The Neural Correlates of Action Representation in the Real World

Magda Mustile

University of Stirling

A thesis submitted for the degree of

Doctor of Philosophy

June 2022

The Neural Correlates of Action Representation in the Real World

Thesis outline

According to the human information processing framework, complex human behaviour is driven by an internal model, also widely known as ‘action representation’, which includes motor and goal related information about a particular action. These action representations are the product of our dynamic interaction with the surrounding environment and constructed through life by knowledge and experience. The cognitive substrate underlying action representation is organised in hierarchical processes, whose role is to predict the consequence of a particular course of actions, ensuring the accomplishment of a goal. However, action representations are flexible and can be dynamically updated and modified online depending on the circumstances in which we act. Furthermore, action representations can also be ‘rehearsed’ when no motor output is required, such as when we imagine an action, i.e., during motor imagery, or when we observe another person performing an action, i.e., during action observation.

Neuroscientific investigations employing the electroencephalogram (EEG) have shown patterns of brain oscillations related to cognitive mechanisms underlying action representation in laboratory-based settings. However, due to the constraints of traditional brain imaging techniques, neuroscientific research is still far from revealing neural correlates of action representation in real world behaviour, particularly in relation to dynamic whole body movements, such as locomotion. Despite the importance of locomotion in daily life, notably little is known about the neural and cognitive processes that support locomotor control. The recent development of portable brain imaging technology provides the unique opportunity of investigating human cognitive processes while participants freely move in the real world environment. In particular, the mobile EEG, employed in the studies presented in this thesis, allows to capture fast changes in brain signals, due to its excellent temporal resolution.

The aim of this thesis is to identify neural markers of action representation during natural locomotor behaviour in real world environments, employing the mobile EEG approach. In three different studies, brain oscillations were analysed in the time frequency domain, while participants executed, imagined, and observed natural locomotor movements. In particular, the analysis focused on event related power spectral changes in the theta (4-7 Hz), alpha (8-12 Hz) and beta (13-35 Hz) frequency bands.

In the first study of this thesis, investigating obstacle avoidance, neural markers of proactive and reactive cognitive control were identified in the theta and in the beta oscillations. Proactive control strategies, reflected in the power increase in the theta frequency band over frontal brain areas, are activated when participants face unexpected changes while moving in the environment, such as the avoidance of unpredictable obstacles on the floor. The findings demonstrated that the action representation is dynamically updated as soon an upcoming obstacle appears, compared to unobstructed walking and when the obstacle is expected. In addition, regardless of whether action representation required updating, a clear beta power increase, also known as beta rebound, was present after obstacles were crossed, reflecting reactive control strategies.

Action representation can be activated also intentionally in absence of motor output, such as when participants perform motor imagery of movements. A large body of evidence has shown that action execution and imagery rely on the same action representation and have overlapping neural substrates, indicating activation of motor processes without overt movements. However, how neural activation in imagery and execution compares for naturalistic whole body movements, such as walking, has not been studied. This issue was addressed in the second study of this thesis. The data revealed similar patterns of cortical activity when participants actually walked and during motor imagery of walking, reflected in the modulations of alpha and beta oscillations, but no overlap with the non-motor control task of counting mentally. However, the results also showed that imagery and execution are cognitively distinct, as indicated by different temporal dynamics of alpha and beta modulation. These dissociations suggest that the activation of the action representation during motor imagery involves not only the kinematic information of the action, that replace the covert motor output, but also spatial information about the environment in which the imagined action is embedded.

The activation of the action representation can also drive the understanding of others' intentions during the observation of other people's actions. Key information when interacting with others is whether someone is moving towards or away from us, indicating whether we may interact with the person. In addition, to determine the nature of a social interaction, we also need to take into consideration the distance of the actor relative to us as the observer. How this information is processed in the brain is largely unknown, at least in part because prior studies have not involved live whole body motion. Consequently, in the third study of this thesis, EEG activity was recorded while participants observed an actor approaching them or moving away. The data showed that distinct cognitive mechanisms encode relevant contextual and social information, such as the distance of the actor and the perspective. It was found that alpha oscillations were modulated by distance, with a stronger decrease of power when the model was near to the observer compared to far, regardless of perspective. By contrast, beta oscillations were found to be modulated by both distance and perspective, with a stronger decrease of power when the model was near and facing the participant (walking towards) compared to when the model was near but viewed from the back (walking away). The dissociation in the neural response to perspective and distance suggests that contextual and social information of the action representation are processed in order to encode the nature of an impending interaction with other people in real world environments.

The findings of this thesis contribute to the understanding of neural and cognitive mechanisms underlying action representation in real world contexts. Previous neuroscientific research has provided useful insight for the understanding of human cognition, using traditional laboratory settings. However, daily living activities in the real world are much more complex compared to laboratory-based tasks. For example, natural locomotor behaviour, is characterised by rhythmical movements but also by high variability depending on the circumstances. Furthermore, the investigation of brain signals for the development of supportive technologies in clinical settings using the EEG, which offers a unique tool for capturing neural markers of cognitive processes, needs to be reshaped around the needs of patients during daily living activities. Indeed, the data of the present thesis point towards the importance of the development of a new dynamic neuroscientific approach, which needs to examine natural behaviour in real world environments. Across the three studies it was demonstrated that mobile EEG recording during different aspects of real world locomotor behaviour is feasible for capturing neural markers of cognitive dynamic control in humans, suggesting new routes for the development of assistive technologies aimed to support patients affected by motor disorders.

Highlights of the experimental studies presented in this thesis

Highlights of Chapter 2

- This is the first study assessing the neural correlates of proactive and reactive control processes during obstacle avoidance in the real world environment employing the mobile EEG.

- The temporal profile of changes in frontal theta and centro-parietal beta oscillations allowed to arbitrate between early selection and late correction mechanisms of proactive control.

- Neural markers of early selection forms of movement control, occurring before the unexpected obstacles, are reflected in frontal theta power increase, which update the internal model in order to face an unexpected change in the environment

- Centro-parietal beta power suppression reflected a late correction mechanism, which prepare and implement the motor execution before stepping over obstacles, compared to unobstructed walking.

- Regardless of whether motor plans required updating, a clear beta rebound was present after obstacles were crossed, reflecting reactive forms of movement control.

- Mobile EEG during real world walking provides novel insight into the cognitive and neural basis of dynamic motor control in humans.

Highlights of Chapter 3

- This first study assessing the neural correlates of motor imagery of whole body dynamic movements (walking) demonstrates a neural overlap with actual execution of walking, evident in matching beta power decrease-increase dynamics and similarity in alpha suppression.

- It is possible to identify the neural signature of the covert process that is motor imagery.

- The spatial distribution of brain activity of imagery compared to the execution of real world dynamic behaviour such as walking, demonstrates a distributed neural network for motor imagery.

- In imagery of real world dynamic behaviour such as walking, the temporal and spatial distribution of brain activity of imagery compared to the execution, highlights the involvement of cognitive mechanisms that go beyond the mere encoding of motor information.

- A parietal decrease in alpha power found in imagery, indexes the integration of visual and motor information for environment-related action representation of real world dynamic behaviour.

Highlights of Chapter 4

- When watching a person approaching or walking away, perspective of the observer and proximity of the agent matters to encode the action performed by other people.

- Heightened neural activation, evident in a selective decrease in beta power when the approaching agent is nearing the observer, demonstrates that during action observation the social information of action representation are processed to understand the nature of the social interaction.

- Modulation of mu rhythms in response to someone approaching, signals the need for a new dynamic neuroscience to understand real life interaction between people.

Acknowledgements

Foremost, I thank my supervisors Magdalena Ietswaart and Dimitrios Kourtis for their support, trust, and patience, for giving me motivation and encouragement throughout my PhD. Their knowledge and guidance were fundamental for this thesis. I could never ask for better mentors and friends like them.

I thank David I. Donaldson and Martin G. Edwards for their advice and teaching throughout my PhD.

I would like to thank Stephen Stewart, Catriona Bruce, Chris Grigson and Samuel Bennet, who supported the implementation of the experimental works presented in this thesis. Their outstanding expertise, technical knowledge, creativity and enthusiasm were essential for my PhD.

I express my gratitude to Simon Ladouce and Gemma Learmonth, for their feedback, support and for sharing their expertise in signal processing and analysis methods.

I thank the University of Stirling for funding this PhD and SINAPSE for the financial support to attend international conferences and visit other labs.

l would like to thank the Psychology Staff and my lab mates, Ilaria, Liivia, Georgia, Laura and Michail for their support and feedback, for their friendship and their inspiring passion for research.

I extend this acknowledgment to all the people that have contributed to my understanding of science and research, who have helped providing material, feedback and insightful questions.

I would like to thank all the participants that took part in the experiment presented in this thesis, providing the data to build my thesis.

I would like to thank my family and my sister, Alessandra, from whom I have been far away for all these years but was always present in my days, supporting me whatever I did, unconditionally.

Author’s declaration

I hereby declare that I am the sole author of this thesis. To the best of my knowledge this thesis contains no material previously published by any other person except where due acknowledgement has been made. This thesis contains no material which has been accepted as part of the requirements of any other academic degree or non-degree program, in English or in any other language.

Scientific dissemination included as Chapters of the present thesis

Magda Mustile, Dimitrios Kourtis, Simon Ladouce, Gemma Learmonth, Martin G. Edwards, David I. Donaldson, Magdalena Ietswaart (2021) Mobile EEG reveals functionally dissociable dynamic processes supporting real- world ambulatory obstacle avoidance: Evidence for early proactive control. *European Journal of Neuroscience*, 54: 8106–8119. doi: https://doi.org/10.1111/ejn.15120 (Chapter 2)

Magda Mustile, Dimitrios Kourtis, Martin G. Edwards, David I. Donaldson, Magdalena Ietswaart (under review). The neural response is heightened when watching a person approaching compared to walking away: evidence of dynamic social neuroscience. *Neuropscychologia* (Chapter 4)

Magda Mustile, Dimitrios Kourtis, Martin G. Edwards, David I. Donaldson, Magdalena Ietswaart (in preparation). The neural substrates of the motor imagery of walking: evidence from mobile EEG**.** (Chapter 3)

Invited talks

Magda Mustile, 'Neural correlates of cognitive processes underlying movement control and action simulation during real world human locomotion: a mobile EEG approach'. Ministry of Science and Culture of Lower Saxony funded workshop (Liebniz University, Hannover) 'Moving forward: developing multi-method experimental approaches to investigate human locomotion in real life to support lifelong self-dependent living', 9 & 16 June 2021

Magda Mustile, 'Walking and obstacle avoidance'. Invited contribution to symposium on Mobile Cognition at the British Psychological Association – BPS - Cognitive Section Annual Conference 2020

Poster presentations

Magda Mustile, Dimitrios Kourtis, Martin G. Edwards, David I. Donaldson, Magdalena Ietswaart. "Providing a neuro-imaging evidence-base for motor neuro-rehabilitation". SINAPSE Annual Meeting, 16-17 September 2021

Magda Mustile, Dimitrios Kourtis, Simon Ladouce, Gemma Learmonth, Martin G. Edwards, David I. Donaldson, Magdalena Ietswaart. “Mobile EEG reveals the neuro-cognitive processes of real world obstacles avoidance”. British Neuroscience Association - BNA - Festival April 2021

Magda Mustile, Dimitrios Kourtis, Simon Ladouce, Gemma Learmonth, David I. Donaldson, Magdalena Ietswaart. “Neuro-cognitive indices of real world ambulatory obstacle avoidance”. Annual SINAPSE Meeting, 19 June 2020

Contents

Chapter 1: General Introduction 1

1.1. From behaviourism to computational approaches of motor control 3

1.2. Computational models of action representation 6

1.3. The emergence of embodied cognition 8

1.4. Actions representation: evidence from apraxia 9

1.5. Action representation and Motor Imagery 12

1.6. Action representation and Action Observation 17

1.7. Brain oscillations 23

1.7.1. Theta and action representation in execution 26

1.7.2. Theta and action representation in Motor Imagery 28

1.7.3. Theta and action representation in Action Observation 30

1.7.4. Alpha and action representation in execution 32

1.7.5. Alpha and action representation in Motor Imagery 34

1.7.6. Alpha and action representation in Action Observation 36

1.7.7. Beta oscillations as sensorimotor rhythm for action 38

1.7.8. Beta and action representation in Motor Imagery 41

1.7.9. Beta and action representation in Action Observation 42

1.8. Mobile approach to study neural correlates of Action Representation 43

1.8.1. Technical challenges 46

1.9. Rationale of the present thesis 51

Chapter 2: Mobile EEG reveals functionally dissociable dynamic processes supporting real world ambulatory obstacle avoidance: Evidence for early proactive control 54

2.1. Introduction 54

2.2. Materials and methods 57

2.2.1. EEG acquisition and analysis 60

2.2.2. Statistical analysis 61

2.3. Results 62

2.3.1. Planning 63

2.3.2. Theta 63

2.3.3. Beta 65

2.3.4. Resetting phase 66

2.3.5. Beta 66

2.4. Discussion 67

2.4.1. Practical implications, technical considerations and future directions 71

2.5. Conclusion 73

Chapter 3: The neural correlates of the imagery and execution in real world dynamic behaviour: evidence for neural overlap but distinct cognitive processes 74

3.1. Introduction 74

3.2. Method 78

3.2.1. Participants 78

3.2.2. Material and procedure 78

3.2.3. EEG recording and processing 79

3.2.4. EEG Analysis 80

3.2.5. Statistical analysis 80

3.3. Results 81

3.3.1. Beta oscillations 81

3.3.2. Alpha oscillations 83

3.4. Discussion 86

Chapter 4. The neural response is heightened when watching a person approaching compared to walking away: evidence of dynamic social neuroscience 92

4.1. Introduction 92

4.2. Methods 95

4.2.1. Participants 95

4.2.2. Material and procedure 96

4.2.3. EEG acquisition and processing 97

4.2.4. Event related spectral perturbation (ERSP) analysis 98

4.2.5. Statistical analyses 98

4.3. Results 99

4.3.1. Effect of perspective and distance 100

4.3.2. Alpha 100

4.3.3. Beta 101

4.3.4. Cortical modulation depending on the perspective of gait phases/cycle 103

4.3.5. Alpha 103

4.3.6. Beta 104

4.4. Discussion 104

4.5. Implications and conclusion of the present study 106

Chapter 5: General Discussion 108

5.1. Summary of findings 108

5.2. Embodied nature of action representation 114

5.3. Relevance of real world setting and mobile approach to study human locomotion 117
5.3.1. Technical challenges of mobile approach 122
5.4. Action representation as a tool for motor disorders 125
5.4.1. Neurofeedback, BCIs and mobile EEG 129
5.5. Conclusion 134
References 136

List of figures

Figure 1.1. 22
Figure 1.2. 25
Figure 1.3. 47
Figure 1.4. 48
Figure 1.5. 49
Figure 2.1. 59
Figure 2.2. 62
Figure 2.3. 63
Figure 2.4. 65
Figure 2.5. 66
Figure 2.6. 67
Figure 3.1. 81
Figure 3.2. 83
Figure 4.1. 96
Figure 4.2. 100
Figure 4.3. 101
Figure 4.4. 102
Figure 4.5. 103

Chapter 1: General Introduction

This thesis is about action representations and their neural correlates. Action representations serve as internal models of our behaviour, constructed through dynamic interaction between body and environment, shaped by knowledge and experience. We rely on action representations in order to act in an everchanging environment. Considering that much of our real world behaviour involves dynamic movements with degrees of freedom that are not tolerated by traditional brain imaging techniques, we have long been constrained in examining how actions are represented in the brain. In this thesis, limitations of traditional brain imagining techniques are overcome by employing a novel mobile EEG approach, which allows the identification of the neural markers of the action representations underlying real world locomotor behaviour.

According to the theory of human information processing, action representations drive a single or series of movements in order to successfully achieve a goal, minimizing errors and optimizing the desired outcome. These operations consist in a complex hierarchy of cognitive mechanisms which plan, update, and predict behaviour. Furthermore, the embodied cognition framework (Barsalou, 2008; Clark, 1999) suggests that cognition, perception, and action are intimately related and that the brain is able to simulate actions and their consequences through the activation of action representation. Indeed, neuroscientific research has provided converging evidence that the brain is similarly activated when we execute, imagine or when we observe other people performing a particular action, suggesting that our cognitive system is activated ‘as if’ we were doing the action (Fadiga et al., 2000).

The findings of the present thesis represent an important development for the study of cognitive and neural processes underlying real world behaviour. The three studies of the present thesis focused on locomotion, which represent intuitively one of the most natural and evolutionary conserved behaviours across species (Ferreira-Pinto et al., 2018). Although it appears a very elementary and pervasive behaviour in daily life, it originates from a complex system which include a close interaction between cortical and subcortical brain structures, such as the cortex, basal ganglia, cerebellum, midbrain and hindbrain, and spinal neurons (Kiehn, 2016; Ferreira-Pinto et al., 2018). Locomotor control is one of the most important acquisitions in human life. It develops slowly during infancy and constitute a fundamental basis for the development of psychological functions (for a review see Anderson et al., 2013). A large body of evidence have shown that locomotion and cognitive functions are intimately related, and that the loss of locomotor abilities is one of the main predictors of cognitive decline in healthy aging (Ataulla h& De Jesus, 2021; Pirker et al, 2017; Jahn et al., 2010) and neurological disease (Richards et al., 1993; Ambrose et al., 2010; Verghese et al., 2002; Beauchet et al., 2016). Indeed, gait impairments characterize a broad range of neurological disorders, such as Parkinson's disease, dyspraxia, Huntington Chorea. Therefore, the investigation of neural markers of cognitive process underlying locomotion deserves attention in order to suggest new insights for clinical practice and health psychology. A key contribution is offered by the present thesis therefore towards the understanding of cognitive processes that drive locomotor behaviour, which can help the future development of robotic assistive technologies for the treatments of different neurological disorders.

