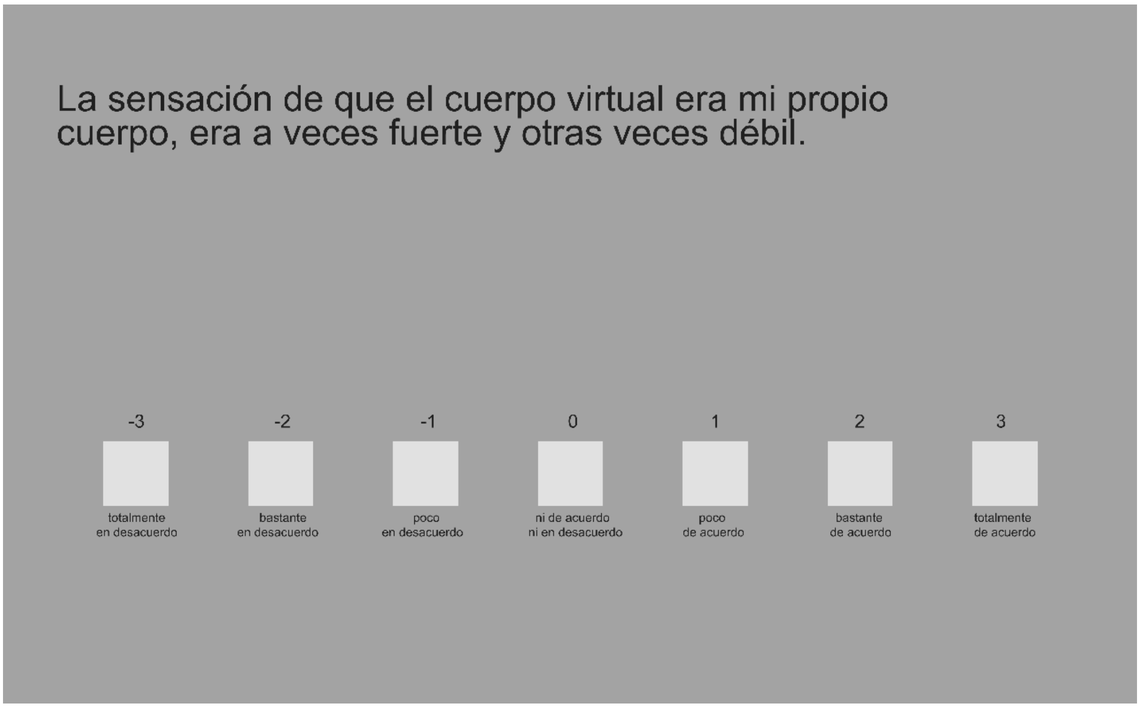

FIGURE A.4: One of the questions of the questionnaire given to participants after the Body condition experiment 1. The Likert scale was the same in all questions. Note that this question was displayed in the Body condition, in the Object condition the question would say "palo sobre la mesa" instead of "cuerpo virtual".

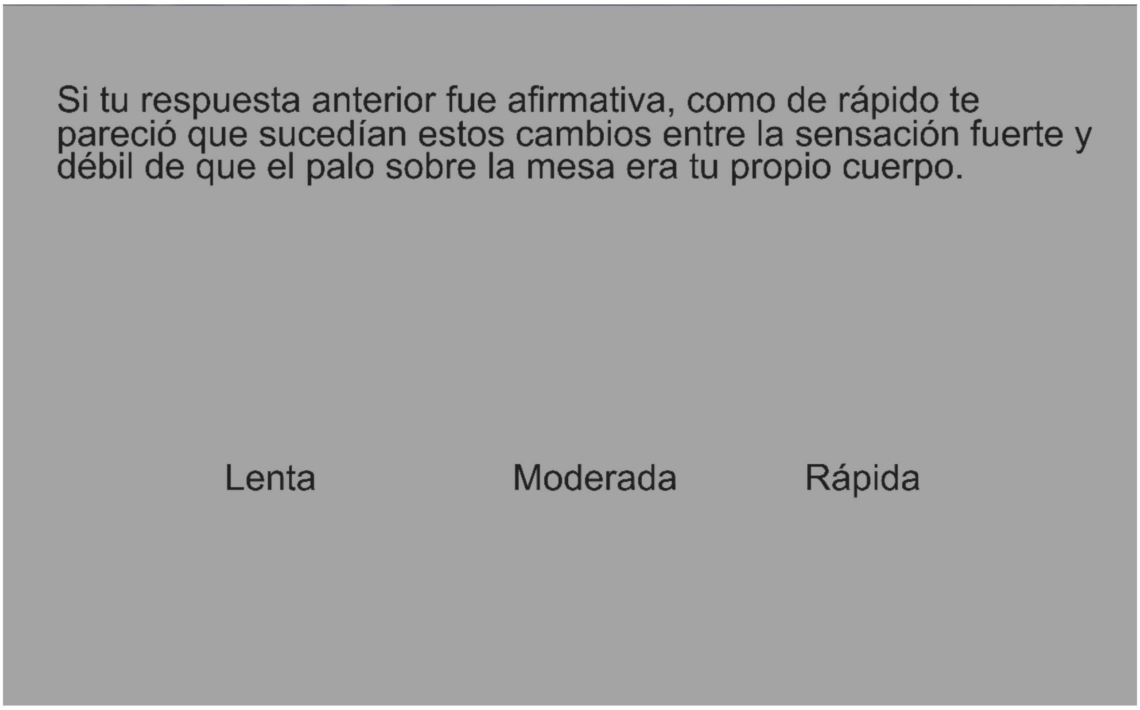

FIGURE A.5: If participants rated the question 2 higher than 0 they were given the question displayed above. Note that this question was displayed after the Object condition, for the Body condition the questionnaire would say "cuerpo virtual" instead of "palo sobre la mesa".

A.2 Individual ratings to questionnaire item MyBody

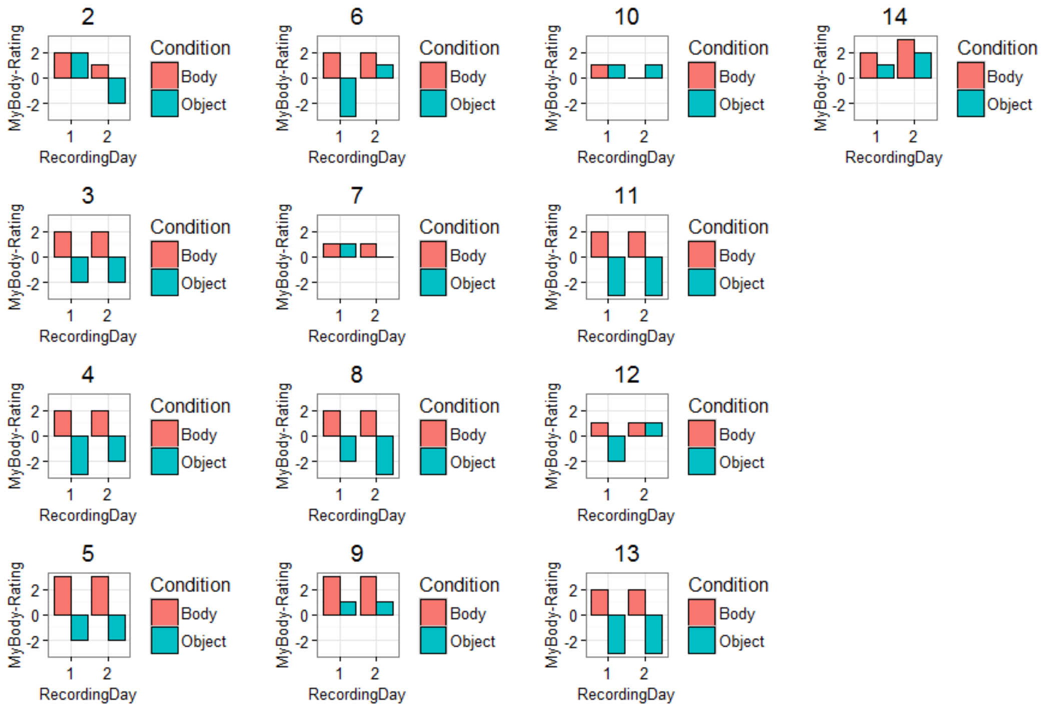

FIGURE A.6: The Effect of Condition and RecordingDay on MyBody ratings. Each graph displays the individual rating of each participant in the different experimental conditions. Numbers on top of individual graphs indicate the participant number.