In the following sections (sections 1.1., 1.2., 1.3.) I will provide an overview of the development of the concept of action representation in theoretical psychological accounts, from behaviourism to embodied cognition. Subsequently (in section 1.4.), neurophysiological evidence of action representation will be discussed in relation to apraxia: a neurological disorder largely characterized by the loss of action representation of movements. Below, it will be also provide an overview of neuroscientific evidence of action representation in relation to motor imagery (section 1.5.) and action observation (section1.6.), each of which will be investigated in experimental Chapters 3 and 4 respectively. An overview of electrophysiological evidence on those brain oscillations targeted in the studies, namely theta, alpha, and beta oscillations, will be provided in relation to action control, motor imagery and action observation (sections 1.7.-1.7.9.). Finally, in the last three sections of the introduction, the mobile approach (section 1.8.), the technical challenges (section 1.8.1.) and the rationale of this thesis (section 1.9.) will be presented.

1.1. From behaviourism to computational approaches of motor control

Action has been conceived as the cardinal element of psychology (Freese & Sabini, 1985). During behaviourism however, the concept of action was replaced with the broad and general term 'behaviour'. The behaviourist account was strongly affected by the cartesian dualism, in which body and mind were conceived as separate entities. This circumscribed the object of psychological investigations, which was limited only to the association between stimulus-response, neglecting the mental dimension. According to behaviourism, psychology as science should only investigate what happens to the body, i.e., what is observable and measurable, which can be mechanistically linked to the physical properties of the environment.

Because of this pervasive account, during 1970-1980, motor theories in psychology were significantly influenced by the neurophysiological approaches, for which human motor acts can be defined as movements and reflexes. According to Giszter (2015) motor acts, in turn are defined by several fundamental building blocks for motion, also named motor primitives, which are kinematics, force interactions with the environment, body kinetics and regulation of impedance (Giszter, 2015). However, this mechanistic perspective assumed a fundamental similarity between human motor behaviour and machines, which perform the same motion monotonously (Rosenbaum, 2009). Our motor behaviour continuously changes, as we need to adapt constantly to a dynamic environment (Rosenbaum, 2009). Critically, conceiving behaviour as motor acts, excluded the covert component of cognitive dimension.

With the emergence of cognitive psychology in the 1950s (e.g., Miller, 1956; Miller, Galanter & Pribram, 1960) this perspective started to gradually change. Miller, Galanter and Pibram (1960) were the firsts to express concerns about the simplistic perspective of behaviour as ‘reflexes’ and they introduced the notion of ‘Plans’. Accordingly, behaviour is guided by Plans, which include motives and knowledge about our own behaviour and the external environment. Plans are primarily voluntary but can become automated, similarly to innate behaviours. More importantly, this perspective constituted the first attempt to introduce the cognitive dimension in the regulation of behaviour. The Plan of Miller and colleagues was similar to a programme, in which a hierarchical process controls the order of sequential operations to perform (Meijer & Roth, 1988).

More specific claims were made in 1988 when Meijer and Roth published ‘*Complex movement behaviour: The Motor-action controversy*’ (Meijer & Roth, 1988). This work aimed to outline in more concrete terms the critical transition occurring during the second half of 1900, from ‘motor’ to ‘action’ theories. As summarised by the authors in their work, a radical theoretical change started with the cognitivist approach, shaping a new notion of action. Differently from the perspective proposed by Miller, Galanter and Pibram (1960) focused on the intentional aspect of behaviour, the new action theories emphasised the role of ‘motor program’ or ‘motor schema’. The new ‘action theories’ (Kelso, 1980; Saltzman & Kelso, 1987) assumed the existence of a ‘motor program’ or ‘schema’, which is set in advance and runs in neural circuits for motor control. This program has a temporal structure, which is an emergent property regulating the timing of the behavioural output and corresponds to a dynamical internal model, for the sequence of different movements.

In the same year, psychological theories were also radically changing after the influential work of the American psychologist Gibson (1979) and to the so-called ecological psychology, which claims the need to include the environment in scientific investigations. The ecological psychology framework traditionally refers the work developed by Gibson (1979), however from a broader viewpoint, this perspective also includes the works of other psychologists such as Brunswik (1943), Neisser (1979) and Bronfenbrenner (1977) who, with some variations, are also proponents of the ecological account. In Gibsonian terms, ecological psychology developed as a branch of ecological science, which emphasizes the reciprocal interaction between organisms and their environments (Gibson, 1979). Indeed, the first assumption of the Gibsonian ecological psychology is that perception is a product of the mutual interplay between the features of the environment - or ecological niche (econiche) - and the animal. The econiche is described in terms of properties or affordances, which are the functional possibilities offered by the environment to the sensorimotor capacities of animals. The perception of affordances is directly linked to action, as it automatically triggers the possible action that an individual can carry out in the surrounding environment, without the need of higher-level processes. Another critical difference between the ecological account and the cognitivist theories, is the existence of an action system, in which sensory and motor processes interact with each other, not anymore in hierarchies of programs (Reed, 1981).

Despite the relevance of the cognitivist account, action theories and ecological psychology, a critical issue remained regarding the denial of mental representation. It was only later, with the development of the human information processing framework, which affected relevantly modern cognitive science, that the concept of representation assumed fundamental importance to define mental and motor processes behind behaviour. In cognitive science, the first theorist to recognise the relevance of the notion of representation was Fodor (1983). In his modular theory, Fodor assumes that the mind is organised in cognitive modules, which are computational devices specialised in specific domains, whose role is to encode input information and transform them in output. Perception is a process whereby the input of the sensory system is converted into a conceptual output: both input and output are conceived as representation, which are then transmitted to the motor system (Sperber, 1994). Certainly, Fodor has the merit to introduce the notion of representation in cognitive science, however in his theoretical framework, they are conceived as conceptual models, rather than action-related information.

It is then with the computational approach and the embodied cognition theory that the term ‘action representation’ assumes the characteristic of being an internal model that guides behaviour. The computational paradigms were inspired by the work of the Russian physiologist Berneistein (1967) who suggested that the motor system creates a model of future actions which is the product of the individual will and the interaction with the environment. Accordingly, for the computational approach, actions are not only biomechanical or physical events, but rather the natural units of our activities; this means that they are directed usually to targeted states, not to movements itself (Prinz in Heuer & Sanders, 2016). Actions depend on different levels of computations that are intrinsically related to the perceptual system. To have a successful behavioural outcome, an action must be guided by an appropriate representation, which is in turn the product of an internal feedforward system that simulates the dynamic interaction between the body and the environment. In this view, the action representation also offers an estimation of the possible outcome of the related behaviour, to minimize errors and increase the chance of success. Predictions are the fundamental pillar of the computational approach to motor control of actions (Wolpert, 1997; Wolpert & Kawato, 1998) which will be described in the next section.

1.2. Computational models of action representation

“Actions are not simply movements. Most of them are whole sequences of movements that together solve a motor problem. Each such chain consists of different movements that replace each other systematically, leading one to a solution for the problem. All the movements, parts of such a chain, are related to each other by means of the problem. If you miss one of the links of the chain, or mix up their order you will fail to solve the problem.” (Bernstein, 1996, p. 146, cited in Grafton & Hamilton, 2007). It is evident from this quote that Bernstein’s perspective highlights an underlying hierarchical structure of motor behaviour. The idea of a hierarchy in motor control was already mentioned between the end of the 19th and the beginning of 20th century’ by Jackson (1874) and Sherrington (1906), who suggested the existence of high and low level neuronal centres which are activated in train during the production of a motor output, but at the same time interact as an integrate system.

The theoretical assumption of a hierarchy in motor control is the core of the motor programming theory and of the computational approach to motor control (Wolpert. 1997; Wolpert & Kawato, 1998). According to Wolpert, motor control can be explained as a hierarchical cascade of processes which translate neural inputs into movement kinematics, in order to produce an observable behaviour. The ground of this theory consists in motor predictions, developed within the framework of forward models, which are causal models through which the system estimates the future state (behaviour) depending on the current state (Wolpert & Flanaghan, 2001; Miall & Wolpert, 1996). By predicting the future outcome of behaviour, a forward model is used to minimize errors in behaviour, select the optimal action and integrate the sensory and motor information into a state estimation, acting like a supervisory system (Wolpert & Flanaghan, 2001; Wolpert & Kawato, 1998). Internal models can be conceived as the computational equivalent to the cognitive construct of action representation or motor primitives of the motor theories (Kawato & Wolpert, 1998). Internal models are the building blocks which constitute the foundation of the motor repertoire, and are shaped by experience and learning (Wolpert. 1997). In particular, the forward models are systems which compare the internal model to the actual outcome. They provide a simulation of behaviour, calculating the dynamic interplay between the current state of the body and the external environment (Miall & Wolpert, 1996).

Computational models are relevant as they show with accurate predictions how behaviour can be implemented in two main states: the covert preparation, which consist mainly of off-line processes, and the overt execution, which designates online processes (Pezzulo & Ognibene, 2012). According to these models, a distal goal can be reached defining in advance the ideal action plan, and then activating the relative motor commands in order to implement the actual movement in time. However, motor control cannot be serial, as we need to constantly update the action representation in response to an ever-changing environment (Pezzulo & Ognibene, 2012).

The serial approach of computational models generally assumes the independence of the behavioural decision, the selection of the action and the execution. This ‘serial’ view has been replaced by parallel models, which highlight the dynamic interplay between processes of motor preparation and execution that can be considered as a continuum, rather than a serial cascade of processes. Pezzulo & Ognibene (2012) proposed a model in which motor control can be considered as a continuous proactive process which integrate past experience, actual predictions and present contextual information in order to successfully achieve a goal. This means that internal models or action representations need to be flexible, and adaptable to different contexts. Evidence on motor adaptations to external perturbations showed that we can switch between different possible action plans depending on the context (Gandolfo et al., 1996). A relevant example is the experiment of Gandolfo et al. (1996) on arm adaptations to force perturbation. In this study, participants had to execute movements towards targets. Movements were either subjected to random force perturbations, which induced a distortion of the postural configuration of the wrist, or executed without perturbation. A first main finding indicated an interference between the two conditions: even when no perturbation occurred, the postural configuration of the wrist appeared modified, showing an 'aftereffect'. As learning proceeded, participants responded with different configurations to the two conditions, indicating that the prediction of the perturbations was then cancelled. These findings showed the ability of the motor system to build an internal model of the external world, selecting the response depending on the external perturbation. However, this model can be dynamically updated and adjusted during experience, correcting the initial prediction based on somatosensory feedback, changing together with the external events. This evidence has provided useful insights for testing hypotheses related to the flexibility of cognitive processes underlying motor control. However, it is clear that controlled settings do not really match real world scenarios and do not represent the complexity of human natural behaviour. Therefore, the aim of the first study of this thesis (Chapter 2) is to investigate cognitive processes underlying action representation during voluntary motor control in real world scenarios, such as online motor adaptations when walking and stepping over predictable and unpredictable obstacles.

1.3. The emergence of embodied cognition

The ecological 'Gibsonian' theory meant a radical change in the approach to study human cognition, firstly because of the rejection of behaviourist dualism, and secondly for claiming the interdependence between action and perception. This view represented an important precursor of the embodied cognition framework, which constituted the alternative to functional computational approaches (Garbarini & Avanzato, 2004). The core of embodied cognition consists in conceiving cognitive processes as shaped by the body and by sensorimotor experience, which are situated in the environment (Varela et al., 1992). In these terms, sensorimotor, perceptual, and motor processes are not separable within the cognitive system. As argued by Gallese (2000), for the embodied cognition, the motor system not only drives the execution of actions but also represents it. The discovery of the canonical and mirror neurons in the monkey's brain (Di Pellegrino et al., 1992; Fadiga & Craghiero, 2003; Gallese et al., 1996; Rizzolatti et al., 1988; Rizzolatti & Fadiga, 1998; Rizzolatti et al., 1996) represented strong evidence for the embodied perspective. The distinctive properties of canonical neurons are relative to their activation during specific hand-object interactions, but also during the observation of an object alone, indicating that they are sensitive to the action afforded by the object. Mirror neurons are activated both during the execution of goal directed movements and during the observation of goal directed movements. The properties of these neurons suggested a match between the execution and the observation of action, which occurs through the so-called 'mental simulation': a process whereby the brain is activated 'as if' the observer was doing a particular action. Mental simulation during the observation of others' actions is based on the rehearsal of the specific action representation in the motor system of the observer, and it has been proposed as a possible mechanism through which we can understand others' behaviour (Rizzolatti & Craghiero, 2004; Rizzolatti & Fogassi, 2014). Within the framework of mental simulation, Jeannerod (2001; 2006) is one of the most relevant representative theorists. He proposed a unifying view of motor cognition, in which motor simulation is not limited to the observation of others' behaviour, but plays a central role during the imagination of an action, also known as motor imagery. His perspective inspired the so-called 'functional equivalence hypothesis', for which action execution, observation and motor imagery share similar neural features and are conceived as functionally similar (Jeannerod, 2001; 2006).

Strong evidence for the existence of a motor simulation mechanism, involving the rehearsal of the action representation in the human brain, came from neuropsychological observations on patients with apraxia. Apraxia is typically determined by a left parietal brain damage and is characterized by impaired execution of learned gestures, despite preserved motor and sensory systems (Heilman & Rothi, 2003). Although the different models proposed have determined a confused taxonomy and definition of the disorder, the investigation of apraxia was highly influential and contributed to the understanding of cognitive mechanisms underlying human motor cognition. In the following section, a brief review of the main models will be reported.

1.4. Actions representation: evidence from apraxia

The term ‘ideo-motor action’ was coined by William B. Carpenter to indicate that action triggered by a ‘chain of ideas’ (Carpenter, 1874 cited in Heuer & Sanders, 2016). As reported by Prinz in ‘Perspectives on perception and action’ (Heuer & Sanders, 2016), Carpenter’s definition of ideomotor action was inspired by the previous theory of Lotze (1852). The similarities between the two approaches is evident from what Lotze wrote in his work ‘Medicinische psychologie oder physiologie der seele’, translated by James: “The spectator accompanies the throwing of a billiard ball, or the thrust of a swordsman, with slight movements of his arm; the untaught narrator tells his story with many gesticulations; the reader, while absorbed in the perusal of a battle scene, feels a slight tension run through his muscular system, keeping time as it were with the actions he is reading of” (Lotze, 1852; cited in James, 1890, p. 525). Later, in ‘Principle of Mental Psychology’, Carpenter characterized ideomotor phenomena as actions arising automatically without any volitional control, underlying the immediate relationship and in some way a correspondence between ideas and actions. This account resembles Lotze’s perspective, whereby perceived or imagined movements immediately affect the execution of corresponding body movement.

The concept of ideomotor actions emerged again with neuropsychological investigations on apraxia during the first years of the 20th century. It was Liepmann (1900, 1905; translation 1977), who suggested that actions are guided by intrapsychic processes, which translates ideas in motor output (Goldenberg, 2003). In the first model proposed by Liepmann, the whole cortex generates the motor ‘idea’, and sends information to left sensorimotor regions, which in turn activate limbs and muscles. According to this schema, the image of a voluntary action is characterised by spatiotemporal features, created by intrapsychic processes which do not include kinetic aspects, but are closer to a visual entity, also called ‘movement formula’ (Goldenberg, 2003, p. 518). As reviewed by Goldenberg, in the second version of his schema, the motor ‘idea’ of Liepmann was clearly defined as a mental image of the movement, generated in posterior visual associative areas, which transmitted the motor commands through central areas via the parietal cortex. A lesion in the parietal cortex would then cause the damage of the idea or of the mental image beyond a particular movement, resulting in the inability to move limbs according to the idea (Goldenberg, 1992). The loss of the mental image of a movement would then be the origin of a motor disorder described as ‘ideomotor apraxia’ which is characterized by a selective impairment in imitative behaviour and in the production of meaningless gestures on command, but with preservation of tool-use movements.

In his last theorization, Liepmann identified another form of apraxia, the so-called ideational apraxia. This form of apraxia is characterized by a loss of the ability to produce purposeful behaviours, and can manifest itself with omissions, erroneous movement sequences and inappropriate tool use. According to Liepmann, in his publication from 1920 (Rothi et al. 1991), differently from ideomotor apraxia, which is the loss of the motor representation, ideational apraxia is characterized by the loss of the meaning of purposeful movement.

Since Liepmann seminal works, the original definition of apraxia has been revisited, and different classifications have been proposed (Geschwind & Damasio, 1985; Heilman et al., 1982; Ochipa et al., 1989; Buxbaum et al., 2003; for a review see Goldenberg, 2009). Despite the confusing taxonomy (see Buxbaum, 2001) there are few general assumptions of Liepmann’s theory that are still accepted: (i) motor acts are stored in the brain as different level of information (ii); motor acts are the results of a chain of processes which combine the different elements of order to generate meaningful behaviours (Jeannerod, 2006; Grafton & Hamilton, 2007); (iii) the role of the parietal cortex in generating action representations which guide the implementation of purposeful movement (Goldenberg, 2009).

The body of evidence on apraxia had a relevant impact on motor cognition theories and the understanding of action's representation. The evidence for an internal representation of movements was furthermore of interest due to the growing approaches based on the human information processing framework (Shiffrin & Schneider, 1977; Schneider & Shiffrin, 1977). According to this account, the cognitive system can encode different information stored in distinct modalities, which are processed by neural circuits functionally connected. In line with this perspective, the first theory of motor representation adopting the human information processing approach, was proposed by Rothi, Ochipa, and Heilman (1991). As suggested by Rothi and colleagues, similarly to language, perceptual information related to gestures and objects are stored in distinct units of semantic knowledge. In order to produce a familiar gesture, the semantic route acts like a working memory buffer supporting the implementation of behaviour by processing the different information stored in memory. Conversely, for new gestures the semantic route can be ignored, and the visual input is directly translated in motor gestures (Rothi et al., 1991; Rumiati & Tessari, 2002). According to this view, different separate units regulate the recognition of objects and actions, and on the other hand the execution of actions. In line with these assumptions, apraxia might be explained as an impairment to access information stored in the different units. However, this model was considered oversimplified and not adequate to explain several observed dissociations, such as the activation of motor areas when naming images of graspable objects (Martin & Chao, 2001; for further discussion see Negri et al., 2007; Buxbaum et al., 2005).

The dissociation about tool-use knowledge received particular interest in motor theories, especially when it was found that in the monkey's brain, neurons of the area F5 and in the intraparietal sulcus respond when the monkey performs a grasping movement but also when the monkey observes the movement performed by another agent or when the object is shown alone (Gallese et al., 1996; for review see e.g., Rizzolatti & Craighero, 2004; Rizzolatti & Wolpert, 200). Functional imaging studies on humans have revealed a homologous fronto-parietal circuit, which is active during the observation of actions (Buccino et al., 2004) and that parietal and premotor areas are active when participants observe graspable objects (Chao & Martin, 1999; Johnson-Frey, 2004). These investigations suggested that a broad fronto-parietal circuit might be responsible for the encoding of information about objects and related actions, stored in the form of 'motor schema' (Garbarini & Adenzato, 2004). In particular, this evidence suggested that the parietal and the premotor areas are possibly the storage of a 'motor vocabulary' needed to execute and recognise objects and related actions (Fadiga et al., 2000). This would be in line with the impairments exhibited by apraxic patients, which usually emerge after parietal lesions that might damage the stored knowledge about objects and related action representation (Buxbaum, 2018).

Notably, several evidence showed that apraxic patients not only manifest deficit at the level of movement execution, but also during motor imagery (Roy et al., 1993; Sirigu et al. 1995; Jeannerod 2006; Buxbaum et al., 2005) and action observation (Pazzaglia et al., 2008; Frenkel-Toledo et al., 2016). For example, Sirigu et al. (1995) showed that patients with left parietal lesions were impaired in predicting time to execute the motor imagery of both simple and complex finger movements compared to healthy participants and to patients with lesions in central motor areas. Buxbaum et al. (2005) showed that patients with ideomotor apraxia present a deficit when they have to imagine a reaching and grasping movement using different grips, compared to healthy participants and non apraxic patients. Similarly, patients with apraxia were shown to have a deficit during recognition of actions performed by other individuals. Pazzaglia et al. (2008) showed that apraxic patients presented a deficit not only during the execution of meaningful gestures but also during the recognition of correct gestures executed by other individuals compared to non apraxic patients. Furthermore, Frenkel-Toledo (2016) showed that patients with ideomotor apraxia fail in imitating reaching and grasping movements compared to patients without apraxia. Taken together, these findings converge towards the idea that apraxic patients might be specifically impaired in evoking action representation not only during the execution but also during recognition. Indeed, it has been proposed that apraxia might be related to an impaired motor simulation due to the difficulty in rehearse the action representation of the movement, which it is thought to occur during both motor imagery and action observation (Jeannerod, 2001; Jeannerod & Decety, 1995).

Taken together, evidence on apraxia strongly suggests the existence of an action representation in the brain, which constitute the core component of motor imagery and action observation, further explored in the sections below.

1.5. Action representation and Motor Imagery

According to Kosslyn, a mental image is an internal representation created at the early stages of perception and emerging when the stimulus is not present (Kosslyn, 2006). Mental images are characterised by the same perceptual properties of the stimulus and can emerge voluntarily (Kosslyn, 1980; 2006). Mental images are similar to internal representations, therefore, given their subjective nature, assessing their properties has been a critical issue for experimental psychology and their relevance was denied until the rise of cognitive science and the theory of human information processing (Boring, 1950; Kosslyn, 1980).

The first psychological account regarding ‘mental images’ focused on visual imagery, and it suggested a correspondence between the perceptual properties of the physical object and the characteristics of the internal mental images (Finke, 1986). This match, which constitutes the core of the so called ‘functional analogy model’ (Finke, 1986; Finke & Kurtzman, 1981; Kosslyn, 1978, 1984), serves as a ‘selective priming’ mechanism, which facilitates the activation of specific neural mechanisms in the visual system. Subsequently, a similar process was proposed also for the representation of motor acts, known as ‘motor imagery’, described as a cognitive process including the anticipation of behavioural outcomes in order to make an action plan and improve motor performance (Decety & Mick, 1988; Decety & Ingvar, 1990; Ingvar, 1985).

Motor imagery has been defined as a particular type of mental image, i.e., it has been regarded as the internal representation of a movement without executing it (Decety, 1996a;

Jeannerod, 1994, 2001; Mulder, 2007). Specifically, motor imagery is the process whereby the action representation of a movement is mentally simulated, producing similar feelings and sensations arising during execution, but without any overt output (Decety & Ingvar, 1990; Beisteiner et al., 1995).

The objective assessment of motor imagery begins with the pioneering mental chronometry experiments by Decety and colleagues (Decety & Michel, 1989; Decety et al., 1989). These investigations showed a match between the temporal organization of real movements and the temporal duration of motor imagery. As reported in these studies, time required to imagine and execute movements, such as writing, drawing or walking, are similar and stable (Decety & Michel, 1989; Decety et al., 1989). Additionally, experimental psychology showed that motor imagery and actual execution of movement share a similar pattern of autonomic changes. Decety et al. (1991) recorded the vegetative response (heart rate and pulmonary ventilation) while participants imagined walking on a treadmill at different speeds. The results indicated the respiration rate and the pulmonary ventilation increased during motor imagery of walking with increased imagined speed, in a similar manner as during action execution.

Another relevant finding concerned the evidence that motor imagery reflects biomechanical aspects of movements (Parson et al., 1987, 1994; Frak et al., 2001). In several studies on mental rotation of hands, Parson et al. (1987; 1994) showed that the time to mentally simulate hand movements from a resting position is similar to the actual movements when they involve common natural postures. However, they also showed that participants needed longer time to imagine less common and more difficult hand postures, suggesting that biomechanical and kinematic aspects of movements are reflected in the mental simulation (Parson et al., 1994). Decety and colleagues (1991) asked participants to walk on beams of the same length but different width, assuming that narrower width would increase the task difficulty and the execution times. They found that time to mentally simulate the task increased with task difficulty, matching the time to actually execute it, both in participants performing the task for the first time, and in participants who had previous knowledge of the task. This was interpreted as a similar adherence of both actual execution and motor imagery to Fitts’ law (Fitts, 1954), which predicts an association between speed and task difficulty (i.e., increased difficulty is associated with longer movement times). However, the presence of the actual execution as an experimental condition, was a confounding factor for these experiments, as participants had tacit knowledge of the motor task. This issue was later addressed in several studies. Decety and Jeannerod (1995) employed a virtual reality paradigm and asked participants to imagine themselves walking in a virtual environment through several gates of different width and placed at different distances. They found that the time to mentally imagine the walk increased with the difficulty of the task (i.e., longer motor imagery times for longer distances) and this effect was not related to the tacit knowledge of the task. The adherence of motor imagery to Fitts' law was also proven in movement involving tools use. Macuga et al. (2012) asked participants to actually execute and imagine moving a pen and two weighted tools (top-heavy and bottom-heavy) tapping in horizontal and vertical trajectories. They found that motor imagery of all the three tool uses conformed to Fitts' law, suggesting an internal shared representation for real execution and motor imagery.

Other evidence related to motor imagery came from neuropsychological patients with apraxia. As mentioned in the previous section of this Chapter, patients with damage to parietal brain areas (Liepmann, 1900; Heilman et al., 1982; Schwartz et al., 1991; Sirigu et al., 1995) might exhibit a deficit in tool use without any sensory or motor impairments. It was then shown that patients with apraxia exhibit also deficit in imagining the movement (Roy et al., 1993; Buxbaum et al., 2005). Buxbaum et al. (2005) compared the actual execution and the motor imagery of grasping movements towards different objects in healthy participants, stroke patients with ideomotor apraxia and stroke patients without apraxia. They found that stroke patients with ideomotor apraxia exhibit a more pronounced deficit in performing motor imagery compared to both stroke without apraxia and healthy participants. Aside from apraxia, other disorders showed deficit in both movement execution and mental simulation, for example, Parkinson's disease (Dominey et al., 1995).

Further evidence of the phenomenological correspondence between action execution and motor imagery came from brain imaging studies. Early investigations showed that during motor imagery the regional blood flow (rCBF) increases in motor areas such as the premotor cortex and supplementary motor areas (Rao et al., 1993; Orgonzo & Larsen, 1979; Roland et al., 1980; Decety et al., 1988; Grafton et al., 1996), and subcortical structure such as the cerebellum (Decety et al., 1990; Lotze et al., 1999; Grafton et al., 1996). Motor evoked potentials (MEPs) studies with transcranial magnetic stimulation (TMS) showed increased corticospinal excitability of the effector involved in motor imagery (Fadiga et al, 1998) without changes in the spinal excitability (Yahagi et al., 1996). The specificity of the activation during motor imagery has been confirmed also by functional magnetic resonance imaging (fMRI) studies (Stippich et al., 2002; Ehrsson et al., 2003), which showed a somatotopic recruitment of the primary motor areas during motor imagery of tongue, finger, and toe movements. Furthermore, a large body of evidence has showed similar activation during execution and motor imagery over a large network including the premotor cortex, prefrontal areas, parietal cortex, and the basal ganglia (Geradin et al., 2000; Grezes & Decety 2001; Hetu et al. 2013; for a recent review see Hardwick et al., 2018).

Despite evidence for neural similarities, much evidence has also highlighted differences between motor imagery and action execution. For example, the mental simulation of a movement might take longer than actual execution (Decety et al., 1989; Louis et al., 2011) especially when participants have to perform novel complex tasks (Calmels et al., 2006; Cerritelli et al., 2020). Participant's expertise (Olsson & Nyberg, 2010; Orlandi et al., 2020; Fink et al., 2009) and posture (de Lange et al., 2006) might also modulate brain activity during motor imagery. For example, Guillot et al. (2009) found that brain activation during motor imagery might differ from execution depending on the imagery ability. Good imagery performers recruit motor parietal and premotor areas, whereas weak imagers recruit more the cerebellum, orbitofrontal areas, and posterior cingulate areas (Guillot et al., 2009). Furthermore, the assessment of the ability of performing motor imagery has also been questioned. Usually, this ability is measured through questionnaires focused on the vividness of the mental image for visual imagery, and on the intensity of the 'feeling' for the kinaesthetic imagery (Roberts et al., 2008; Williams et al., 2012; Williams & Cumming, 2011). Although these questionnaires have been proven to be a valid tool for assessing motor imagery ability, they are not enough to determine whether participants are effectively performing the mental task. This is mainly due to the covert nature of motor imagery and to the fact that these tools are generally self-reported scales, which are prone to several psychological biases, such as social desirability, self-protection bias or tendency to the mean (Gabbard & Lee, 2014; Dahm, 2020). Additionally, it has been suggested that for complex motor tasks, visual imagery is easier to perform compared to kinaesthetic imagery; thus, it is possible that it can be involuntarily used by participants (Guillot et al., 2004).

Furthermore, in a recent meta-analysis, Hardwick et al. (2018) showed a rather small overlap between brain activation during action execution and motor imagery. In particular, this meta-analysis revealed a prominent recruitment of frontal areas during motor imagery, which are usually less active during execution. Two possible explanations have been proposed for this difference: the higher recruitment of frontal areas might be related to the increased working memory demands during motor imagery of complex movements (Rottschy et al., 2012; Wollenweber et al., 2014) or alternatively, to the inhibitory mechanisms (Blasi et al., 2006; Coxon et al., 2016; Nigel et al., 2015) which prevent the activation of corticospinal pathways during motor imagery (Crammond et al., 1997).

In light of the evidence for a questionable functional equivalence between execution and motor imagery, an alternative model has been recently proposed by Glover and Baran known as the 'Motor Cognitive Model'. The Motor Cognitive Model (Glover & Baran, 2017) provides a cognitive framework for motor imagery mechanisms. Whilst it does not deny the functional analogies, it suggests that motor imagery and actual execution also differ depending on the different motor stages and on the action being executed/simulated. At the stage of the movement preparation, the motor representation of an action is generated employing similar cognitive mechanisms in both motor imagery and actual execution. During the execution stage, the actual movement automatically activates visual and sensory feedback to monitor the movement online, whereas during motor imagery these processes are not activated due the absence of the physical movement. The model also poses a distinction between motor imagery of highly developed and poorly developed motor images. Highly developed motor representations are the results of well-known and strongly practiced actions, which are recalled easily and do not need a great amount of cognitive effort. Poorly developed motor representations are instead newly learned actions, which require more control and conscious effort during their recall. As proposed by Glover and Baran (2017), highly developed motor images would elicit greater similarities between motor imagery and actual execution, not only during the planning but also during the execution. Highly developed images are more likely to produce the match between time to execute and imagine the movement, differently from poorly developed images that require additional control. In summary, this model suggests that the planning phase of movement, is the common ground between motor imagery and action execution.

The cognitive substrate of motor imagery has been difficult to assess primarily because of the methodological limitations, which allow the investigation unrepresentative and minimal movements. Indeed, the evidence of neural correlates of cognitive mechanisms underlying motor imagery has been recorded in tasks in which participants are seated or lying down in a scanner and imagining the performance of simple movements such as finger tapping or dorsiflexion of the foot (Pfurtscheller et al., 2006a, 2006b; Neuper et al., 1999; Hashimoto et al., 2013; Solis-Escalante et al., 2008, 2012; Muller-Putz et al., 2010). Furthermore, EEG studies on motor imagery, usually analyse brain activity with a limited number of channels and cognitive dimension is not considered at all for (Leeb et al., 2007; Pfurtscheller et al., 2003). For example, whole body dynamic movements in the natural environment have not yet been investigated. As suggested by the embodied cognition framework, action representations are dynamic entities, which include not only the kinematic aspects of the action, but also the information about the state of the body and the information coming from the external world (Varela et al., 1992). Indeed, much evidence has shown how the brain states and cognitive processes are influenced by the environment (Gramann et al., 2011; 2014). Thus, in order to understand the complex cognitive substrate of motor imagery, it is necessary to look at natural actions, corresponding to what we actually do in the real world. Therefore, the aim of the second study (Chapter 3) of this thesis is to test the functional equivalence hypothesis on whole body dynamic natural movement applying a mobile approach.

1.6. Action representation and Action Observation

Moving and acting in the environment also means that we need to interact with others and understand their actions. The idea that humans are sensitive to movements performed by others is something that is not recent in psychology. As shown by developmental psychology, human infants are attracted by faces, body posture and body parts (for a review see Marshall & Meltzoff, 2015). Through the observation of others' actions, infants can learn and can build their knowledge about the world and about the meaning of particular motion patterns. As suggested by the observational learning account (Bandura et al., 1966; Bandura, 2008), infants acquire social skills through imitation (Meltzoff, 1988; 1996; 2017; Meltzoff & Prinz, 2002 Kuhl et al., 1996; Heimann, 1989; Nadel & Butterworth, 1999; Uzgiris, 1981). According to Meltzoff (2002; 2017), to learn a particular behaviour, infants need to evaluate the match between their own action and the action observed (Meltzoff, 2002; 2017). In other words, infants need a representational system to compare what they observed and their own motor transformations. This perspective supports the idea that understanding others is based on the activation of the action representation system which works through 'mental simulation' of the action observed.