A.3 Questionnaire ratings of selected participants

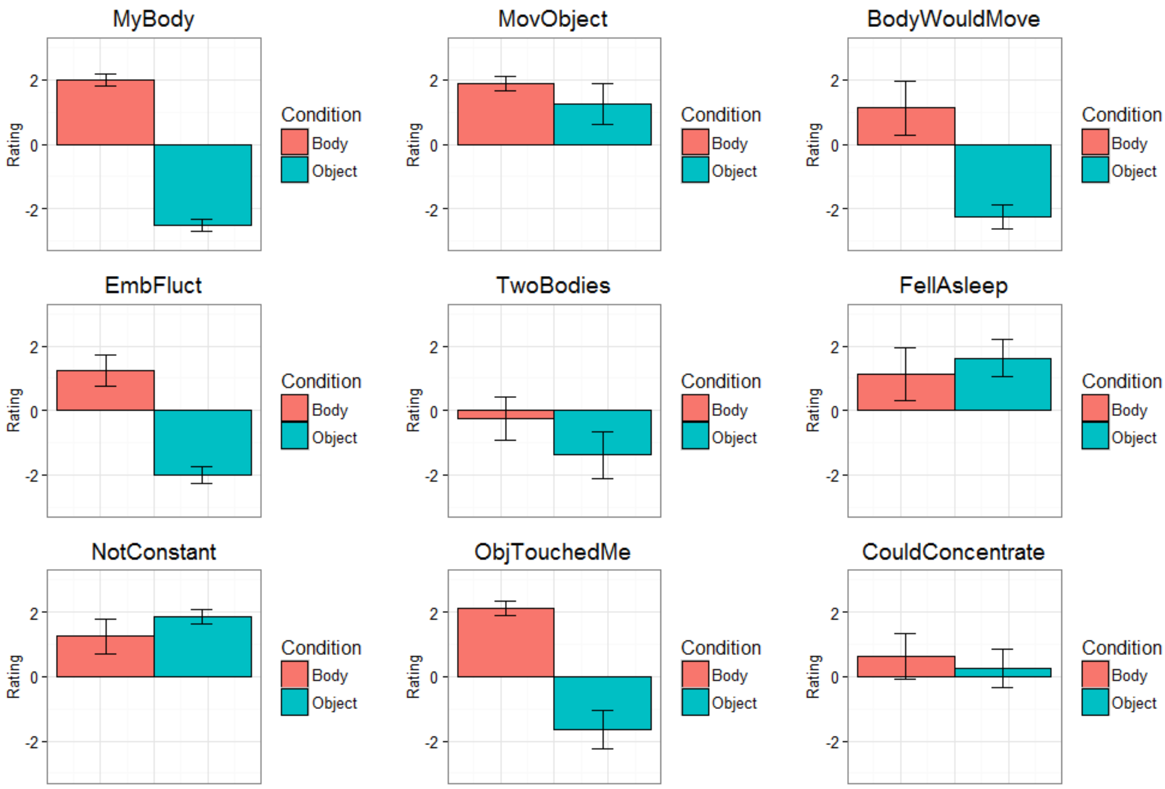

FIGURE A.7: The Effect of Condition on questionnaire ratings in selected group of participants (N = 8). Those participants that had ratings higher than 1 (Body condition) or lower than -1 (Object condition) in the MyBody item were selected (one recording day).

A.4 Correlation between ISF and behavior at selected electrodes

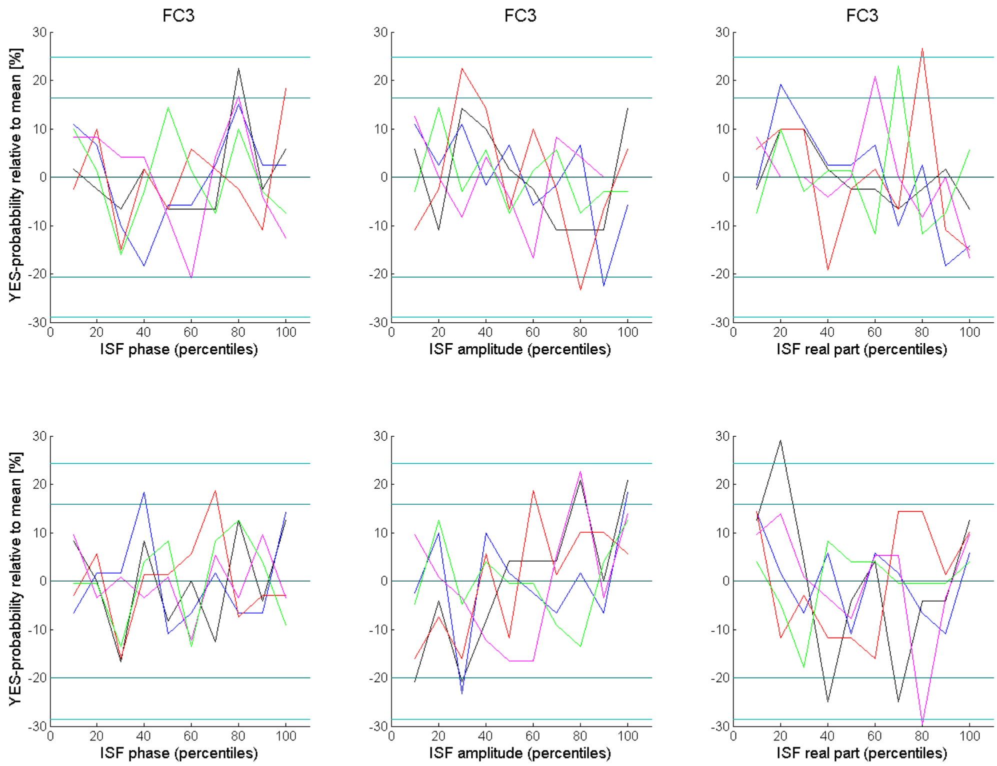

FIGURE A.8: Change in Yes-response probability as a function of phase (A), amplitude (B), and real part (C) of the ISF recorded at electrode FC3. Y-axis indicates the change in Yes-probability relative to the mean. The top row displays the Body and the bottom row the Object condition. The statistical significance of hit probability was estimated for each bin using the cumulative binominal distribution. 0.005, 0.05, 0.95, and 0.995 values are indicated by horizontal lines. The axes range from -π to π (A), from 0 to maximum amplitude (B), and from minimum to maximum of the ISF EEG (C).

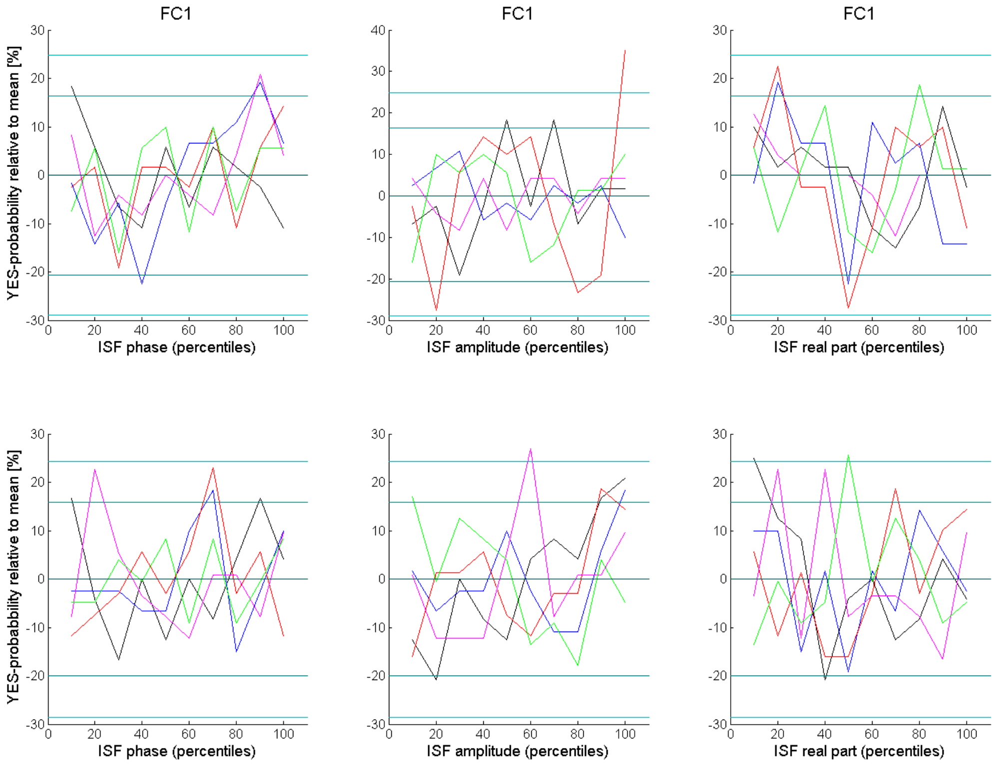

FIGURE A.9: Change in Yes-response probability as a function of phase (A), amplitude (B), and real part (C) of the ISF recorded at electrode FC1. Y-axis indicates the change in Yes-probability relative to the mean. The top row displays the Body and the bottom row the Object condition. The statistical significance of hit probability was estimated for each bin using the cumulative binominal distribution. 0.005, 0.05, 0.95, and 0.995 values are indicated by horizontal lines. The axes range from -π to π (A), from 0 to maximum amplitude (B), and from minimum to maximum of the ISF EEG (C).