The hypothesis of a 'mental simulation' has then found the most important foundation in the late '80s when it was found through single cell recording that neurons of the F5 premotor area of the monkey's brain become active both during the execution of particular goal-direct hand movements such as grasping or retrieving a piece of food (Rizzolatti et al., 1987), but also when the monkey observed the same movement performed by another agent (di Pellegrino et al., 1992; Gallese et al., 1996). As reported by di Pellegrino et al. (1992), they ‘incidentally’ observed that these neurons, today widely known as ‘mirror neurons’, were activated by the observation of meaningful, object-directed actions performed by the experimenter, even if the monkey was not performing any overt movement. From this first observation, a large body of evidence has tried to understand this peculiar property of the neurons of the area F5 of the monkey’s brain. A first crucial finding was that the area F5 contains neurons that are selectively activated when the monkey observes an object alone, also called ‘canonical’ neurons, and other neurons are active during the observation of goal directed actions, performed both by a conspecific or by a human, also called ‘mirror’ neurons (Rizzolatti et al., 1987; Rizzolatti et al., 1996; Gallese et al., 1996). Gallese et al. (1996) compared the neural activation when presenting objects alone requiring different grip (precision grip, finger prehension, whole hand prehension) but also when observing action relate to food grasping (presenting the food to the monkey, putting it on a surface, grasping it, giving it to a second experimenter or taking it away from him), food manipulation and manipulation of other objects and other movements (waving, lifting arms). They found that the activation of mirror neurons was triggered by actions in which the mouth or the hand of the experimenter interacted with an object. These neurons only fired when the monkey observed and performed the same action, suggesting that mirror neurons’ function is related to the internal representation of the movement (Gallese et al., 1996; Jeannerod 2001) which encodes the essential elements of the action, such as the agent of the action or the specific motor aspects, acting as a ‘motor vocabulary’ (Gallese et al., 1996). This has led to relate the main function of the mirror neurons to the understanding of action performed by others.

Further evidence suggested that mirror neurons might respond also to different levels of the action. Umiltà et al. (2001) recorded the activity of mirror neurons of the area F5 in the monkey brain while observing a ‘fully visible’ action towards an object, and while observing a ‘hidden’ action toward an object, i.e., the critical part of the hand-object interaction was not visible. They showed that most of the mirror neurons fired similarly in both conditions, meaning that they responded also when the monkey had to infer the goal of the action withoit observing it, suggesting a specialized mirror function in action prediction (Umiltà et al., 2001). Kohler et al. (2002) demonstrated that mirror neurons fired both when the monkey performed a hand action (tearing action, dropping a stick) but also when the monkey heard the sound related to that specific action. Fogassi et al. (2005) compared the activation of monkey's mirror neurons during the observation of grasping actions with different purposes, i.e., grasping a piece of food for eating, grasping a piece of food for placing it in a container and grasping a solid object to place it. They found that mirror neurons of the inferior parietal lobule discharged selectively according to the goal of the observed grasping action. In other words, seeing a particular grasping action in relation to different goals, activates the same neurons that code the execution of that specific action, allowing the monkey not only to recognise, but also to predict the action outcome. This was further supported by evidence of mirror neurons activation during grasping actions performed with different effectors. In two independent investigations, Umilta' et al. (2008) and Rochat et al. (2010), recorded the activity of mirror neurons while the monkey observed a grasping action performed both with hands and with a tool (pliers) by the experimenter. They found that mirror neurons were activated in both conditions, even when the action performed, required a different precision movement (closing vs opening) or a different tool (spearing food using a stick).

The results obtained from monkeys and the parallel development of brain imaging techniques, led to a wide number of investigations aimed to find the homologous mirror neuron system also in humans. Interestingly, the first scientific evidence was provided in 1950, when Gastaut & Bert (1954, but see also Cohen-Seat et al., 1954) recorded the cortical activity while participants observed a movie. They reported the blocking of the rolandic 'mu rhythm' (8-12 Hz) when participants observed biological motion, a pattern usually observed during movement execution. In the human brain, area F5 corresponds to Broca's areas. Gallese and colleagues in 1996 speculated that this area might possibly represent the locus of the matching mechanism between execution of action and observation.

First studies on humans targeted the premotor cortex using TMS. Fadiga et al. (1995) used the TMS to stimulate the motor cortex and recorded the MEPs from four muscles of the hand during the observation of grasping, of the object presented alone, of simple arm movements and a dimming light detection task (detect the dimming of a visual stimulus on the screen). They found that the observation of movement performed by other individuals increased the motor excitability, and that this pattern of motor activation during observation of others' movement was similar to the pattern of muscle contraction during the actual execution of the specific movement. In particular, observing grasping actions elicited greater activation in the opponens pollicis, whereas during the observation of arm movement, the facilitation effect was found in muscles involved in arm elevation, but not in the opponens pollicis. Similarly to theories proposed in animal studies described above, this finding suggested that action observation has a role in facilitating the motor response. This interpretation was further supported by Strafella and Paus (2000) and Maeda et al. (2002) studies. Strafella and Paus (2000) found similar results recording MEPs while participants observed handwriting and arm movements in the specific muscles involved in the execution of the two actions (i.e., first dorsal interosseous and the biceps). Similarly, Maeda and colleagues (2002) found a match between the MEPs elicited in the specific finger muscle involved in the observed action.

EEG and neuromagnetic (MEG) studies also found evidence of a match between brain activity during observation and execution of actions in humans. Cochin et al. (1998) measured the cortical response using EEG while participants observed video projections showing objects, still and moving cartoons, and gymnastic exercises performed by a human model. They reported that during the observation of human movements, alpha and beta rhythms desynchronise over central and centro-parietal areas, a pattern that has been regarded as the index of motor activation during the execution of movements (Pfurtscheller & Klimesch, 1992; Pfurtscheller et al., 1996a, 1996b, see Chapter 4 for further discussion on alpha and beta oscillations during action observation). Hari et al. (2000), used MEG to investigate the activation of the motor cortex during the execution and the observation of manipulative actions, and during rest. They found that the precentral motor cortex was similarly activated during the execution and the observation of the movements compared to rest, although to a weaker extent during action observation.

A large body of brain imaging studies has then extended these findings, showing that a broad range of brain areas are active during the observation of others’ actions. Rizzolatti et al. (1996) measured the rCBF employing the positron emission tomography (PET) scanning while participants observed a grasping movement towards an object (geometric solid and common small/large objects), while executing the grasping movements towards the same objects and while observing the object alone. They showed that the observation of grasping movements significantly activated the inferotemporal cortex and the left inferior frontal gyrus. Decety et al. (1996) asked participants to imitate or recognise meaningful actions and meaningless actions performed by an experimenter while measuring the rCBF through PET. They found that when subjects observed the action with the purpose of recognizing them, there was an increased activation of the right parahippocampal gyrus, whereas in the condition in which they had to imitate, there was an increased activation of the right dorsolateral prefrontal cortex and of the pre-supplementary motor areas. Furthermore, they found that meaningful action activated the inferior frontal gyrus, middle temporal gyrus and the orbitofrontal regions, which were more active compared to meaningless actions. Similarly, Grezes et al. (1998) in a PET study, found a different activation of brain areas when observing meaningful and meaningless actions, the former involving activation of the inferior frontal gyrus and the fusiform gyrus and latter involving the activation of the superior and the inferior parietal lobe and the cerebellum.

These findings demonstrated that a broad range of brain areas is involved in action observation, which were then confirmed by the fMRI investigations. Iacoboni et al. (1999) scanned participants while observing and then imitating finger movements that were shown in a video and while executing the same movements in response to visual cues. They found that different brain areas including the left inferior frontal cortex and the superior parietal lobule, were active during both observation and imitation. Buccino et al. (2001) investigated brain activation during the observation of object- and non-object related actions performed by a model with different body effectors, such as mouth, arm, hand, and foot. They found that action observation of movements performed with different body parts activated the frontal premotor brain areas in a somatotopic manner. Furthermore, they found that object related actions elicited a somatotopic activation of the parietal areas, confirming the role in the perception of manipulable objects (Buccino et al., 2001). Johnson-Frey et al. (2003) further demonstrated that the dynamic hand-object interaction is not essential to activate the mirror neuron system in humans and that only the static image of hand-object interaction is enough to elicit a mirror response. They analysed the brain response using fMRI while participants observed static images of objects being either grasped or just touched. The results indicate a greater response of the inferior frontal areas during grasping images compared to touching images, suggesting that the inferior frontal cortex might be relevant for action-relevant perceptual properties.

Despite the large number of neuroscientific investigations on action observation, experimental paradigms have been affected by a lack of ecological validity. For example, typically, studies on action observation have employed recorded videos in which only targeted body parts were shown to participants (Cochin et al., 1998; Ulloa & Pineda, 2007; Zarka et al., 2014; Angelini et al., 2018; Kilner et al., 2006; 2009). It has been suggested indeed that brain activity in response to recorded videos might be reduced in comparison to live actions (Rizzolatti & Fogassi, 2014). Furthermore, as one of the most accredited hypotheses for the action observation is related to the understanding others’ action goals

(Schippers & Keysers, 2011; Hamilton, 2013; Buccino et al., 2001, 2004; Wheaton et al., 2004; Rizzolatti & Fogassi, 2014) it is crucial to investigate cognitive mechanisms related to action observation in contexts that resemble real world dynamics. This means that to better understand the meaning of the mirror neuron system it is necessary to use experimental paradigms aimed to disentangle the different factors that might affect cognitive processing, in settings that reproduce what happens during real life action observation. Thus, the aim of the third study of this thesis (Chapter 4) is to investigate neural correlates of whole body dynamic action observation.

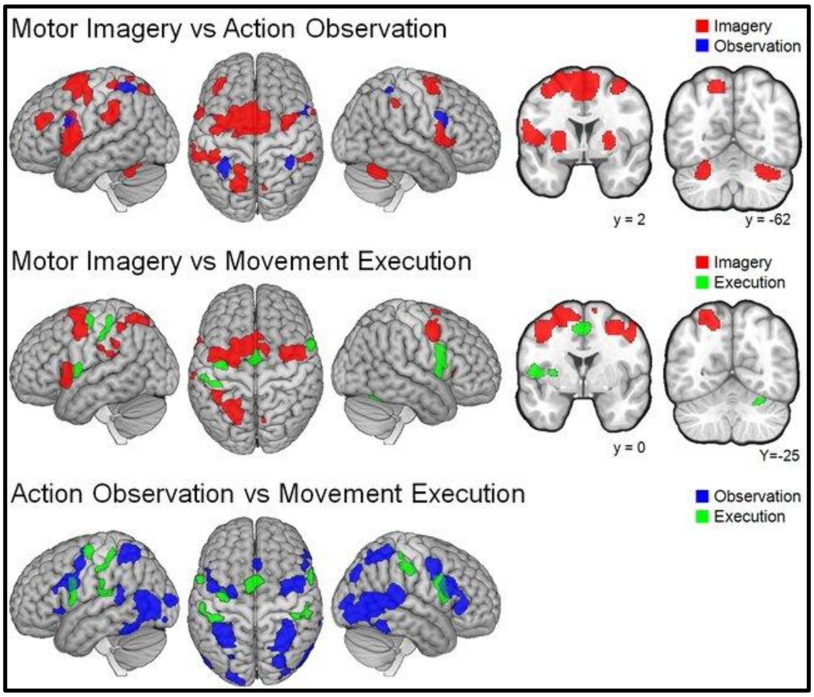

Figure 1.1. Contrast analysis taken from Hardwick et al., 2018. The figure shows the overlap between motor imagery, action observation an movement execution across cortical and subcortical areas emerged from the meta-analysis conducted by the authors.

1.7. Brain oscillations

The development of the human information processing framework (Boring, 1950; Kosslyn, 1980) and the theories of motor control (Wolpert. 1997; Wolpert & Kawato, 1998) signified an important step forward for modern neuroscience. The first important consequence of this theoretical revolution was the idea that the brain works as a predictive machine, that processes regular features of the external environment and uses this information to predict events and solve problems (Wolpert. 1997; Wolpert & Kawato, 1998). The ability of the brain to work as a predictive machine is supported by complex processes, which above all include the organization and the retention of information (Buzsáki et al., 2013). These processes allow the brain to maintain a trace after the disappearance of the input, and take place thanks to the continuous online modification of synaptic connections over a broad number of functional brain circuits (Buzsáki et al., 2013; Buzsáki, 2006). Another important ability of the brain is the integration and the organization of local processes into the global system, also known as bottom-up communication (Buzsáki et al., 2013; Tononi et al., 1998). This communication can take place also in the other direction, from the global to the local level, establishing the so called top-down control (Engel & Fries, 2001). To support these processes, a powerful exchange of information between local and global structures, is necessary. Furthermore, in order to produce complex computations and generate behavioural output, brain processes need to interact in parallel with each other, integrating data coming both from the sensory system and from the external world (Buzsáki et al., 2013; Cisek & Kalaska, 2010; Gallese, 2000).

One the most accredited hypotheses regarding how the information are organized, retained, and integrated from local areas to the global system, regards brain oscillations, which are thought to mediate and support these processes (Buzsáki, 2006; Buzsáki et al., 2013). Brain oscillations are ubiquitous phenomena in the nervous systems, and they are evolutionary preserved across species (Buzsáki et al., 2013). This suggests that they might underlie some fundamental brain processes such as the encoding of sensory information and the generation of specific behaviours (Singer, 2017). All the brain structures have the intrinsic ability to generate oscillations which propagate within the central nervous system. This knowledge emerges primarily from animal models and from studies on patients who received deep brain stimulation (DBS) surgery. The implanted electrodes can record oscillations from single neurons, neuronal assembly, and local field potentials (LFP). Although different techniques have been used to investigate brain oscillations in humans (i.e., electrophysiology both in vitro in vivo and MEG), the principal methodology employed by cognitive neuroscience is the EEG, which provide a non-invasive recording of ongoing oscillations over the scalp with a high temporal accuracy.

The frequency of brain oscillations depends on the properties of different neurons, and it covers a range between 0.05 Hz to 500 Hz (Buzsáki, 2010). However, the classical taxonomy of human brain rhythms includes slow frequency bands, namely delta (0-4 Hz), theta (4-8 Hz) and alpha (8-12 Hz), and high frequency bands, such as beta (13-35 Hz) and gamma (35-90 Hz). Single neurons as well as neuronal assemblies, can generate rhythmic activity both in a specific frequency range or within multiple frequencies (Hutcheon & Yarom, 2000). This suggests that specific timing of oscillations might represent the information exchange between different networks (Buzsáki & Draguhn, 2004; Buzsáki, 2010). Typically, slow waves are generated by broad distributed and prominent membrane-potential changes, whereas fast oscillations are generated by narrower neuronal assemblies and by smaller changes in the membrane action potential (Singer, 2017; Buzsáki, 2010; Buzsáki et al., 2013; Fries et al., 2007). The type of oscillations produced by a particular brain area depends on the characteristics of the specific neurons, which can have frequency preferences and oscillate either spontaneously or in response to specific stimuli. Generally, spontaneous brain oscillations are the index of excitatory and inhibitory postsynaptic potentials, which can be characterized by cyclic or temporary changes in excitability. For example, pacemaker cells are characterized by regular fluctuation, and are involved in the control of rhythmical behaviour, such as locomotion, respiration, and heart frequency (Marder & Buchner, 2001; Grillner, 2006). However, neurons can oscillate in response to determined stimuli: indeed, the role of oscillations in supporting cognitive processes has been assessed through different experimental paradigms aimed to measure cortical activity elicited by specific cognitive tasks (Buzsáki, 2010;Buzsáki et al., 2013).

The most important evidence for the association between oscillations and cognitive processes, is the synchronized activity of neural networks during perceptual and sensory processing (Engel et al., 2001; Ward, 2003). Synchrony is necessary when information needs to be retained or integrated, and it is usually visible as a coherent brain activity in the EEG (Hutcheon & Yarom, 2000; Varela et al., 2001). The strength of neuronal synchronization depends on the velocity of signal conduction, which is globally mediated by low frequency ranges, such as theta or alpha frequency ranges (Buzsáki et al., 2013). According to Buzsáki (2010) synchrony is defined by the time window in which information is retained, whereas successive events that evoke identical responses can induce non-synchronous activation of neural networks. For example, synchronous and asynchronous activity in the basal ganglia can induce the so-called event-related desynchronization/synchronization over cortical areas (Gatev et al., 2006). This pattern of synchronization and desynchronization is generally accepted as the modulatory activity of communication between (and within) the cortex and other subcortical structures.

The event-related spectral desynchronization was firstly described by Pfurtscheller & Aranibar (1977) in the alpha and in the beta frequency bands, and is commonly accepted as the index of the activation of the corresponding cortical area. In contrast, the event-related spectral synchronization is associated with the reduction of cortical activation (Pfurtscheller & Aranibar, 1977). Both phenomena can be studied by analysing the power spectral changes in the frequency domain, by which the power spectral changes of the EEG activity are averaged, and time locked to events. This analysis, also known as time-frequency analysis, is usually represented by a two-dimensional image called event related spectral perturbation (Pfurtscheller & Da Silva, 1999; Makeig et al., 2004, see Figure 1.2).

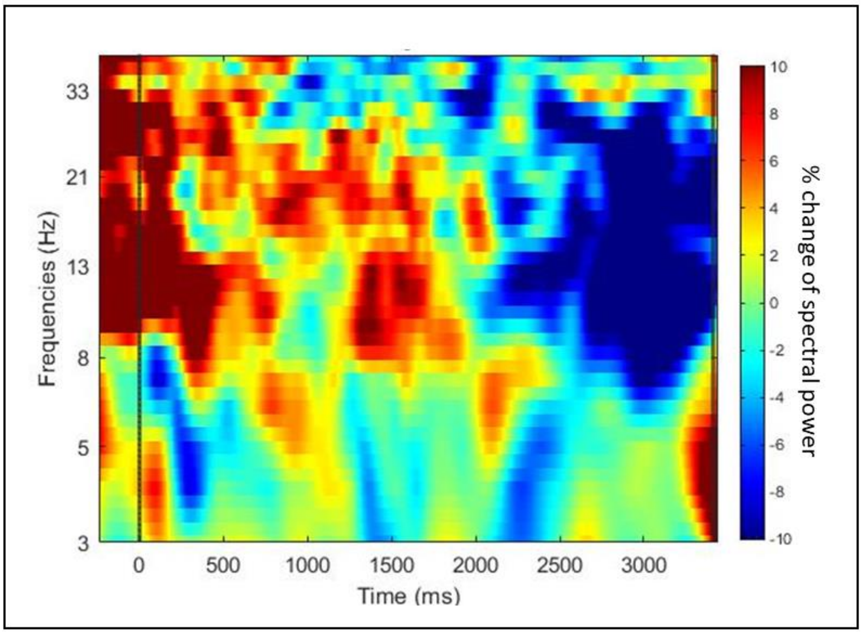

Figure 1.2. Mean event-related changes in spectral power (ERSP) computed as the percentage change from baseline, during the epoch of interest at frequencies ranging from 3 to 35 Hz. The image shows an increase of power in the frequency range of 10-35 Hz during the first 500ms, and a decrease in power around 2500ms and lasting until 3500ms in the frequency range of 7-33 Hz.

One of the principal pieces of evidence of previous EEG investigations is that distinct oscillations in particular frequency ranges are generated by specific tasks, suggesting a functional specialization (for a recent review see Klimesch, 2018). The first example was reported by the pioneering studies of Berger (Berger, 1929) who observed different power spectral changes in the alpha frequency band during rest with eyes closed compared to rest with eyes open. Following this first observation, EEG investigations have aimed to identify the functional significance of brain oscillations by analysing the frequency domain using the event related spectral perturbation in response to cognitive tasks. However, mostly cognitive functions are investigated in isolation, therefore multiple interpretations have been proposed for the same oscillatory range, resulting in separate and distinct hypotheses for the same frequency band. For the purpose of this thesis, only evidence regarding theta, alpha and beta oscillations bands will be discussed in relation to action control, motor imagery and action observation, which are the focus of the three studies reported in Chapter 2, 3 and 4 respectively. Therefore, in the following sections, previous evidence regarding the interpretation of theta, alpha and beta oscillations will be discussed in relation to action representation during voluntary actions, motor imagery and action observation.

1.7.1. Theta and action representation in execution

The role of slow oscillations in the theta frequency range (6-12 Hz in rats, 4-7 Hz in humans) have been for long the centre of an animated debate. Mainly, electrophysiological evidence of theta oscillations has been collected on animals. The first hypothesis about the role of theta oscillations in the brain associated these slow waves to arousal, following the observation of cortical and hippocampal theta activity during the administration of noxious stimuli in anesthetized rabbits (MacLean et al., 1952; Green & Arduini, 1954). Subsequently, theta waves were recorded in both rats and cats during active behaviour, such as locomotion, spatial orientation, and memory tasks (Vanderwolf, 1967, 1969). These observations were then consistently reported in a large body of animal studies, involving rats, guinea pigs, dogs, cats, gerbils and suggested a role for theta oscillation in the preparation of voluntary behaviour (Kramis et al., 1975). This view was then followed by an alternative hypothesis developed by Bland (1986) who suggested the role of theta waves in integrating sensory motor information during behaviour in rats.

In humans, theta activity has been difficult to record, mainly because this rhythm is not as prominent as the hippocampal theta of animals. Furthermore, it is difficult to establish an relation between functions exploited by cortical oscillations in animals and humans, as the same cognitive function might be subserved by distinct frequency ranges. For example, theta oscillations over the visual cortex in rodents exhibit some similarities with human alpha rhythm (Senzai et al., 2019). Additionally, another difficulty for a univocal interpretation is represented by the pervasive presence of theta rhythm in different cognitive tasks (Cruikshank et al., 2012). Indeed, theta oscillations have been regarded as the index of different cognitive functions, such as attention (Aftanas & Golocheikine 2001; Banquet 1973; Brookings et al. 1996; Ishihara & Yoshii 1967; Mizuki et al. 1982; Mundy-Castle, 1957; Nakashima & Sato 1993; Smith et al. 2001), memory (Gevins et al. 1997; Gruber et al. 2008; Jensen & Tesche 2002; Klimesch et al. 2001; Krause et al. 2000; Onton et al. 2005; Sederberg et al. 2003), spatial navigation (Caplan et al. 2001, 2003; de Araujo et al. 2002;

Ekstrom et al. 2005; Kahana et al. 1999, 2001). Similarly to animal models, theta oscillations have been proposed to underlie sensorimotor integration, in analogy with Bland’s hypothesis (Caplan et al. 2003). This perspective is supported by several evidence that showed that during the planning and the initiation of a motor response, theta activity increases over the motor brain areas (Tombini et al., 2009; Mehring et al., 2003; Perfetti et al., 2011; Cruikshank et al., 2012).

Neuroscientific evidence on humans has also pointed to the role of theta activity in action monitoring in relation to the error-related negativity (ERN). The ERN is a negative event related potential, also known as error negativity (Ne), which has been consistently reported to occur with the appearance of erroneous responses (Ghering et al., 1990; Gehring et al., 1993, 1995; Falkestein et al., 1991; Dehaene et al., 1994). The ERN peaks approximately around 150 ms after the incorrect response, and it is temporally aligned with the onset of the electromyographic (EMG) signal in the muscle involved in the response (Botvinik et al., 2000). In the seminal studies of Gehring et al. (1993) and Dahaene et al. (1994), the ERN was observed during the performance of the Eriksen Flanker task (Eriksen & Eriksen, 1974; Coles et al., 1985), known to induce erroneous responses. In both studies, the ERN was recorded following incorrect responses but not correct ones. Furthermore, the ERN was maximal over medial prefrontal brain areas, specifically over the anterior cingulate cortex and the supplementary motor areas, suggesting that these areas might play a key role in the online monitoring of performance (Ghering et al., 1990; Gehring et al., 1993; Dahaene et al., 1994). After these studies, different perspectives emerged regarding the role of the ERN. The first hypothesis (Falkestein et al., 1991; Ghering et al., 1990; 1993) pointed towards a response checking process. According to this interpretation, the ERN represents the correlate of a cognitive mechanism which detects the mismatch between the actual (erroneous) response and the action representation of the required response. The second hypothesis suggests that the ERN is not related to comparative processes but arises when a task induces the competition between different conflictual responses, which more likely generates erroneous performances (Carter et al., 1998). However, a third perspective supported by evidence of the occurrence of the ERN both during correct and incorrect responses (Scheffers et al., 1996; Vidal et al., 2000; Luu & Tucker 2001) pointed towards a general mechanism for the evaluation of action consequences, of both correct and incorrect responses (Luu et al., 2003; Vidal et al., 2003).

A critical finding was provided by Luu & Tucker (2003) who revealed that the ERN shows association with the midline frontal theta for both correct and incorrect responses during the performance of the Eriksen Flanker task. This association was consistently reported by other studies, which suggested that midline frontal theta could be the generator of the ERN (Luu et al., 2004; Trujillo & Allen, 2007; Cavanagh et al. 2009) and might index the monitoring of action outcomes (Cavanagh et al., 2009; 2010). Specifically, midline frontal theta might signal the need for an online behavioural adaptation, especially after erroneous responses (Cavanagh et al., 2010). This perspective is further supported by the observation of increased theta activity over mid-frontal and sensorimotor areas during challenging balance tasks (Slobounov et al., 2009; Sipp et al., 2013) and in response to external perturbations (Peterson & Ferris, 2018). Most of these findings reported the increase of power over the anterior cingulate cortex that has been related to detection of errors and online monitoring of actions (Anguera et al. 2009; Slobounov et al. 2009; Sipp et al., 2013).

1.7.2. Theta and action representation in Motor Imagery

The original account of motor imagery changed substantially over the past 30 years due to the growth of scientific evidence. Recently, a multidimensional perspective regarding motor imagery as has been proposed (Eaves & Cumming, 2018). According to this view, cognitive processes underlying motor imagery include different functions, namely generation, inspection, transformation, and maintenance. Generation includes the process of producing a transient mental image from sensorimotor long-term memories, created during previous experience. Inspection involves the shift of attentional focus on perceptual properties, to extract and encode relevant information. Transformation involves the manipulation of the features of the motor image. Finally, maintenance is defined as a supporting process for the other functions which ensure the achievement of the required goal.

The multidimensional account, which is based on a computational approach developed by Kosslyn (2006) for visual mental images, received strong support from brain imaging studies. These investigations revealed the involvement of a broad frontoparietal-striatal network in motor imagery tasks, suggesting that motor imagery involves a large range of cognitive functions, such as working memory, action monitoring, predictive coding, attention, and sensorimotor integration. In line with the multidimensional model of motor imagery, this chain of cognitive mechanisms would ensure the different steps, i.e., generation, inspection, transformation, and maintenance of the motor image (Guillot et al., 2014; O’Shea & Moran, 2017; Eaves & Cumming, 2018). Furthermore, recent EEG studies (Van der Lubbe et al., 2021) suggested that motor imagery involves more executive control compared to actual execution, which support the different operations included in the multidimensional model (Eaves & Cumming, 2018).

As mentioned in the previous section, a neural correlate for executive functions has been identified in theta rhythm. Theta rhythm over frontal areas has been associated with action monitoring, error prediction, and generally to top-down cognitive control (Cavanagh et al., 2010). It has been proposed that theta oscillations might reflect cognitive control processes also in motor imagery. This is supported by several electrophysiological evidence showing increased theta activity in skilled participants. Weeber & Doppelmayr (2016) examined the effects of motor imagery training in a dart throwing task. EEG activity was recorded at the beginning and at the end of the 15 training sessions. At the end of the training, they found significant higher theta increase in middle frontal electrodes compared to the first session only in the group of participants that underwent the motor imagery training, but not in a control group that received no training. Other studies from sports literature showed that midline frontal theta is associated with top-down cognitive control during movements (Baumester et al., 2008; Doppelmayr et al., 2008; Luchsinger et al., 2016). Baumester et al., (2008) observed a higher theta power in experts compared to novices during golf-putting. Doppelmayr et al. (2008) found that midline frontal theta was higher in expert shooters compared to novices just before rifle shooting. Similarly, Luchsinger et al. (2016) showed a larger increase of midline frontal theta in experts compared to novice skiers towards the shooting.

Conversely, other evidence showed different findings in experts and novices. Manicucci et al., (2020) found that participants with low-score in kinaesthetic imagery ability measured with the Movement Imagery Questionnaire (MIQ-3, Hall &Martin, 1997) exhibit less theta power over frontocentral brain areas, which might indicate the need for a greater cognitive effort to perform the imagery task compared to high-score participants. These findings are in line with the study conducted by Ahn et al. (2013). They showed that theta oscillations were associated with the brain computer interface (BCI) user performance, and that increases in theta power were associated with illiterate users, suggesting recruitment of additional attentional resources. Similarly, Trambaiolli et al. (2019) reported higher theta power in ‘literate’ participants performing a motor imagery task requiring them to move a cursor on a screen using neurofeedback. They found that good performers exhibited a higher theta power compared to ‘illiterate’ participants.

These findings offered two possible interpretations. According to the first hypothesis, theta oscillations might represent the recruitment of greater attentional resources in good motor imagery performer, which is supported by evidence of the association between theta oscillation and attentional processes (Haufler et al., 2000; Kubota et al., 2001; Luu et al., 2003; Nakashima & Sato, 1993; Sauseng et al., 2006). The second hypothesis argues that theta activity during motor imagery might reflect the feedback of the performance, supported by evidence that shows how theta activity might signal the evaluation of action outcomes (Cavanagh et al., 2009; 2010). In these terms, the higher theta power in good performers would mean a greater engagement in feedback and learning compared to bad performers. Van der Lubbe et al. (2021) examined the involvement of frontal areas using a Go/No-go discrete sequence task in which participants had to perform a sequence of five finger movements pressing different keys of a keyboard with the left or the right hand. The participants had to execute, imagine, or withhold the movement. They found a higher frontal-central theta increase of power during the motor imagery condition, compared to the execution and the inhibition of movements. The findings suggest a greater engagement of attentional processes and effort during motor imagery, but also a possible involvement of top-down cognitive control processes (Sauseng et al., 2005, 2006; Luu et al., 2003).

1.7.3. Theta and action representation in Action Observation

The role of theta oscillations has been investigated also in relation to action observation. Preliminary studies on children aged 2-7 years, showed that during action observation of biological movements a prominent theta band suppression occurred over frontal, temporal and central brain areas compared to the observation of both static objects and objects in movement (Cochin et al., 2001). These findings were further confirmed on children aged 5-7 years, in which a prominent theta band suppression was found over central, parietal, and temporal areas during action observation (Martineu et al., 2008) This evidence suggests that theta oscillations might represent the neural marker of the development of mirror functions in the cognitive system, which starts from slow oscillations, and it is replaced by faster frequency ranges during the adolescence, such as alpha rhythm (8-12 Hz, Oberman et al., 2013).

Furthermore, studies on neurotypical human adults also reported theta desynchronization during action observation tasks. Frenkel-Toledo et al. (2016) investigated cortical activation during rest, execution, and observation of reaching and grasping hand movements and observation of non-biological movements (i.e., a ball rolling on a surface). The data indicated a stronger theta suppression occurring during action observation of hand movements compared to non-biological movements. Urgen et al. (2013) investigated theta oscillations during action observation of five upper body actions performed by a human agent, a human-like robot and a robot. They found that the observation of the movements performed by the robot elicited a stronger increase in the theta power over frontal and central electrodes compared to the humanoid and android movements. In both studies, theta oscillations have been proposed to index cognitive processes that are distinct from the action simulation processes occurring during action observation. It has been suggested that theta rhythm might be related to the encoding of the action representation in working memory(Duzel et al., 2005; osipova et al., 2006; Zion-Golumbic et al., 2010; Klimesch et al., 2010). Additionally, consistently with previous studies which associated theta activity with semantic linguistic congruence (Hald et al., 2006; Davidson & Indefrey, 2007; Bastiaansen et al., 2008; Shahin et al., 2009), Urgen et al. (2013) pointed out a possible specific role for theta activity in integrating perceptual information and semantic memory during the observation of actions.

An alternative explanation regarding the role of theta oscillations during action observation has been proposed by Babiloni et al. (2017). They examined the functional connectivity of theta oscillations over premotor and frontal brain areas during action observation and execution of reaching and grasping movements towards different objects through the electrocorticographic (ECoG) recording in epileptic individuals. The results indicated a stronger functional connectivity in both delta and theta frequency range (3-8 Hz) occurring within prefrontal and premotor networks during the execution of reaching and grasping movements compared to their observation. According to Babiloni (2017), theta and delta oscillations are involved in enhancing neural connections between distant brain areas, depending on task-related demands. In other words, higher functional connectivity would promote coordination within a broad neural circuit, especially in conditions requiring additional cognitive resources. This explanation is furthermore consistent with the sensorimotor integration account, which highlight the role of theta oscillations in the integration of motor programs and sensory information for the online monitoring of action outcome (Bland & Oddie, 2001; Caplan et al., 2003; Ekstrom et al., 2005).

1.7.4. Alpha and action representation in execution

In the early 20th century, Hans Berger observed that when adults relax with eyes closed, a rhythmic activity around 10 Hz emerges from posterior scalp regions (Berger, 1933). This observation suggested that in absence of external visual stimulation or motor output, the brain produces a resting rhythm, characterised by power suppression (Kuhlman, 1978). Following this observation, the alpha power suppression over posterior brain areas was interpreted as the index of bottom-up processing (Klimesch et al. 2007). However, this interpretation was then questioned by the evidence that alpha oscillations can be also suppressed in absence of visual stimulation in a dark room with eyes open (Adrian & Matthews, 1934; Penfield & Jasper, 1954; Moosman et al., 2003). Moreover, alpha power suppression is not only observed over occipital scalp areas, but also over central brain regions during movements (Pfurtscheller, 1989; Pfurtscheller & Berghold, 1989), over frontal sites during semantic processing (Klimesch et al., 1997; 1999), and over parietal areas during memory tasks (Klimesch et al., 2006). Walter (1950) was the first to indicate that each individual's alpha rhythm is the outcome of different oscillatory patterns, corresponding to the 'most highly synchronised process over the largest superficial area' (Walter, 1950 cited in Guntekin & Basar, 2007). According to Walter's account, Galambos (1992) classified the alpha 'rhythms' in two general categories: spontaneous alpha (generated spontaneously in the brain) and induced alpha (induced by external sensory stimuli). Subsequently, Basar et al. (1997) highlighted the necessary use of the term 'alphas' and indicated four main dynamics for alpha patterns, which can be spontaneous, evoked, induced and emitted. Spontaneous patterns reflect an integrative process of different brain functions. Induced patterns are defined as initiated but not time-locked to a stimulus. Evoked reflects the pattern of alpha activity time-locked to a stimulus. Emitted indicates a pattern of activity observed in anticipation of the external stimulation.