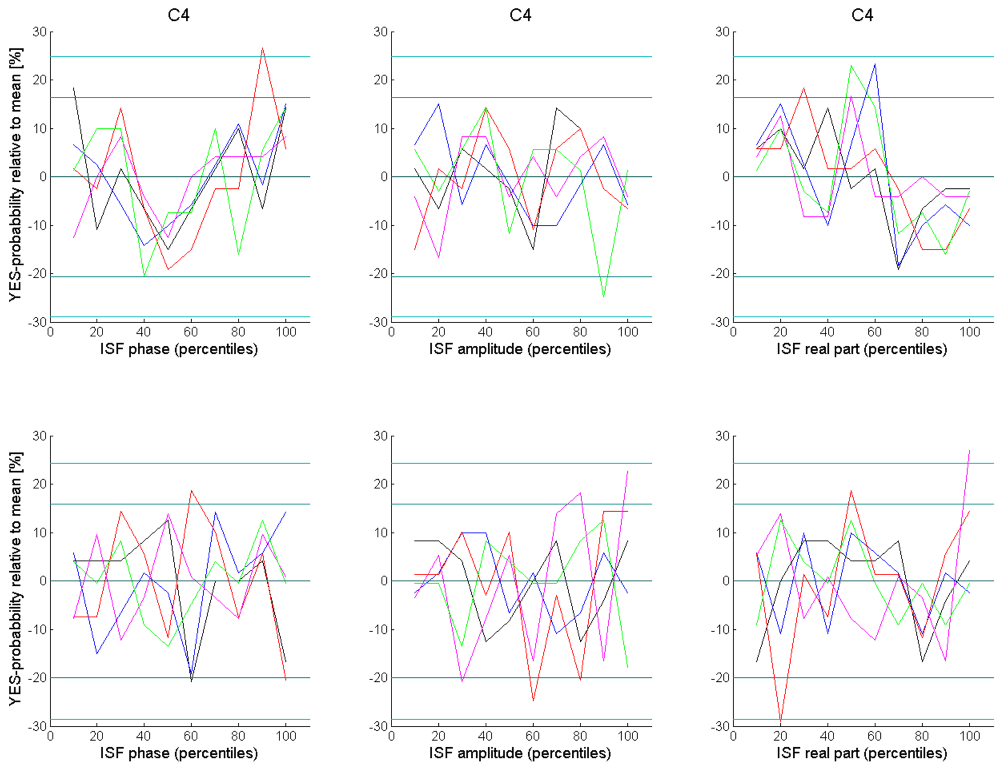

FIGURE A.10: Change in Yes-response probability as a function of phase (A), amplitude (B), and real part (C) of the ISF recorded at electrode C4. Y-axis indicates the change in Yes-probability relative to the mean. The top row displays the Body and the bottom row the Object condition. Each line color indicates the changes in Yes-response probability of one participant. The statistical significance of hit probability was estimated for each bin using the cumulative binominal distribution. 0.005, 0.05, 0.95, and 0.995 values are indicated by horizontal lines. The axes range from -π to π (A), from 0 to maximum amplitude (B), and from minimum to maximum of the ISF EEG (C).

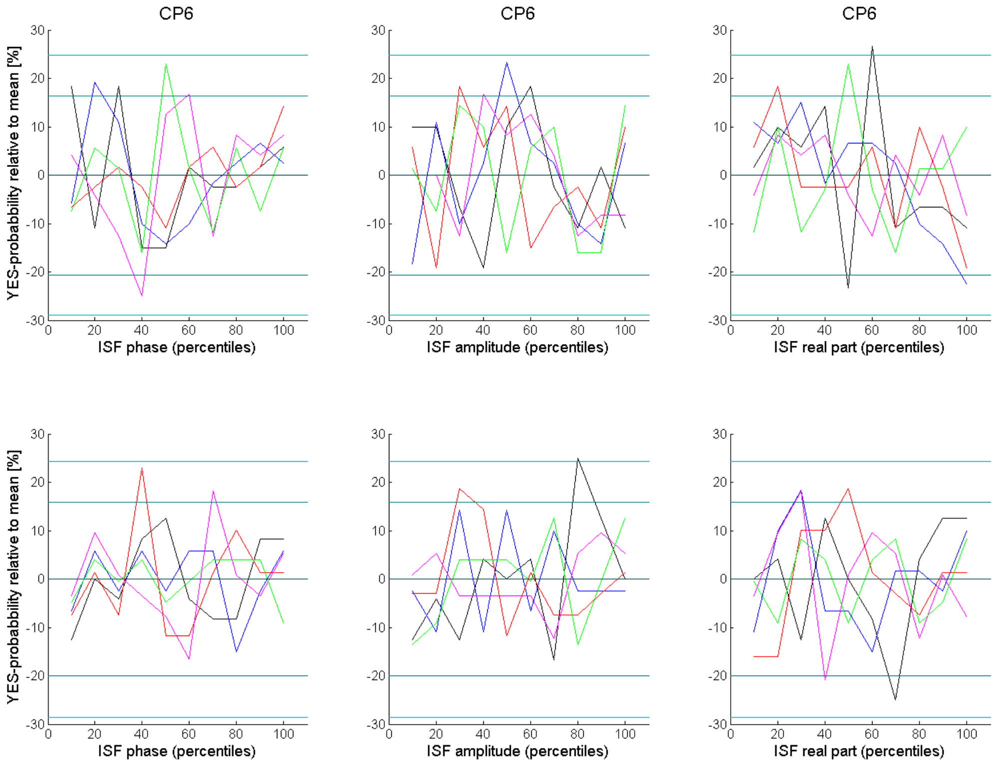

FIGURE A.11: Change in Yes-response probability as a function of phase (A), amplitude (B), and real part (C) of the ISF recorded at electrode CP6. Y-axis indicates the change in Yes-probability relative to the mean. The top row displays the Body and the bottom row the Object condition. Each line color indicates the changes in Yes-response probability of one participant. The statistical significance of hit probability was estimated for each bin using the cumulative binominal distribution. 0.005, 0.05, 0.95, and 0.995 values are indicated by horizontal lines. The axes range from -π to π (A), from 0 to maximum amplitude (B), and from minimum to maximum of the ISF EEG (C).