Since these observations, different hypotheses about the functional and cognitive meaning of alpha have been proposed. A popular hypothesis suggested by Pfurtscheller et al., (1996) is that alpha might reflect the general activation of the brain, i.e., an 'idling' rhythm of the brain, which has been indicated as the state of the brain when no external stimulation is provided (Adrian &Matthews, 1934). The general premise to this account is that brain areas engaged in a given task, display event-related desynchronization, whereas brain areas that are not related to the task and represent a potential interference, present event-related synchronization. As suggested by Klimesch (2012), a strong support for this account, is provided by the evidence that alpha suppression is usually observed in response to different tasks (Pfurtscheller & Lopes da Silva, 1999), it is widespread over the scalp and it usually lasts until the end of the task, suggesting that alpha power suppression might reflect active processes (Kaufman et al., 1990, 1992; Michel et al., 1994). Differently, alpha event-related synchronization represents the neural correlate of a specific localised idling rhythm, which can be recorded over brain areas that have 'nothing to do' (Adrian & Mattews, 1934, cited in Pfurtscheller et al., 1996b). This observation was supported by the evidence that areas that are not related to the processing of information related to the task at hand present alpha power synchronization. For example, alpha power synchronization can be observed over hand areas during foot movements (Pfurtscheller & Neuprer,1994) and during visual stimulation (Brechet & Lecasble, 1965; Pfurtscheller & Klimesch,1992).

Within motor cortical areas, alpha oscillations have been observed during preparation and execution of movements. As mentioned before, around 2 seconds prior to the movement onset, a strong desynchronization in the alpha band (8-14 Hz) appears contralaterally in the motor cortex and then becomes bilateral with the movement execution. The alpha suppression is sustained during movement and gradually dissipates around 2 seconds after movement cessation (Gastaut, 1952; Pfurtscheller & Aranibar, 1979; Toro et al., 1994; Pfurtscheller & Berghold, 1989; Stancák & Pfurtscheller, 1996; Jurkiewicz et al., 2006; Heinrichs-Graham et al., 2013). The cortical activation observed prior to the movement onset has been suggested to represent the preparation of the relevant sensorimotor circuits needed to implement the actual execution of the movement (Georgopoulos et al., 1989; Pfurtscheller et al., 1997).

However, a controversial finding for the idling rhythm hypothesis, is that alpha synchronization can be observed also during the active performance of a task. As reviewed in Klimesh (2012), in memory tasks in which a particular piece of information needs to be retained before providing the appropriate response, alpha power synchronization occurs over parietal areas (Schack et al., 2005). Moreover, alpha synchronization can be observed over motor areas during motor tasks that require inhibition of movement (Hummel et al., 2002) or during the motor imagery of movements (Neuper et al., 1999; Pfurtscheller & Neuper, 1997). These observations support a possible role of alpha synchronization in inhibitory top-down processes (Klimesch et al., 2012).

Another hypothesis has been proposed by Pineda (2005) which highlights the role of alpha rhythm in linking perception and action. This hypothesis is supported by evidence of alpha power suppression over the sensorimotor cortex during execution, motor imagery and action observation of movements (Pfurtscheller, 1992; Pfurtscheller et al., 2000; Babiloni et al., 1999; Pineda et al., 2000). Alpha oscillations over central sensorimotor areas, also called 'mu rhythm', have been proposed to signal the modulation of sensorimotor areas driven by the mirror neuron system. The hypothesis regarding alpha mu rhythm as a common denominator between perception and action, proposed by Pineda, accounts also for the existence of multiple alpha rhythms in the brain and the global-local organization. According to this view, functionally specialised local networks produce alpha oscillations independently. When they become coupled, a coherent and global alpha modulation can be observed over a distributed system that includes the independent sources. This local-global entrainment is coherent with the pattern of desynchronization and synchronization of alpha patterns observed over the scalp across different tasks (Pineda, 2005 but see also Wiener, 1955, 1956). Thus, global synchronization might represent a gating system which encodes different representations, such as visual and auditory information, into action representations, facilitating the local entrainment of different brain areas and translating 'seeing' and 'hearing' into 'doing' (Pineda, 2005).

1.7.5. Alpha and action representation in Motor Imagery

As mentioned before, the event related desynchronization in the alpha rhythm over the sensorimotor cortex is usually observed prior and during the execution of a movement (Gastaut, 1952; Pfurtscheller & Aranibar, 1979; Toro et al., 1994; Pfurtscheller & Berghold, 1989; Stancák & Pfurtscheller, 1996; Jurkiewicz et al., 2006; Heinrichs-Graham et al., 2013). In the middle 20th century, clinical studies reported a blocking of the rolandic 'wicket' alpha rhythm during passive movements, after spoken orders or tactile stimulations (Chatrian et al., 1959). The blocking of sensorimotor alpha rhythm was also reported when movements were imagined with the phantom limb in amputated patients (Klass & Bickford, 1957; Gastaut et al., 1965).

Since these studies, a large body of evidence reported a suppression of alpha oscillations over motor areas also when there is no overt motor output, i.e., during motor imagery (Babiloni et al., 1999; Pfurtscheller & Lopes da Silva, 1999; Crone et al., 1998b; Miller et al., 2007). In particular, the series of experiments performed by Pfurtscheller and colleagues, had a large impact on the scientific debate about the investigation of neural correlates of motor imagery. In their seminal studies during 1996-1997, Pfurtscheller and colleagues asked participants to imagine a movement performed either with the left or the right hand. During the task, a power suppression in the alpha band was observed over the contralateral primary sensorimotor hand area, similarly to the alpha event-related desynchronization observed during the preparation of the real hand movement. This suggested that motor brain areas are similarly activated when planning a movement and when imagining performing the same movement. At the same time, an alpha synchronization was observed ipsilateral in the sensorimotor hand area. The alpha power increase in the ipsilateral hand areas, has been interpreted as the inhibition of irrelevant brain processes. This pattern has been later called ‘focal ERD/surrounding ERS’ (Suffczynski et al., 1999).

Despite the great impact of these studies on the understanding of neural correlates of motor imagery, previous investigations did not consistently report this pattern in the alpha frequency range. In Pfurtscheller et al., (2001) only a subset of the participants showed the expected imagery-related EEG activity. Furthermore, in other studies (Pfurtscheller et al., 2005 and Pfurtscheller & da Silva, 1999) they reported a high intra-subject variability within the activated frequency bands. A possible explanation to this inconsistency regards the type of motor imagery performed by participants. Indeed, two main kinds of imagination have been related to motor imagery, as described by Annet (1995). The imagination of movements can be performed either from a first-person perspective, ‘with an interior view’, i.e., kinaesthetic imagery, or from a third person perspective, as an ‘external observer’, i.e., visual imagery (Sekiyama, 1983). To test this hypothesis, Neuper et al. (2005) compared participants' performance during the execution and imagination of hand movements (clenching a ball with the right hand) both in the kinaesthetic and in the visual imagery modality. The results indicated that distinct patterns of power suppression and power increase of alpha and beta oscillations occurred during the two imagery modalities. Specifically, only the kinaesthetic imagery showed the expected event related desynchronization/synchronization pattern over the sensorimotor hand area in the alpha and in the beta frequency ranges, whereas the visual imagery modality did not show evidence of this pattern. These findings were later corroborated by other EEG investigations (Cremades, 2002; Cremades et al., 2007; Stecklow et al., 2010) and brain imaging studies (Solodkin et al., 2004; Guillot et al., 2009). Cremades (2002) examined cortical responses in expert and novice golfers during visual and kinaesthetic imagery of golf putting movements. They found a larger suppression of alpha power during kinaesthetic compared to visual imagery in experts compared to novices. Similarly, Stecklow et al. (2010) investigated the cortical activity in volleyball athletes and non-athletes during motor and visual imagery of a volleyball attack movement and a hand clapping movement. They found a prominent alpha desynchronization in athletes during kinaesthetic imagery of volleyball movements compared to non-athletes. This evidence showed that alpha activity might be modulated by the perspective but also by the knowledge of movement and the level of expertise. Indeed, several recent studies found similar results (Niedermeyer, 1977; Gerloff et al., 1998; Martin et al., 2017; Nishimura et al., 2018; Ruggirello et al., 2019). Furthermore, alpha oscillations during motor imagery have been found to be modulated by the complexity of the imagined movement. Zabielska-Mendyk et al. (2018) found that in expert pianists, alpha desynchronization was larger for complex movement compared to simple ones, whereas in non-professional pianists the level alpha suppression did not discriminate between complex and simple movements.

1.7.6. Alpha and action representation in Action Observation

In 1954, Gastaut and Bert proposed to study the cortical activity with the EEG in situations that are close to real life and far from the static position of traditional experiments. Therefore, they investigated the cortical activity during the observation of a ‘newsreel’ showing biological motion, such as ski jumps, boxing matches, and bike races. The analysis of the EEG activity showed an alpha rhythm desynchronization over central brain areas, interpreted as the index of the identification of the human actors observed.

Since these pioneering studies, the alpha desynchronization during observation of other movement has been regarded as the index of the downstream activation of the mirror neuron system on sensorimotor areas (Muthukumaraswamy & Johnson, 2004a) and has been consistently reported in EEG studies on action observation. Cochin et al. (1999) examined the EEG response in 20 healthy participants during the execution and observation of pincer movements executed with fingers by a model, and resting state. They showed that both the execution and the observation of the movement elicited a decrease in the alpha spectral power over frontal and central electrodes, which are thought to be included in the mirror neuron system in humans. Babiloni et al., (2002) suggested that alpha rhythms might have different roles depending on the spatial distribution over cortical areas. They compared the cortical activity during the execution of finger extension and the observation of the same movement in 10 healthy participants. They reported a stronger blocking of alpha rhythm over parietal and occipital areas compared to execution, but not in central areas. Additionally, they found an alpha increase of power only after movement observation over parietal sites. Frontal alpha suppression was found to be contralateral to the observed movement whereas execution was characterized by an ipsilateral alpha desynchronization. As suggested by the authors, whereas the alpha rhythm over frontal areas might be related to the activation of sensory information about the movement facilitating the understanding of the observed action, posterior parietal cortex alpha suppression might signal the integration of visual and motor information of the observed actions, as the parietal cortex receive input both from motor areas and occipital cortex. These findings opened the possibility of multiple roles of alpha rhythms within the action observation network.

Other studies instead suggested that the alpha rhythm over central areas might be highly specialized and related to the processing of specific movement parameters. Muthukumaraswamy & Johnson (2004b) reported stronger suppression of alpha oscillations over primary sensory and motor areas, during the observation of a precision grip towards an object compared to the observation of a flat hand extension movement. In a separate similar experiment, Muthukumaraswamy et al. (2004) tested the hypothesis that alpha power might be modulated by the goal of the observed movements, rather than the movement parameters. They compared the cortical activation between execution, flat hand extension, precision grip with no object and precision grip towards an object. Confirming the previous findings, the alpha power suppression was found to be generally stronger when participants observed the precision grip compared to the flat hand extension. However, they also found that the precision grip towards an object elicited a more prominent alpha suppression than an empty precision grip. This suggested that alpha oscillations over sensorimotor areas, as the index of the mirror neuron system in humans, respond to the observation of goal-directed behaviours, compared to non-goal-oriented actions (Jonson-Frey et al., 2003; Schippers & Keysers, 2011; Hamilton, 2013; Buccino et al., 2001, 2004; Wheaton et al., 2004; Rizzolatti & Fogassi, 2014).

Within the mirror neuron system framework, alpha oscillations have been also related to social interactions (Tognoli et al., 2007; Kilner et al., 2006). Tognoli et al. (2007) investigated alpha oscillations during visually mediated social interactions. EEG activity was recorded during visually guided and not-visually guided social interaction conditions. In the visually guided social interaction condition, participants observed another person movement and then performed the same (coordinated action) or a different action (not coordinated action). In the not-visually guided social interaction condition, participants were not able to observe others’ movements. The data demonstrated that alpha rhythm is more suppressed during the observation of others' actions regardless of the coordination, compared to actions that are not fully visible. As suggested by Urgen et al. (2013), these findings support a role for alpha in matching visual input with the semantic motor representation stored in memory, which is in line with the hypothesis for a function of integrating perpetual, memory, and motor information into a meaningful action representation (Pineda, 2005).

1.7.7. Beta oscillations as sensorimotor rhythm for action

Described for the first time by Berger (1929) and Tonnies (1934), the suppression of beta (13-30 Hz) oscillations has been commonly reported over the sensorimotor cortex during the planning and the execution of movements compared to rest (Neuper et al., 2006; Pfurtscheller & Berghold, 1989; Pfurtscheller & Lopes da Silva, 1999). Mainly, beta rhythm has been reported along with alpha oscillations, as an index of sensorimotor processing (Hari & Salmelin, 1997; Pfurtscheller & Lopes da Silva, 1999; Bauer et al., 2006; Schubert et al., 2009; Jones et al., 2010; Van Ede et al., 2011). Aside from movement execution and preparations, other investigations reported beta modulation also in relation to different kind of cognitive processing, such as memory (Sederberg et al., 2006; Tallon-Baudry et al., 1998; Deiber et al., 2007), inhibition (Tempel et al., 2020), reward (Massar et al., 2014) and temporal predictions (Meijer et al., 2016).

Due to their extensive presence over the brain, the origin of beta oscillations has been an object of debate. There are two possible hypotheses related to the neural origin of beta rhythm, which are respectively indicated as the local generator model and the subcortical model. Accordingly with the local generation model, beta oscillations originate from the cortex (Jensen et al., 2005; Roopun et al., 2006; Kramer et al., 2008; Kopell et al., 2011; Sherman et al., 2016) and their role is to maintain long-distance inter area communication (see Koppel et al., 2000). Another perspective sees beta oscillations originating in the basal ganglia and propagating then in the cortex (Holgado et al., 2010; McCarthy et al., 2011).

Regarding the functional significance of beta oscillations within the sensorimotor cortex, two main models have been proposed. Sensorimotor beta rhythm has been firstly interpreted as an idling state (Pfurtscheller et al., 1996a; Neuper & Pfurtscheller, 2001). Similarly, to alpha oscillations, considered as the idling rhythm of the visual cortex, beta rhythm has been proposed as the idling rhythm of the sensorimotor cortex (Kuhlman, 1978; Pfurtscheller et al., 1996). This interpretation followed the observation that beta oscillations synchronise over motor areas that are not needed for a given task (Pfurtscheller et al., 1996a, 1996b) whereas during movements, beta desynchronized over motor areas contralateral to the movement performed (Pfurtscheller et al., 1995; van Wijk et al., 2012). Indeed, it is widely accepted that beta desynchronization over sensorimotor brain regions is the index of motor activation and may reflect the planning and the execution of voluntary movements compared to passive states (Neuper et al., 2006; Pfurtscheller & Berghold, 1989; Pfurtscheller & Lopes da Silva, 1999; Chung et al., 2017; Allen and MacKinnon, 2010; Kilavik et al., 2013; Pfurtscheller et al., 1994). In the post movement phase, the beta suppression is followed by a power synchronization over the same sensorimotor areas. This beta increase was associated with a deactivation or inhibition of neural networks not involved in that specific moment (Neuper & Pfurtscheller, 2001).

The second perspective suggests that beta oscillations index the maintenance of the current cognitive and motor state, also called the ‘status quo’ hypothesis (Engel & Fries, 2010; Jekinson & Brown, 2011). According to this model, beta activity might signal an active process which promotes the feedback processing and recalibrates the motor system after a change (Engel & Fries, 2010; Baker, 2007). This account is supported by evidence showing that beta increase of power also known as beta rebound, promotes the existing motor set at the expense of new potentially interfering events or movements. Indeed, during periods of enhanced beta synchronization movements have been shown to be slower (Gilberston et al., 2005), whereas postural control is enhanced, suggesting that beta rebound promotes the maintenance of steady-state force output (Androulidakis et al., 2006). Furthermore, it has been demonstrated that altered oscillatory patterns in the beta frequency band might induce slowing of movements, as reported in clinical studies on patient with Parkinson’s disease (Joundi et al., 2012; Pogosyan et al., 2009: Brown, 2007; Heida et al., 2014; Heinrichs-Graham et al., 2013; Little & Brown, 2014; Espenhahn et al., 2017). Beta rebound has been associated also with inhibition of movement initiation (Gilbertson et al., 2005; Zhang et al., 2008) and decreased corticospinal excitability (Chen et al., 1998).

However, the beta rebound is not only observed over sensorimotor areas after movement, but also during the active performance of other tasks. For example, several studies have reported beta increases over frontal, parietal and temporal brain regions during the online maintenance of information in working memory (Liebe et al., 2012; Wimmer et al., 2016; Deiber et al., 2007). Furthermore, beta rebound has also been reported during decision making tasks, before providing a motor response (Kaiser et al., 2001; Zhang et al., 2008). In line with this evidence, Spitzer & Haegens (2017) recently proposed an integrative view that takes in account the multiple roles of beta oscillations. According to this perspective, beta rhythm has been suggested to represent the index of an endogenous processing which supports the activation of cortical representation of task-relevant contents (Spitzer & Haegens, 2017).