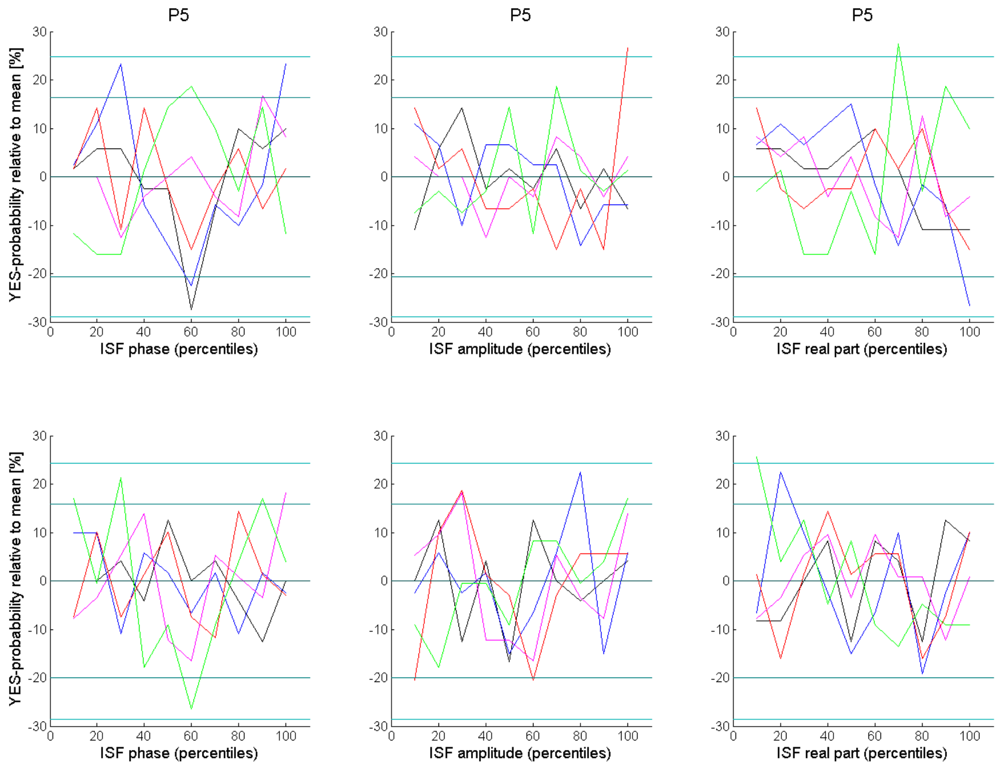

FIGURE A.12: Change in Yes-response probability as a function of phase (A), amplitude (B), and real part (C) of the ISF recorded at electrode P5. Y-axis indicates the change in Yes-probability relative to the mean. The top row displays the Body and the bottom row the Object condition. Each line color indicates the changes in Yes-response probability of one participant. The statistical significance of hit probability was estimated for each bin using the cumulative binominal distribution. 0.005, 0.05, 0.95, and 0.995 values are indicated by horizontal lines. The axes range from -π to π (A), from 0 to maximum amplitude (B), and from minimum to maximum of the ISF EEG (C).

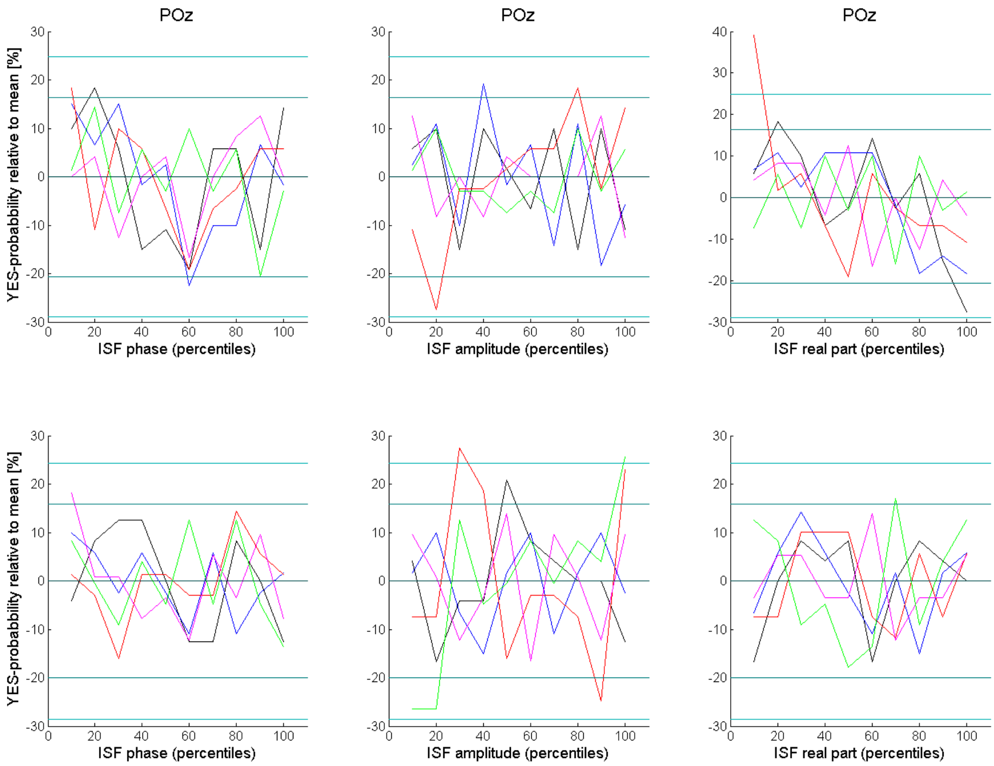

FIGURE A.13: Change in Yes-response probability as a function of phase (A), amplitude (B), and real part (C) of the ISF recorded at electrode POz. Y-axis indicates the change in Yes-probability relative to the mean. The top row displays the Body and the bottom row the Object condition. Each line color indicates the changes in Yes-response probability of one participant. The statistical significance of hit probability was estimated for each bin using the cumulative binominal distribution. 0.005, 0.05, 0.95, and 0.995 values are indicated by horizontal lines. The axes range from -π to π (A), from 0 to maximum amplitude (B), and from minimum to maximum of the ISF EEG (C).

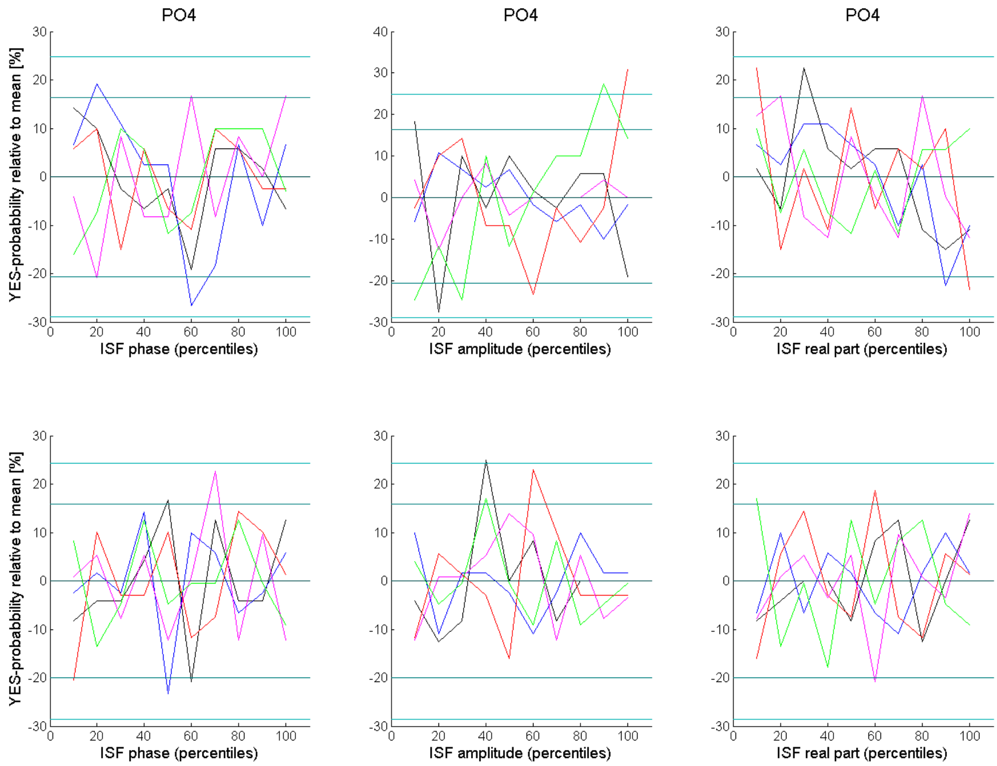

FIGURE A.14: Change in Yes-response probability as a function of phase (A), amplitude (B), and real part (C) of the ISF recorded at electrode PO4. Y-axis indicates the change in Yes-probability relative to the mean. The top row displays the Body and the bottom row the Object condition. Each line color indicates the changes in Yes-response probability of one participant. The statistical significance of hit probability was estimated for each bin using the cumulative binominal distribution. 0.005, 0.05, 0.95, and 0.995 values are indicated by horizontal lines. The axes range from -π to π (A), from 0 to maximum amplitude (B), and from minimum to maximum of the ISF EEG (C).

Appendix B

Supplementary material of experiment 2

B.1 Consent form and questionnaire

B.1.1 Consent form

The following Figures B.1–B.3 and B.2 display the consent form, which was read and signed by each participant before participating in the experiment. The original size of each page was DIN A4.

IDIBAPS BEAMING

INFORMACIÓN PARA LOS PARTICIPANTES

Este experimento forma parte de una larga serie de estudios para comprender las respuestas de la gente dentro de un entorno virtual. Este estudio ha sido aprobado por el Comité Ético de Investigación Clínica de la Corporación Sanitaria Hospital Clínic de Barcelona.

Por favor lea esta información y siéntase libre de preguntar cualquier duda a los experimentadores. Sin embargo los aspectos específicos que buscamos con este estudio no podrán ser comentados con usted antes de terminar la sesión. Intentaremos que el conjunto del estudio nos lleve el menor tiempo posible.

Por razones de seguridad, mujeres embarazadas, pacientes con epilepsia y personas que vayan a conducir coches/motos/bicicletas o a trabajar con maquinaria compleja o peligrosa inmediatamente después del experimento, no pueden participar en este estudio.

Usted va a usar un sistema de Realidad Virtual (RV) compuesto por un sistema de posicionamiento y unas gafas o casco de RV. El equipo de visión puede ser usado sobre sus propias gafas. Además del equipo usado para navegar por el entorno virtual, y dependiendo de la prueba específica que le sea asignada, es posible que le coloquemos un equipo fisiológico diseñado para medir su actividad muscular, cerebral, cardiaca, respiratoria o corriente galvánica de la piel, todas ellas respuestas que usted tendrá al navegar en un entorno virtual.

Usted recibirá una serie de estímulos térmicos (calor) durante varias fases del estudio. Usted deberá simplemente pulsar un pulsador cuando el estímulo se vuelva doloroso, para detener el estímulo. El nivel de fuerza y el número total de estímulos ha sido ajustado previamente para evitar cualquier posible inconveniente. Esta técnica estándar es utilizada en numerosos estudios clínicos internacionales.

IMPORTANTE

Cuando la gente usa un sistema de RV, algunas personas podrían experimentar cierta sensación de mareo o estrés. Algunos tipos de video podrían llegar a generar un episodio epiléptico, como se ha informado que ocurre en algunos videojuegos.

La información que hemos reunido nunca será mostrada de forma que pueda usted ser identificado individualmente. La información será transmitida de forma agrupada y estadística. Si se escribe un artículo de investigación, podría emplearse algún comentario verbal que usted haya hecho, aunque siempre de forma anónima.

Por favor tenga en cuenta que si en algún momento usted no desea continuar participando en el experimento, recuerde que es libre de salir sin tener que dar explicaciones.

1

CONTINUA →

FIGURE B.1: Consent form pages 1 of experiment 2.

IDIBAPS BEAMING

Procedimientos que cada participante deberá comprender y aceptar:

- Se le pide que lea, comprenda y firme su consentimiento informado. Si usted lo firma, el estudio contará con su participación. Recuerde que usted puede abandonar dicho estudio en cualquier momento sin tener que dar razón alguna para ello.
- Apague el móvil antes de usar el equipo.
- Durante la prueba se le puede pedir que responda a un número de preguntas de manera verbal o sobre papel.
- A usted se le podrán colocar una serie de sensores para medir su actividad muscular, cerebral, cardiaca, respiratoria y temperatura corporal.
- Usted se moverá en un entorno virtual usando un casco de realidad virtual o unas gafas estereoscópicas para ver en 3D en una pantalla. La prueba puede realizarse tanto de pie como sentado.
- En la pantalla verá un cuerpo virtual. Es posible que se le pida concentrar su atención en alguna parte durante unos minutos o realizar una tarea sencilla (por ejemplo, mover el brazo o la mano, señalar hacia un objeto, etc.).
- Al acabar el experimento tendrá una conversación con el experimentador sobre su experiencia, mientras se revisa la grabación realizada. Durante todo este tiempo, usted puede ser grabado en video y audio.
- Finalmente deberá contestar a un breve formulario. (OPCIONAL)
- Por favor, no comente el estudio con otros durante los próximos 3 meses.
- [redacted]

Si tiene alguna cuestión relacionada con el estudio, por favor contacte con nosotros:

- Dr. Matteo Martini (matteomartini1@gmail.com)
- [redacted])
- Dr. Maria V. Sánchez-Vives (msanche3@clinic.ub.es)
- [redacted])

2

FIGURE B.2: Consent form page 2 of experiment 2.

BEAMING
Being in Augmented Multi-Modal Naturally-Networked Gatherings

CONSENTIMIENTO INFORMADO DEL PARTICIPANTE

El voluntario deberá leer y contestar cuidadosamente las siguientes preguntas:

¿Ha leído toda la información sobre este estudio?	**SI**	**NO**
¿Ha tenido la oportunidad de preguntar y comentar cuestiones sobre el estudio?	**SI**	**NO**
¿Ha recibido respuestas satisfactorias a todas las cuestiones?	**SI**	**NO**
¿Ha recibido la suficiente información sobre este estudio?	**SI**	**NO**
¿Ha comprendido que usted es libre de abandonar este estudio…		
• … en cualquier momento?	**SI**	**NO**
• … sin dar ninguna razón?	**SI**	**NO**
¿Ha comprendido y aceptado los riesgos asociados con el uso de la Realidad Virtual?	**SI**	**NO**
¿Está de acuerdo en tomar parte en este estudio?	**SI**	**NO**
¿Está de acuerdo en ser monitorizado fisiológicamente?	**SI**	**NO**

Nombre y apellidos del investigador que le ha informado sobre el estudio (escriba siempre en MAYÚSCULAS): ………………………………………………...

Nombre y apellidos del participante: …………………………………………......

Yo certifico que no tengo epilepsia y que no conduciré ni coches, ni motos, ni bicicletas, ni usaré maquinaria compleja que pueda ser peligrosa inmediatamente después de acabado el estudio.

Firma del participante: **Firma Investigador:**

Fecha: …………………… **Fecha: ……………………**

FIGURE B.3: Consent form page 3 of experiment 2.

B.1.2 Questionnaire

The following seven questions were read out loud to the participant in random order.

1. Tuve la sensación de que estaba recibiendo los golpecitos en el lugar en el que se encontraban mis dedos.
2. Parecía como si el tacto que yo sentía en los dedos fuera causado por la bola que tocaba los dedos virtuales.
3. Sentía como si la mano virtual fuera mi propia mano.
4. Tenía la sensación de tener más de una mano.
5. Parecía como si los golpecitos que estaba sintiendo vinieran de algún lugar entre mi propia mano y la mano virtual.
6. Parecía como si mi mano real se volviera virtual.
7. En una escala de 1–10 cuanto fuerte tuviste la ilusión de que la mano virtual fuera tu propia mano?

B.2 Results

Pain threshold analysis: Although residuals in the mixed model used to analyze the HPT were bell shaped, they were not normal distributed ($W = 0.884$, $P < 0.0001$). A plot of the fitted values against the residuals identified 8 data points that were clear outliers (see Figure B.4). We removed these data points and reran our model. Similar as the model reported in the results section, this model shows a clear significant main effect of distance ($z = —3.03$, $P = 0.002$) and has normal distributed residuals ($W = 0.995$, $P = 0.997$), confirming that the effects in the model reported in the results section were not due to the not normal distributed residuals.

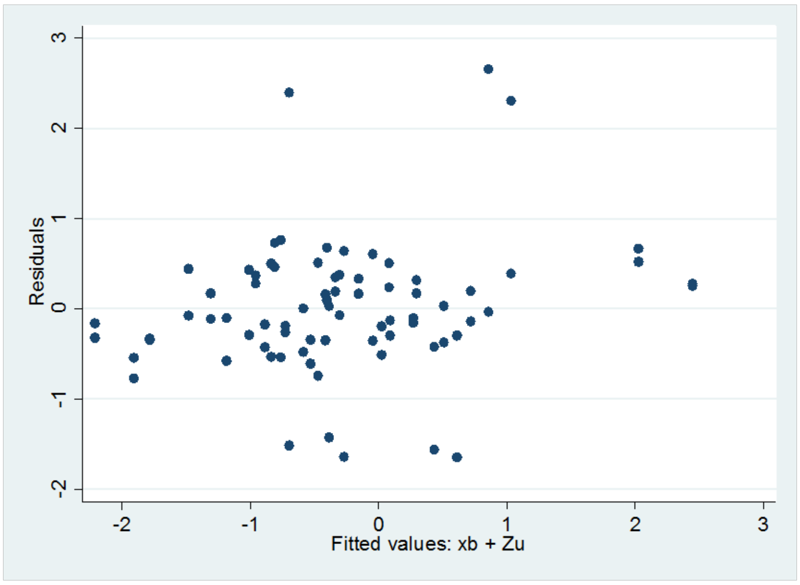

FIGURE B.4: Plot of fitted values against residuals.