Movement-related beta desynchronization is typically observed bilaterally over sensorimotor areas, whereas the beta rebound occurs ipsilaterally over the sensorimotor cortex (Salmelin and Hari, 1994; Stancák & Pfurtscheller, 1996). As mentioned above, whereas beta desynchronization has been related to the activation of sensorimotor areas, beta rebound has been related to inhibition, as an "idling" state (Engel & Fries, 2010) and to content-specific activation (Spitzer & Haegens, 2017). However, these findings have not been consistently reported, as several evidence showed that both beta desynchronization and the beta rebound might be affected by different variables. For example, Tan et al. (2014) showed that the amplitude of the beta rebound is inversely related to the magnitude of movement errors. Other evidence relates beta activity to attentional process and online processing (Sauseng & Klimesh, 2008; Gola et al., 2013). Chung et al. (2017) suggested that not only beta power, but the coordination of modulation of different frequency bands (alpha and theta) within the sensorimotor and parietal cortex are necessary for online update of the system, error monitoring and accuracy of motor performance. In an experiment with healthy controls and Parkinson's disease patients, Nelson et al. (2018) showed that the pattern of beta desynchronization/synchronization is directly related to motor memory retention and neural plasticity during the learning of a motor task. Kaiser et al. (2001) suggested that beta desynchronization before movement may represent the selection process of possible movements to carry out. Furthermore, Tzagarakis et al. (2010) and Doyle et al. (2005) showed that beta suppression may be related to movement uncertainty: beta desynchronization is greater when choices are limited to narrower range of movement alternatives (e.g., subjects already know which side of the body to move) compared with a higher range of possibilities. The functional significance of the 'up and down' of beta oscillations over the sensorimotor cortex still deserves further investigation**.**

1.7.8. Beta and action representation in Motor Imagery

The first evidence of similar dynamics of beta oscillations during movements and during the absence of motor output was reported in 1954 by Jasper and Penfield. They observed a suppression in the beta frequency range over the contralateral sensorimotor cortex during a tactile stimulation. Later, it was also found that beta event-related desynchronization/ synchronization patterns can be observed also during the anticipation of a tactile stimulation without motor output (van Ede et al., 2010). In the MEG study, van Ede et al. (2010) manipulated the expectation of tactile stimulation on the hands. They showed that just prior (330ms before) and following tactile stimulation, a beta power suppression occurred over the contralateral sensorimotor cortex and a beta rebound in the time interval between two consecutive stimulations. The involvement of beta modulation during the passive motor states was largely corroborated in the series of experiments carried out by Pfurtscheller and colleagues in the ’90s. As described in the first experiment (Pfurtscheller & Neuper, 1997) during motor imagery of finger movements, there was a suppression of both alpha and beta rhythms over central areas contralateral to the movement side. At the same time, a concomitant synchronization in the alpha and beta frequency ranges appeared over the ipsilateral central side.

A similar pattern has been reported across different EEG investigations on motor imagery (Salmelin et al., 1995; Pfurtscheller & Neuper, 2001; Salenius et al., 1997; Schnitzler et al., 1997; McFarland et al., 2000); although there is a certain level of variability among studies. In Pfurtscheller et al. (2005) for example, only a subset of participants displayed a clear beta rebound after the termination of imagery of hand or foot movements. Interestingly, the beta rebound was absent after imagery of tongue movements. The lateralization of the beta rebound has also not been confirmed across the studies. Several investigations reported the beta rebound over the ipsilateral areas during motor imagery of both right and left hand (Pfurtscheller et al., 1997b; Parasuraman & Rizzo, 2008), whereas Pfurtscheller et al. (2005) reported a contralateral beta rebound after hand motor imagery. Further research highlighted that the variability in the pattern of beta activity during motor imagery might be related to multiple factors. A possible explanation regards the parameters of movement. For example, Nam et al. (2011) found that the extent of the lateralization of beta power decrease and increase during motor imagery might be associated with movement duration. They compared cortical activation during brief and continuous motor imagery of both left and right hands and found a stronger contralateral power decrease and larger ipsilateral power increase in the beta frequency range in the brief motor imagery compared to the continuous motor imagery. The complexity of the movement to be imagined also plays a relevant role. Zabielska-Mendyk et al. (2018) found that beta desynchronization was larger in motor imagery of complex finger tapping movements compared to simple ones**.**

1.7.9. Beta and action representation in Action Observation

Typically considered as sensorimotor rhythm, beta oscillations have been related to pure motor domain. However, since their presence also occurs during tasks that do not require a motor output, i.e. during motor imagery, their possible involvement in action observation has been considered.

First investigations on beta oscillations during action observation have been carried out using MEG. Hari et al. (1998) examined cortical activity during the manipulation of a small object, the observation of the same movement performed by another individual, observation of moving and static objects and rest. The data showed that during both the execution and the observation of a movement, a similar beta suppression occurred over the precentral motor cortex. Cochin et al. (1998) recorded cortical activity during the observation of static landscapes, moving and static objects and animals and gymnastic exercises performed by humans. The data showed a decrease of power in the alpha frequency band over central areas but also a parallel posterior beta suppression, specifically over centroparietal and occipital areas during the observation of human movements compared to the other conditions. In an EEG experiment, Babiloni et al. (2002) investigated the cortical activation during both the execution and the observation of aimless finger movements (i.e., finger extension). The results showed that during execution and observation of aimless movements, beta power similarly decreased over premotor and primary motor areas, suggesting a mechanism related to the evaluation of the match between the observed action and one’s own execution. Furthermore, Avanzini et al. (2012) showed that the upper beta desynchronization was modulated by the speed of the observed movement, suggesting the encoding of the kinematics aspect of behaviour.

This evidence suggested a possible involvement of beta oscillations in visual perception of biological motion. However, different evidence suggested a role for beta beyond the visuo-motor match, but also in action understanding and the mirror neuron system. Järveläinen et al. (2004) In an MEG study, they compared the brain activation during execution and observation of both goal-direct-tool use movements (using chopsticks to move small objects) and non-goal directed tool use movements (using chopsticks without any goal). They found that goal direct tool use movements elicited a stronger suppression in beta power over the primary motor cortex compared to non-goal direct tool use. This would suggest a role for beta in encoding the goal of the action rather than the visual properties, in line with the account that considers the mirror neuron system for the understanding of actions performed by others. A further demonstration for a role of beta in the understanding of other actions is provided by Kilner and colleagues, which showed that beta (Kilner et al., 2009) was modulated by the perspective of the observer in respect to a model performing an action. Indeed, Kilner and colleagues (2009) found a stronger beta power suppression over sensorimotor areas contralateral to the side of the screen in which the movement was performed, but only the model was facing forward the participant, compared to the condition in which the model was facing away. This finding has been interpreted as a modulation in visuospatial attention driven by the social relevance of the observed action.

1.8. Mobile approach to study neural correlates of Action Representation

In the mid-20th century, Gastaut & Bert (1954) measured cortical activity during the observation of a cinematographic projection, claiming that to understand neural correlates of human cognitive processes, research needs to investigate contexts and actions that are close to real life, rather than simple and minimal behaviour studied in the traditional laboratory setting. This perspective was also generally pursued by theorists of ecological psychology, who highlighted the need for ecological validity in experimental paradigms (Brunswick 1943; Neisser, 1979; Bronfenbrenner, 1977). The changes proposed by the ecological account were directed towards a more naturalistic approach, through which cognitive processes are not anymore studied separately from the environment, even if without replacing the importance of controlled laboratory experiments. Indeed, naturalistic research should illuminate the properties of the laboratory experiments in ecological contexts, adapting each setting to the different research questions. This aspect was further sustained by theories of embodied cognition which extended the focus of research on the dynamic interplay between cognition, body and environment (Barsalou, 2008; Clark, 1999).

In the past two decades, the study of human mind and behaviour has been remodelled by the development of portable technologies. The emergence of mobile devices has brought the so-called Mobile Brain body Imaging (MoBI) research field, which aims to study natural behaviour in real world environments. The MoBI approach offers the exclusive possibility to revisit traditional experimental paradigms, in which participants are usually required to perform tasks in laboratory rooms, usually motionless, while seated in front of a computer screen or while lying down in a scanner. The MoBI approach provides the novelty of measuring neural correlates of human cognitive processes during complex natural behaviour in real world scenarios, bringing a totally new conception of neuroscientific research.

The MoBI framework is clearly embedded in the embodied perspective, adopting a methodological approach that is grounded on the concurrent study of mind and body (Makeig et al., 2009). Cognitive processes are intimately related to perception and action, and they need to be investigated in the natural environment. Indeed, several studies demonstrated that the environment and the state of the body affects brain activity and cognitive processes during both active behaviour (Gramman et al., 2011; 2014; Maimon et al., 2010) and imagination (Rizzolatti et al., 2002; Nunez & Srinivasan, 2006). Therefore, in order to understand human cognition, the concurrent recording of signals coming from the brain and the body is necessary. This represents one of the main challenges of the MoBI approach, which employ the synchronization between signals provided by different devices (e.g., EEG, EMG, eye tracking) in real world settings (Gramann et al., 2011; Makeig et al., 2009; Artoni et al., 2018; Ladouce et al., 2017). Meeting this challenge requires the development of more advanced technological solutions, such as the creation of wearable and easy-to-apply sensors, which allow the recording of high-quality signals during natural movements.

Although traditional brain imaging techniques such as fMRI or PET still represent the most powerful methodologies to study brain changes with high spatial resolution, direct measures of behaviour are more suitable to explore natural behaviour while individuals move freely within the environment. Techniques such as the near infrared spectroscopy (fNRIS) and the mobile EEG are the new frontiers of the mobile approach. The fNRIS employs sensors that measures changes in blood haemoglobin concentrations, which index the activity of the local brain areas. Although fNRIS provided relevant insights in the understanding of active human behaviour such as walking (Miyai et al., 2001; Suzuki et al., 2004, 2008; Harada et al., 2009) and obstacle avoidance (Maidan et al., 2018), it offers a low temporal resolution, not suitable to detect very fast changes in neural signals underlying cognitive processes. Differently, the mobile EEG represents a good compromise to explore neural oscillations underlying cognitive processes, as it provides a non-invasive recording of brain signals with an excellent temporal resolution, albeit with poor spatial accuracy.

Mobile EEG recordings have been previously applied in several research fields, such as sport performance (Park et al., 2015), environmental psychology (Mavros et al., 2016; Aspinall et al., 2015) neuro aesthetic (Djebbara et al., 2019), architecture (Djebbara et al., 2019) and neuro ergonomics (Wascher et al., 2021). There is a growing interest in neural recordings during locomotion and mobile EEG has been used during active walking task. However, previous MoBI investigations on walking took place on a treadmill and generally they did not actually explore cognitive mechanisms, which are largely involved in the control of locomotion (Gwin et al., 2011; Seeber et al., 2014; 2015; Bulea et al., 2015; Wagner et al., 2012; 2016). Indeed, a large body of evidence demonstrated that the control of locomotion involve a complex interplay between subcortical structures and cortical structures (Dietz and Duysens, 2000; Dietz, 2003; Nielsen, 2003; Drew et al. , 2004; Drew et al., 2008; Grillner et al. , 2008). However, until the emergence of mobile technologies, cognitive and neural processes related to human locomotion have been assessed through classical brain imaging techniques, which require the participants to sit or to lie down performing simple rhythmical movements with the feet (Luft et al., 2002; Dobkin et al., 2004; Mehta et al., 2009) or during the performance of motor imagery of walking (Jahn et al. , 2008; Wagner et al. , 2008; Wang et al., 2008; Jahn et al., 2009). It is clear, that tasks performed with the constraints of the scanner do not resemble real walking, which requires more complex cognitive dynamics such as the whole body postural control and the integration of sensory feedback from the body with external information coming from the surrounding environment.

The application of the mobile EEG technique in the study of human locomotion has seen somewhat of a proliferation in the context of the MoBI framework. Indeed, mobile EEG has been applied in outdoor spatial navigation (Reiser et al., 2019), speed control (Bulea et al., 2015), gait adaptations (Wagner et al., 2016), running and cycling (Gwin et al., 2011; Zink et al., 2016), attentional allocation while walking (Ladouce et al., 2019) or walking over different terrains (Luu et al., 2017). Furthermore, one of the most striking pieces of evidence provided by mobile studies showed that cortical activity is coupled with the gait cycle (Gwin et al., 2011; Seeber et al., 2014; 2015).

The interest in locomotion has also had a critical impact in clinical practice, where the mobile EEG could perhaps be used for neurofeedback and brain computer interface (BCI) systems. Neurofeedback is a technique whereby a user learns to control their own brain signals associated with behaviour, whereas BCI systems employ the brain activity as input signals to control external devices, such as prosthesis or exoskeleton (Wolpaw, 2002). The use of both systems has been increasingly applied in rehabilitative settings, as they represent a potential tool for patients with limited mobility (Millan et al., 2008; Hatsopoulos and Donoghue, 2009; Kim et al., 2011; Leuthardt et al., 2009; Scherberger, 2009; Zich et al., 2015; for a review see Kranczioch et al., 2014). Although the mobile EEG has been largely applied to investigate cognitive control of locomotion, the contribution to the understanding of human motor cognition has remained limited, especially in real world settings. Therefore, the aim of this thesis is to provide real world evidence of neural correlates of human motor processes related to motor cognition and action representation using the mobile EEG approach.

1.8.1. Technical challenges

The mobile EEG offers an exciting and unique opportunity for the understanding of human cognitive processes in real world settings. However, there are still several drawbacks, which mainly include the difficulty of removing motion artifacts and noise from the EEG recording. The development of potential solutions has seen in the past few years critical improvements. Indeed, several offline techniques have been proposed in order to reduce the interference created by noise and artifacts during real world recordings. One of the most used signal processing techniques is the independent component analysis (ICA, Bell & Sejnowski, 1995). The application of ICA has the potential to identify and separate artifacts related to eye, head and neck movements, cardiac activity, line noise from brain signals. The ICA has proven to be a successful technique in both traditional and MoBI investigations (Makeig & Jung, 1996; Makeig et al., 2002, 2004; Jung et al., 2000). The research group of the Swartz Center for Computational Neuroscience of the University of California San Diego has been the main promoter of solutions for the analysis of mobile EEG data, and recently another technique, called IClabel, has been proposed. IClabel is an automated tool which allows to identify and classify independent components (IC) after the ICA decomposition. This tool provides a consistent and statistically based categorization of ICs through a comparison with a large database of EEG dataset (Pion Tonachini et al., 2019, see Figure 1.3 and 1.4).

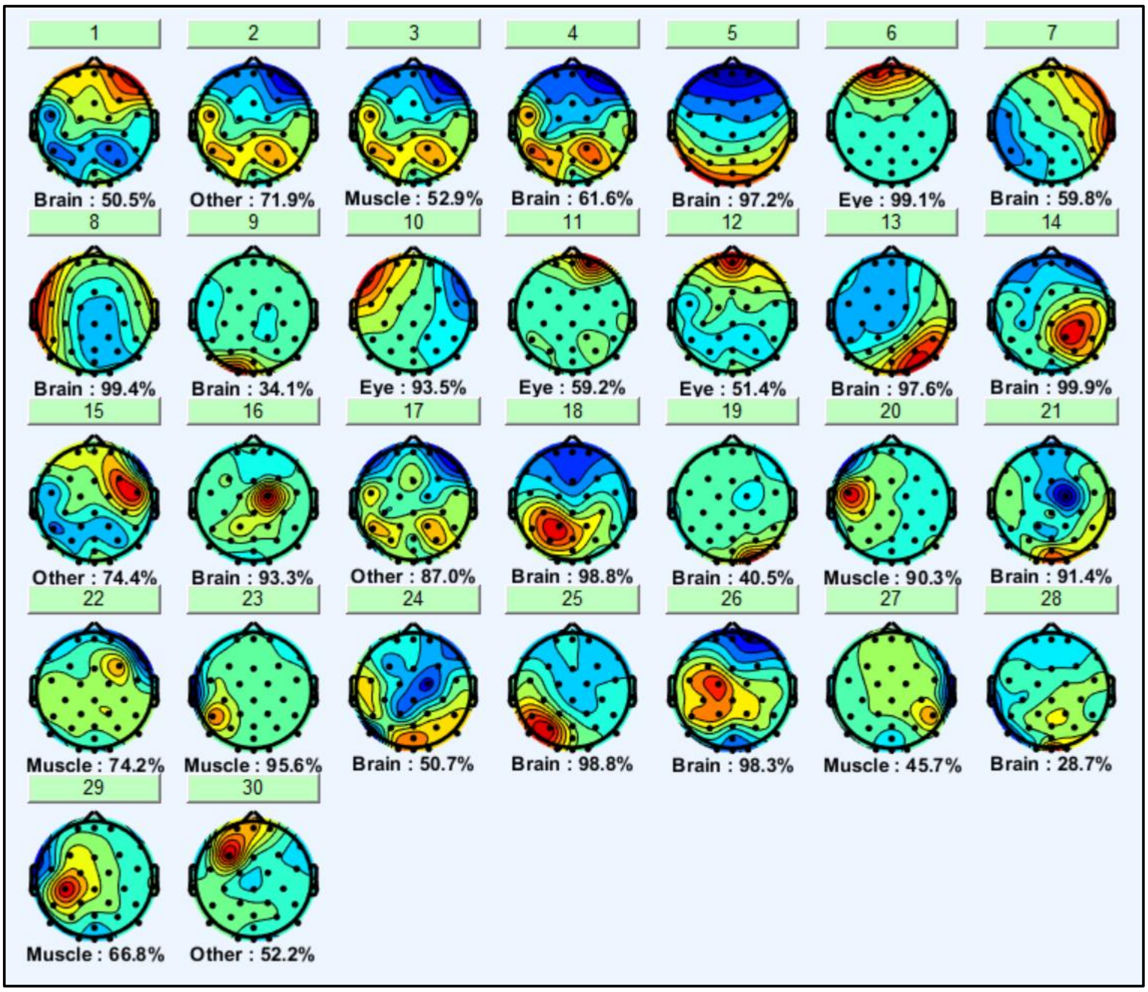

Figure 1.3. Scalp map projections obtained using IClabel plugin of EEGLAB (Pion Tonachini et al., 2019). The figures shows an example of the visualization of ICs labels offered by the algorithm.