There was no effect of repeated assessments of pain thresholds on the HPT measure.

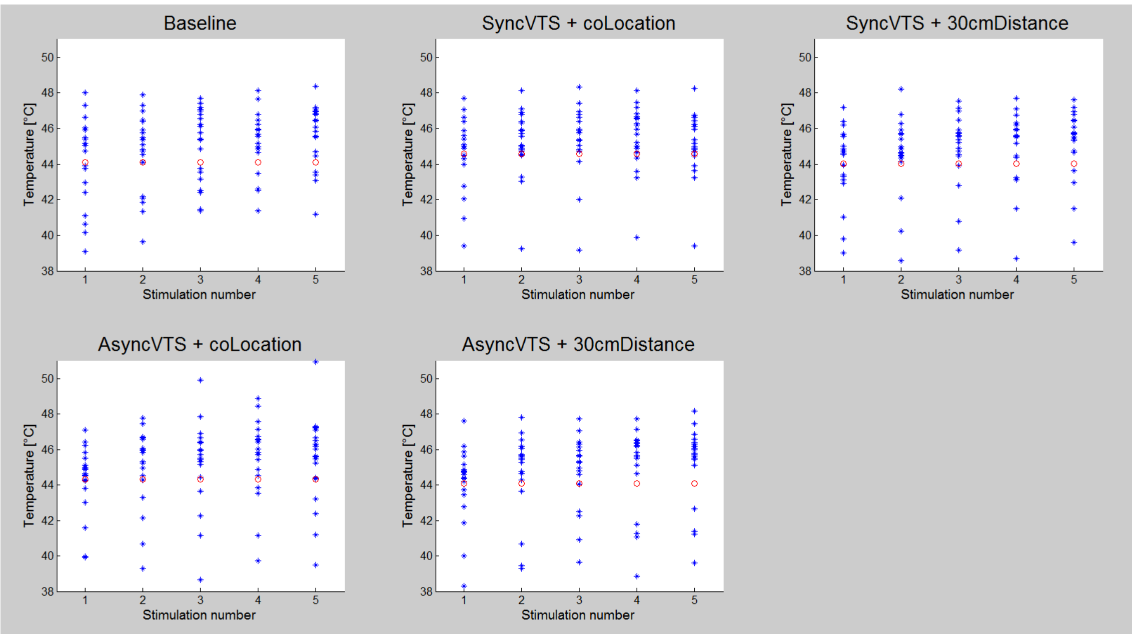

FIGURE B.5: Individual HPT responses in °C of the 19 participants in each experimental condition, including the baseline. Blue dots represent the individual responses and red circles the mean values. The mean values do not follow a linear trend of time, thus showing that the measure of heat pain threshold was not affected by the number of repetitions.

Appendix C

Supplementary material of experiment 3

C.1 SSVEP Simulink models

C.1.1 SSVEP training

Figure C.1 displays the Simulink model of the SSVEP training.

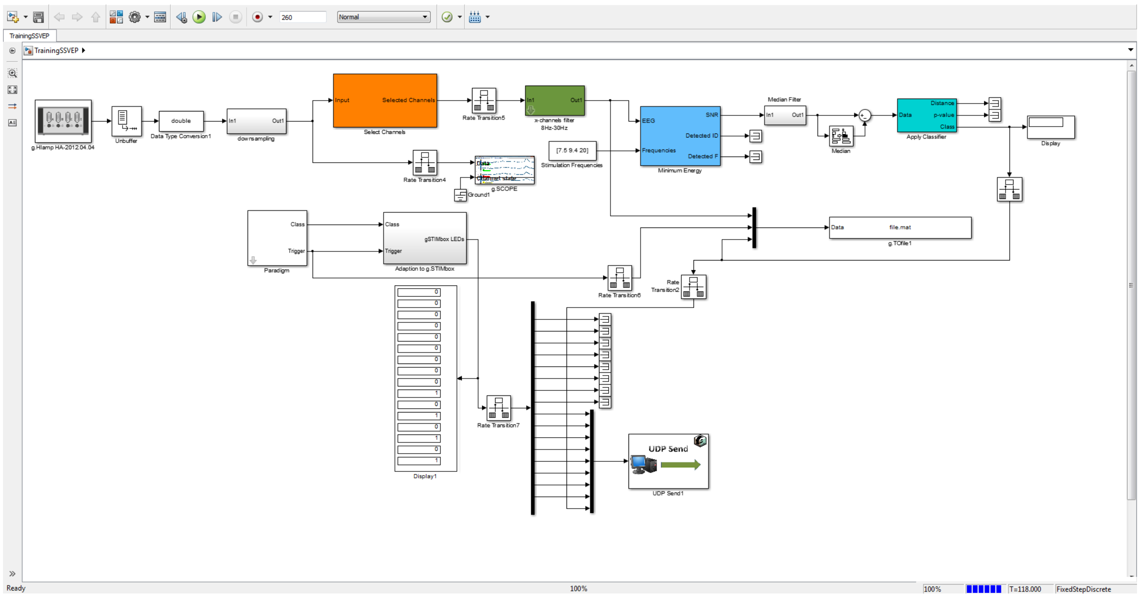

FIGURE C.1: Simulink model of SSVEP training.

C.1.2 SSVEP condition

Figure C.2 displays the Simulink model used for SSVEP training.

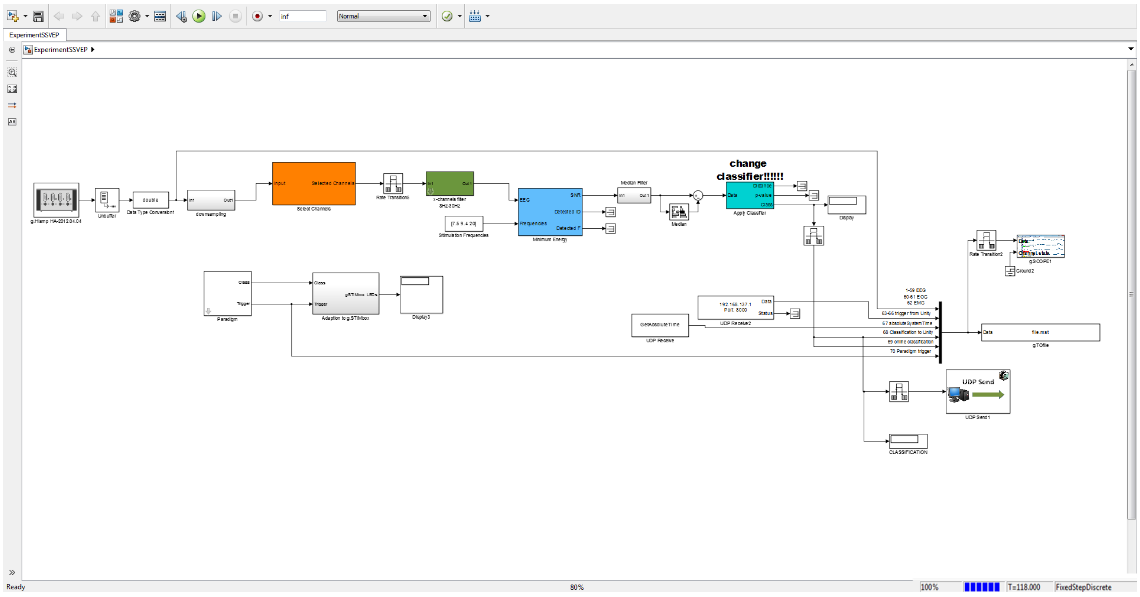

FIGURE C.2: Simulink model used for SSVEP condition.

C.2 Motor imagery Simulink models

C.2.1 MotorImagery training

Figure C.3 displays the Simulink model of the MotorImagery training.

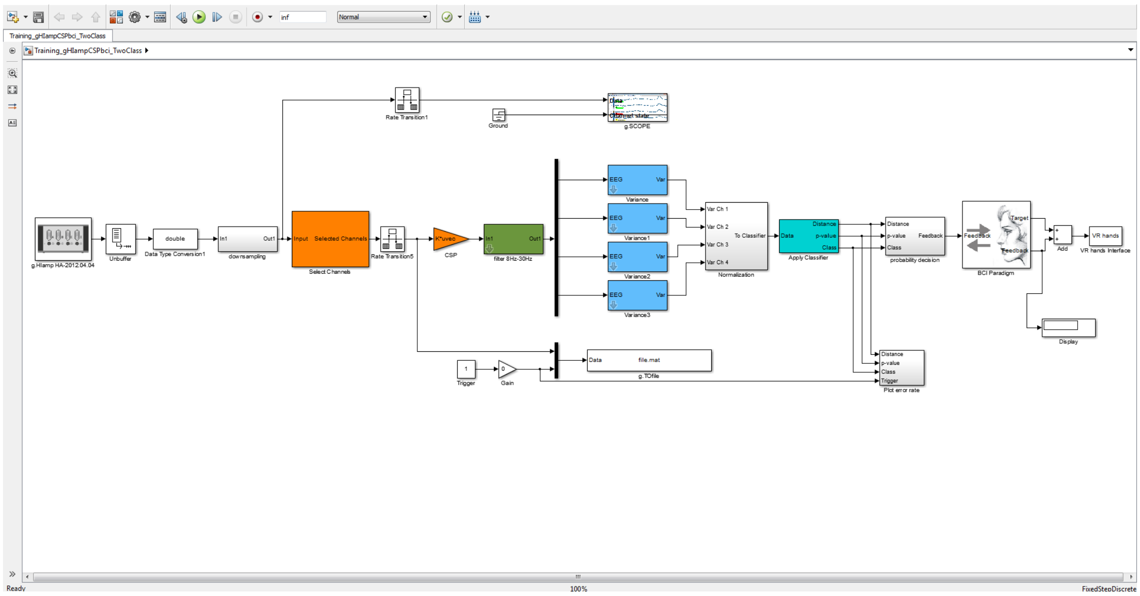

FIGURE C.3: Simulink model of MotorImagery training.

C.2.2 MotorImagery condition

Figure C.4 displays the Simulink model of the MotorImagery condition.

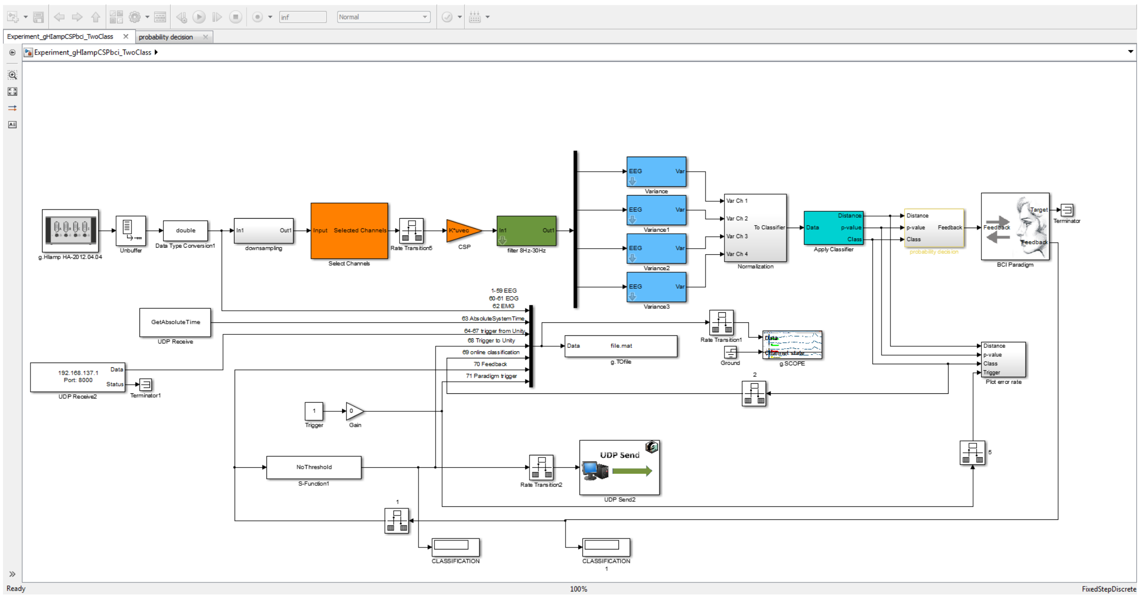

FIGURE C.4: Simulink model of MotorImagery condition.

C.2.3 Consent form and questionnaire

Consent form

The following figures C.5 and C.6 display the consent form, which was read and signed by each participant before participating in the experiment. The original size of each page was DIN A4.

Questionnaire

The follwing Figures the questions are disp

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INFORMACIÓN PARA LOS PARTICIPANTES

Este experimento forma parte de una larga serie de estudios para comprender las respuestas de la gente dentro de un entorno virtual. Este estudio ha sido aprobado por el Comité Ético de Investigación Clínica de la Corporación Sanitaria Hospital Clínic de Barcelona.

Por favor lea esta información y siéntase libre de preguntar cualquier duda a los experimentadores. Sin embargo los aspectos específicos que buscamos con este estudio no podrán ser comentados con usted antes de terminar la sesión. Intentaremos que el conjunto del estudio nos lleve el menor tiempo posible.

Por razones de seguridad, mujeres embarazadas, pacientes con epilepsia y personas que vayan a conducir coches/motos/bicicletas o a trabajar con maquinaria compleja o peligrosa inmediatamente después del experimento, no pueden participar en este estudio.

IMPORTANTE

Cuando la gente usa un sistema de RV, algunas personas podrían experimentar cierta sensación de mareo o estrés. Algunos tipos de video podrían llegar a generar un episodio epiléptico, como se ha informado que ocurre en algunos videojuegos.

Procedimientos que cada participante deberá comprender y aceptar:

- Se le pide que lea, comprenda y firme su consentimiento informado. Si usted lo firma, el estudio contará con su participación. Recuerde que usted puede abandonar dicho estudio en cualquier momento sin tener que dar razón alguna para ello.
- Apague el móvil antes de usar el equipo.
- A usted se le colocarán una serie de sensores para medir su actividad cerebral (EEG), muscular (EMG) y ocular (EOG). Estos valores fisiológicos están medidos por medio de sensores que solo captan la actividad fisiológica y por tanto nunca procuran algún tipo de estimulación.
- Usted verá un entorno virtual usando un casco de realidad virtual o unas gafas estereoscópicas para ver en 3D en una pantalla.
- En la pantalla verá un cuerpo virtual. Es posible que se le pida concentrar su atención en alguna parte durante unos minutos o realizar una tarea sencilla (por

1

FIGURE C.5: Consent form page 1 of experiment 3.

IDIBAPS

ejemplo, mirar hacia un punto del campo visivo, o pensar con mover el brazo, etc.).

- Durante la prueba se le puede pedir que responda a un número de preguntas de manera verbal o sobre papel.

- La información que hemos reunido nunca será mostrada de forma que pueda usted ser identificado individualmente. La información será transmitida de forma agrupada y estadística. Si se escribe un artículo de investigación, podría emplearse algún comentario verbal que usted haya hecho, aunque siempre de forma anónima.

- Por favor, no comente el estudio con otros durante los próximos 3 meses.

- Se pagarán 20 euros por su participación.

Si tiene alguna cuestión relacionada con el estudio, por favor contacte con nosotros:

- Birgit Nierula (bnierula@gmail.com)
- Dr. Maria V. Sánchez-Vives (msanche3@clinic.ub.es)
- Dr. Mel Slater (melslater@ub.edu)

2

FIGURE C.6: Consent form page 2 of experiment 3.

IDIBAPS

CONSENTIMIENTO INFORMADO DEL PARTICIPANTE

El voluntario deberá leer y contestar cuidadosamente las siguientes preguntas:

¿Ha leído toda la información sobre este estudio?	**SI**	**NO**
¿Ha tenido la oportunidad de preguntar y comentar cuestiones sobre el estudio?	**SI**	**NO**
¿Ha recibido respuestas satisfactorias a todas las cuestiones?	**SI**	**NO**
¿Ha recibido la suficiente información sobre este estudio?	**SI**	**NO**
¿Ha comprendido que usted es libre de abandonar este estudio…		
• …en cualquier momento?	**SI**	**NO**
• …sin dar ninguna razón?	**SI**	**NO**
¿Ha comprendido y aceptado los riesgos asociados con el uso de la Realidad Virtual?	**SI**	**NO**
¿Está de acuerdo en tomar parte en este estudio?	**SI**	**NO**
¿Está de acuerdo en ser grabado en video?	**SI**	**NO**
¿Está de acuerdo en ser grabado en audio?	**SI**	**NO**
¿Está de acuerdo en ser monitorizado fisiológicamente?	**SI**	**NO**

Nombre y apellidos del investigador que le ha informado sobre el estudio (escriba siempre en MAYÚSCULAS): …………………………………………..

Nombre y apellidos del participante (escriba siempre en MAYÚSCULAS): ………………………..

Yo certifico que no tengo epilepsia y que no conduciré ni coches, ni motos, ni bicicletas, ni usaré maquinaria compleja que pueda ser peligrosa inmediatamente después de acabado el estudio.

Firma del participante: **Firma Investigador:**

Fecha: …………………… **Fecha: ……………………**

La información obtenida de su experimento nunca será publicada individualmente. Los datos serán analizados en grupos y aquellos comentarios verbales, en el caso que se publiquen, serán presentados de forma anónima.

3

FIGURE C.7: Consent form page 3 of experiment 3.

C.2.4 Questionnaire

The following five questions were presented to the participant in random order on a computer screen. Questions one and four are displayed in Figures C.8 and C.8.

1. Sentía como si el brazo derecho fuera mi propio brazo.
2. Sentía como si fuera yo el que producía el sonido (cuando la mano tocaba el botón).
3. Sentí que por descuido golpee los objetos con mi brazo cuando cayeron de la mesa.
4. Sentía como si el movimiento del brazo virtual fuera ...
5. Sentía como si el brazo virtual se moviera por su propia cuenta.

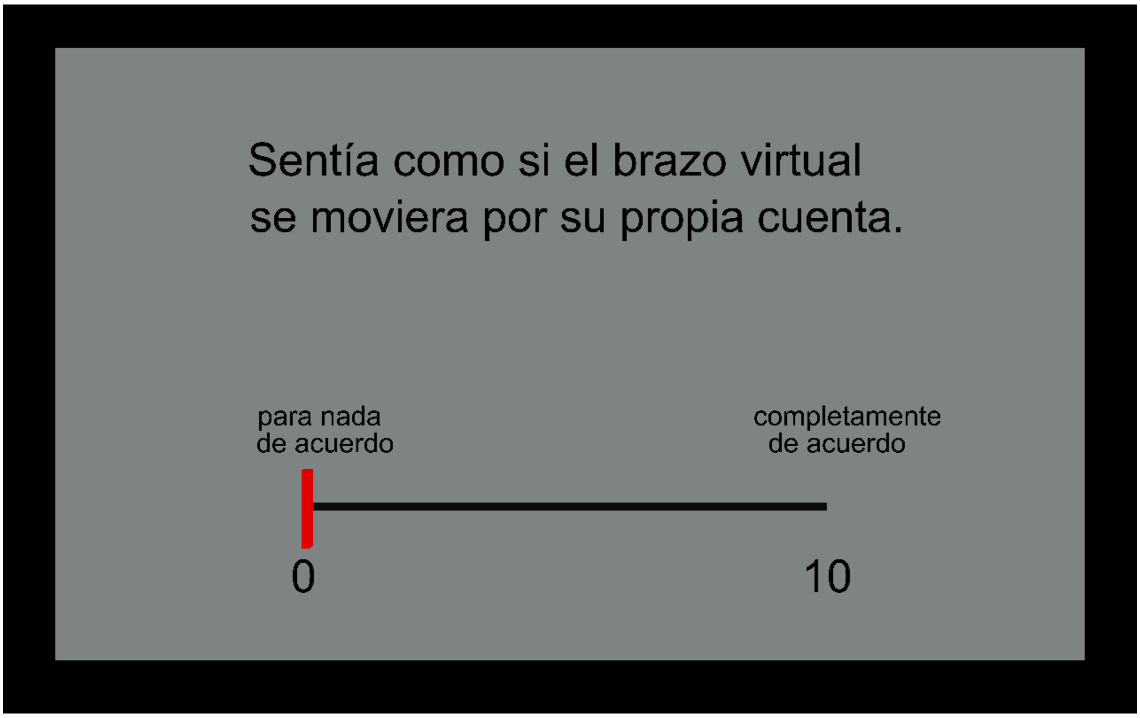

FIGURE C.8: One question from the questionnaire given to participants after each experimental condition. The answering bar looked the same in questions 1–3 and 5.

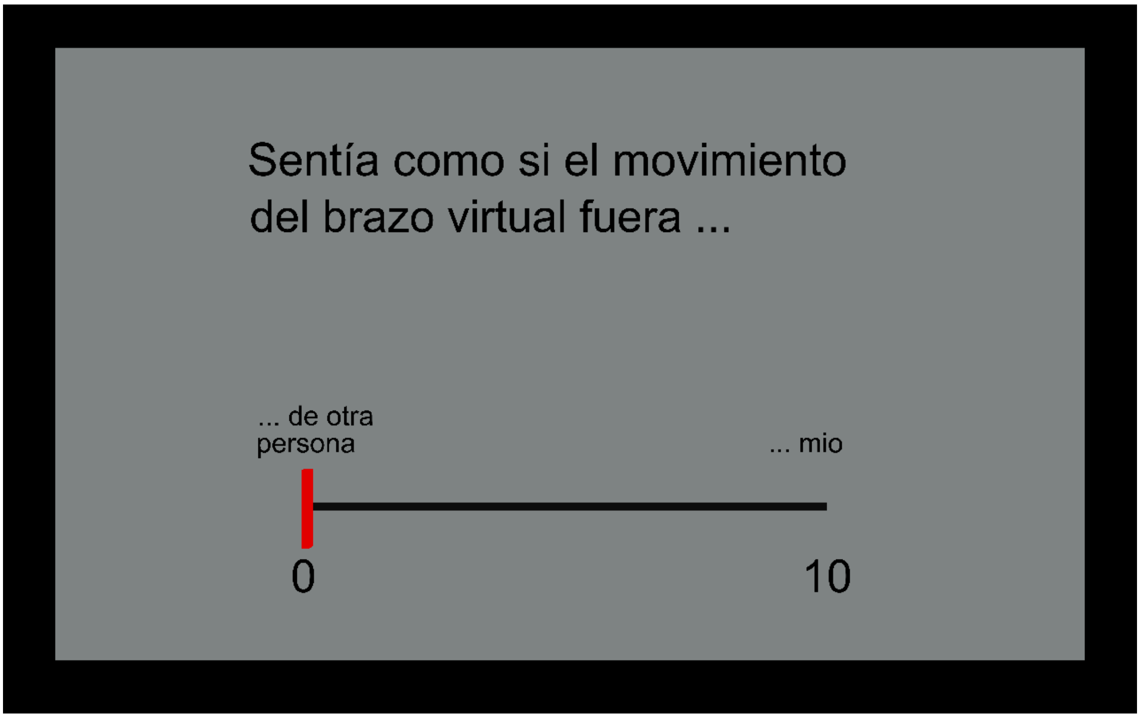

FIGURE C.9: Question 4 from the questionnaire given to participants after each experimental condition.

The following questions were presented to the participant inside the virtual environment on a virtual computer screen. Questions 1–4 were targeting responsibility and question 5 control.

1. Sentía como si fuera yo quien ha roto el lapicero...
2. Sentía como si fuera yo quien ha roto la taza de café...
3. Sentía como si fuera yo quien ha roto el vaso...
4. Sentía como si fuera yo quien ha roto el florero...
5. Sentía como si fuera yo quien controlaba el movimiento del brazo virtual.

C.3 Results

C.3.1 Model comparisons for agency related measures

Questionnaire ratings were analyzed using a multilevel mixed-effects ordered logistic regression with fixed-effects "condition" and random effects "individual subject". ERD% was analyzed using a repeated measure ANOVA with fixed effect "condition". To both models we stepwise added the fixed effects "MAp", "EMp", "MAo", and "EMo" as covariates and checked with Likelihood ratio tests which model fitted the data best. This model was then used for statistical comparisons. The following Table displays the fixed effects of the model that fitted the data best for each measure.

TABLE C.1: Fixed effects, P value of Likelihood ratio test, Akaike's information criterion (AIC) of statistical model with the best fit to the data, and AIC with the basic model that includes only the fixed effect "condition"

Measure	**Fixed effects**	**P value**	**AIC (best fit)**	**AIC (basic model)**
Questionnaire responses				
Control	Condition	n.s.	346.2	346.2
Responsibility	Condition + EMp	.033	365.9	368.5
MySound	Condition	n.s.	354.0	354.0
TouchedObject	Condition + EMp	.024	373.8	376.9
MyMovement	Condition	n.s.	380.0	380.0
ERD%				
Preparation phase	Condition	n.s.	459.8	459.8
Motor observ. phase	Condition	n.s.	459.8	459.8