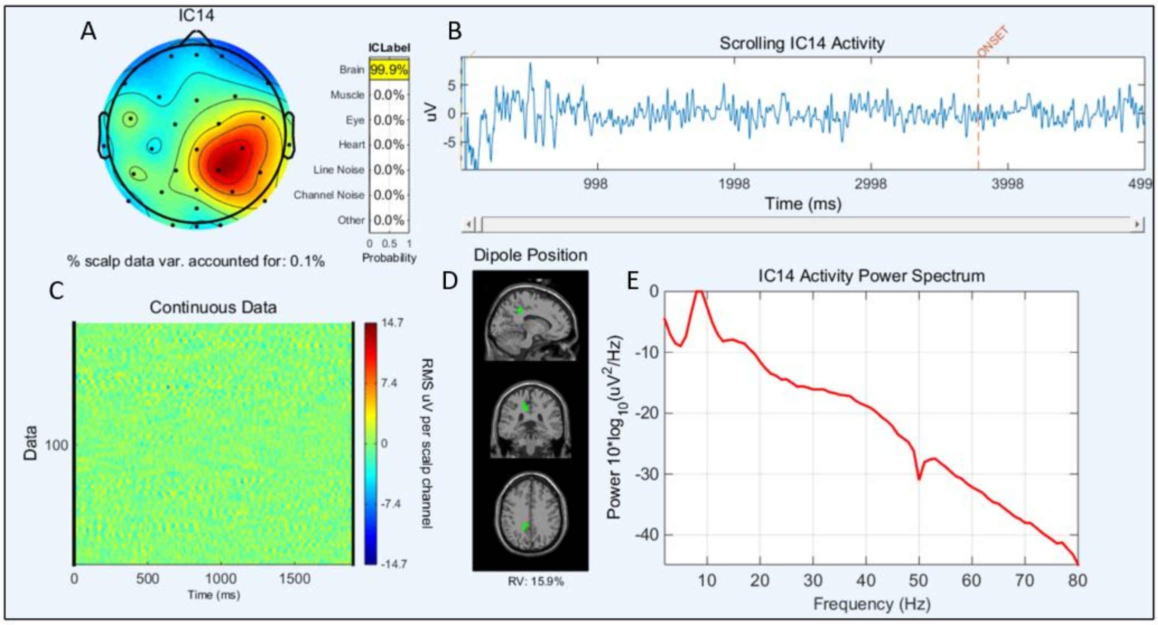

Figure 1.4. Image of a single IC properties obtained with IClabel (Pion Tonachini et al., 2019). Panel A illustrates the Scalp Topography; Panel B shows the component Time Series; Panel C shows the

ERP (event related potential) of the continuous data; Panel D represents the Dipole Model Plot which shows the estimated location of brain equivalent current dipoles with the residual variance reported in percentage (RV); Panel E illustrates the Activity Power Spectrum of the IC averaged across the entire dataset.

Another main challenge of the MoBI approach, is represented by the online synchronization of the mobile EEG with other portable devices such as EMG, eye tracking or force sensors for gait measurements (Gramann et al., 2011; Makeig et al., 2009; Artoni et al., 2018; Ladouce et al., 2017). The combined application of different portable devices opens the door to several problems that need to be addressed in order to provide a reliable recording of brain and body signals. Firstly, the sampling rate of different devices represents a critical issue for a reliable synchronization between fast brain events recorded by the mobile EEG (which uses a sampling rate of up to 2000 Hz) such as evoked potentials or oscillations, and body signals, such as gait measurements or gaze dynamics (usually, recorded with a sampling rate of 50 Hz). A second aspects concerns the time drifts occurring during recordings, which cannot be systematically predicted. To solve these issues, recently, an opensource project called Laboratory Streaming Layer (LSL, Kothe, 2014) has been successfully applied to synchronize signals of different devices using a network. LSL provide a real time data stream acquired from different hardware, allowing a concurrent time stamp of the different streams. It has been used to integrate different EEG systems, eye tracking and motion capture (Gramman et al., 2014). However, LSL requires access to the Application Programming Interfaces (Artoni et al., 2017) which is not always feasible due to the restrictions related to licenses of the different devices.

An alternative solution to LSL, is to use a wired strategy employing the TTL port, connecting physically the different devices with cables through the respective amplifiers during the online recordings. However, this solution might overcomplicate the experimental setup, as in this case the devices should be connected with cables throughout the experimental session. For example, some devices such as the EMG, might have a fixed amplifier, whereas the mobile EEG amplifier is usually placed in a backpack worn by the participant; also, using long cables might affect free movements within the experimental settings. As suggested by Artoni et al., (2018) a possible solution would be aligning the start of the recording and the end, delivering just the initial pulse and the last to both the devices.

In the study reported in Chapter 4 of the present thesis, we employed the strategy of the TTL port, following the suggestions of Artoni et al. (2018), to synchronize signals of gait parameters and cortical activity, recorded respectively through mobile EEG and the Pedar-x foot pressure insoles system (Figure 1.5).

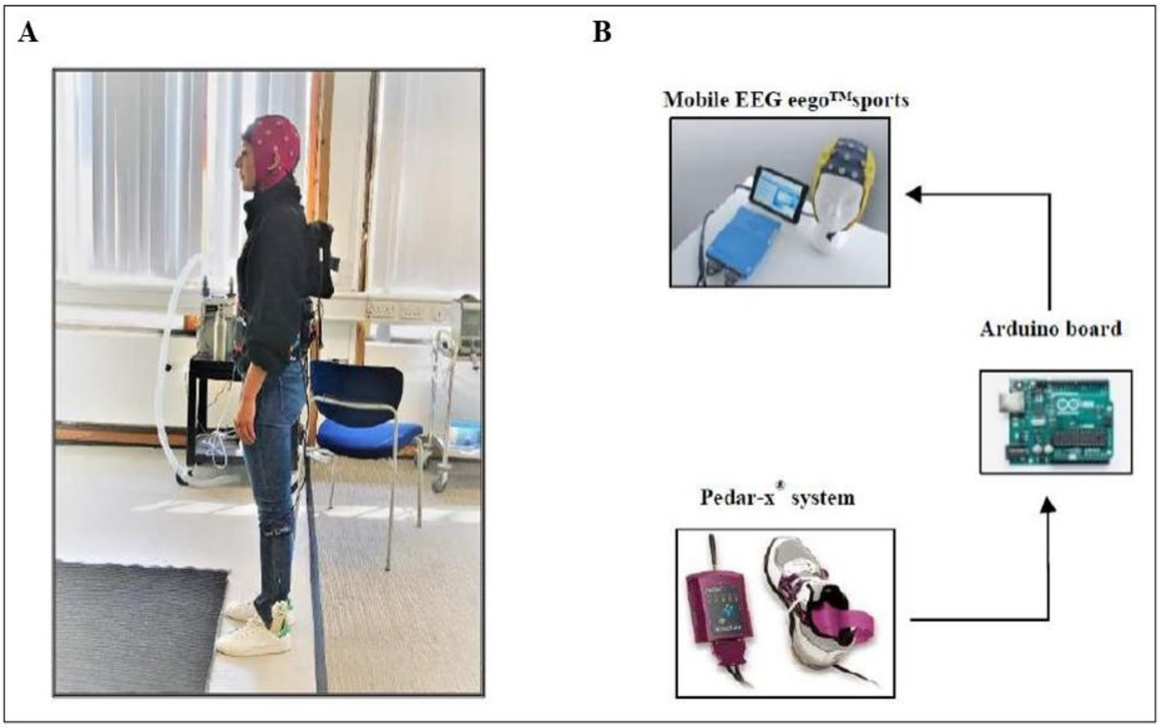

Figure 1.5. Panel A: An example of the experimental setup used in Chapter 4. The participants wore the mobile EEG and the foot pressure insoles system. Panel B: schematic representation of the synchronization strategy used in Chapter 4. At the beginning of the recording, a pulse was sent by the amplifier of the Pedar-x, to the amplifier of the EEG, through an Arduino system.

Before applying this strategy, the feasibility and reliability of the synchronization was tested. The discrepancy in the sampling rate between the two devices led to opt for a one-way communication from the Pedar-x (50 Hz) to the EEG (up to 2000 Hz), setting the former at a higher sampling rate that allowed a better and more accurate reference for later offline synchronisation. To obtain a continuous synchronization between signals, the amplifier of the Pedar-x, wired to the laptop, had to be connected to the amplifier of the EEG placed in the backpack worn by the participant, with a long cable. This strategy offered the advantage of having repetitive pulses delivered to the EEG, although impractical during free movements experiments. The solution to this issue was to deliver only the first pulse of the recording to use as a clock pulse for offline synchronisation. As both the amplifiers employ different connection standards, the main issue encountered was how to make the two devices communicate with each other. The adoption of the Arduino system, connected on one side to the TTL port of the two amplifiers, was a good choice to solve the issue. Its use has been recently proposed by Artoni et al. (2018) who showed it can be an effective strategy to align data from the EEG and the EMG when the real time streaming data application is not available.

Lastly, a critical aspect of investigating cortical oscillations during naturalistic rhythmical movements such as locomotion, is represented by the discrepancy between brain and gait rhythms. A large body of evidence has demonstrated the coupling between gait and cortical activity (Gwin et al., 2011; Seeber et al., 2014, 2015). This coupling has been found also during sensory stimulation. Indeed, as shown by a broad literature, when a rhythmical stimulus is presented, the brain produces an oscillatory response that simulate the rhythmical structure of the stimulus (Schroeder & Lakatos, 2009; Obleser & Kayser, 2016; Chemin et al., 2018). The alignment between brain signals and rhythmical stimuli is thought to reflect the attempt of the brain to predict the structure of events (Arnal & Giraud, 2012; Helfrich et al., 2019). The coupling between brain oscillations and rhythmical stimuli has been indeed investigated in different fields, such as music perception (Nozaradan et al., 2015), speech (Vanthornhout et al., 2018; Obleser & Kayser, 2019) and gait control (Gwin et al., 2011; Seeber et al., 2014, 2015).

Although the coupling between oscillations and rhythmical movements constitute a compelling perspective for the MoBI approach, the issue of synchronising brain activity and rhythmical behaviours is particularly challenging. The main difficulty arises from the high intra and inter individual variability that characterises the temporal structure of gait events, i.e., the heel strikes, which are not perfectly periodic. Furthermore, in real world experiments investigating locomotion, the speed of participants clearly affects the duration of each trial, influencing the temporal occurrence of experimental events. This issue represented one of the main critical challenges of the present thesis, which focused on natural walking. For example, in Chapter 2 where unexpected obstacles were presented on the floor when participants crossed motion sensors placed on the path, the variable speed of participants did not allow the alignment between different trials. This issue was encountered also in Chapter 3 and 4 of the present thesis, where the speed of participants affected the length of the trial making trivial the segmentation of EEG data.

A solution for this issue is represented by the time warping technique (Sakoe & Chiba, 1978). Time warping is a method to stretch and align periodic brain signals to events of variable duration (Sakoe & Chiba, 1978; Chemin et al., 2018). This approach makes possible to shrink or to extend the EEG signal to match the time interval between events that are not perfectly periodic (Chemin et al., 2018). In other words, the time warping makes possible to solve the high variability of natural rhythmical movements, such as gait. This technique has been applied in the studies of the present thesis, through the use of the *newtimef()* function in EEGLAB (Delorme & Makeig, 2004). The *newtimef()* function apply a linear time warping to the median of the events of the trials computed across participants and conditions. This methods was furthermore applied to align the timepoints of the heel strike in the analysis of Chapter 4. The time warping is applied after the computation of the time frequency transform, in order to avoid the alteration of the original signal.

1.9. Rationale of the present thesis

To summarise, the high temporal resolution of the EEG makes it particularly suitable to investigate oscillatory patterns in the brain to identify neural markers underlying human cognitive functions. However, to date, electrophysiological investigations have been critically limited by the methodological constraints and technical difficulties investigating real world behaviour. What we know about neural markers of cognitive processes has been tested in laboratory settings, in which poorly informative stimuli are employed in psychological paradigms to study complex human behaviours and cognitive processes. The main limitation of previous investigations is represented by brain imaging technologies, which require participants to lie down in a scanner or to sit and imagine movements normally performed when upright, or to sit motionless during EEG recordings while, for example, imagining walking. In this thesis, we employ a novel approach, namely the mobile EEG to investigate cognitive processes during naturalistic behaviour in real world environments. More specifically, in three studies, the neural markers of action representation are analysed during covert and overt human naturalistic behaviour, such as when we need to face unexpected change in the environment, when we have to imagine walking down a room, and when we observe a person approaching or moving away from us. Neural oscillations in the theta (4-7 Hz), alpha (8-12 Hz) and beta (13-35 Hz) frequency bands are analysed in the time frequency domain, through the assessment of the event related spectral perturbations.

In the first study, neural correlates of action representation during natural obstacle avoidance are investigated. This study aims to provide the first real world evidence for the assumptions of the proactive cognitive control account (Braver, 2012; Pezzulo & Ognibene, 2012). Participants were required to walk freely down a room and step over expected and unexpected obstacles displayed as images projected onto the floor. The results showed that avoiding unexpected obstacles induced increases in frontal theta, associated with early proactive control of action, which updates the action representation when facing a dynamic change in the environment. Furthermore, it was demonstrated that the adjustment of movements is made just before crossing the object but not when there is nothing on the floor. These dynamics are suggestive of a late mechanism of proactive control, which is reflected in power suppression of the beta frequency range over sensorimotor areas, signalling motor preparation. Finally, a clear beta rebound was evident only after obstacles were crossed, reflecting the resetting of the motor system and the activation of reactive processes of cognitive control.

In the second study, the neural correlates of action representation during motor imagery are investigated, comparing motor imagery to actual execution of walking and a mental counting as a control task. In particular, this study aims to test the functional equivalence hypothesis (Jeannerod, 1994, 2001) using whole body dynamic natural movements, which received little attention in previous research due to noted methodological constraints. The results indeed revealed similar patterns of cortical activity during actual walking and motor imagery, reflected in modulations of beta oscillations, but with minimal overlap with the non-motor control task of mentally counting. However, the results also showed interesting differences, as beta power modulation during motor imagery of walking showed a distinct temporal profile. Furthermore, we also found a different modulation in the alpha frequency band, which was characterised by a stronger decrease of power in the motor imagery condition compared to actual execution and mental counting, but only at the beginning of the trial. This would suggest a dissociation between cognitive processes related to the activation of action representation during motor imagery and actual execution, reflected in distinct modulations in the alpha and in the beta frequency bands.

In the third study, it is investigated whether the distance of a model and the perspective of the observer might modulate neural correlates associated with the activation of action representation during action observation. Brain activity was recorded through the mobile EEG while participants observed a model walking towards or away from them. The results showed that the alpha frequency band is modulated only by the distance, as a stronger decrease of power occurs only when the model is near to the observer compared to the 'far' distance, regardless of perspective. Crucially, differently to previous literature, beta was found to be modulated both by distance and perspective - as a stronger decrease of power occurs when the model is near but facing the participant (walking towards) compared to the condition in which the model is near but viewed from the back (walking away). This suggests that in real world action observation, relevant aspects of the action representation are needed to process others' actions, such as the perspective of the observer and the distance in space of the agent.

The studies reported in this thesis will provide the first evidence for distinct neural correlates underlying action representation in real world human behaviour. Importantly, the cortical activity underlying cognitive processes related to action representation will be investigated using the new mobile EEG approach, which provides a characterization of the temporal profile of brain oscillations related to a given task. Crucially, the mobile approach allows the investigation of natural behaviour in the real world, revealing cognitive processes that could not be studied before with the traditional brain imaging techniques. In this thesis, investigations will be focused on locomotion, which is undoubtedly one of the most natural motor behaviours (and the most constrained by brain imaging techniques to date). Although apparently simple, locomotion is a complex whole body movement, generated by substrates which includes brain areas critically involved in cognitive processes. In the three studies presented, different aspects of real world locomotor behaviours will be explored, such as when walking and facing unexpected changes in the environment, imagining walking down a room, and observing another person approaching or walking away or towards us. These behaviours are regulated by cognitive mechanisms which share a similar core component, which is the internal representation of the action.

Chapter 2: Mobile EEG reveals functionally dissociable dynamic processes supporting real world ambulatory obstacle avoidance: Evidence for early proactive control.

2.1. Introduction

Moving safely through the environment while walking requires continual monitoring and adjustment of planned behaviour, including the ability to make fast online motor transformations in response to dynamic changes such as the appearance of unexpected obstacles. The skill of negotiating the constraints of the environment while walking is inherently complex; it develops slowly throughout infancy (Mowbray & Cowie, 2020) and is progressively lost in aging and motor impairments such as Parkinson's disease (Holtzer et al., 2014; Peterson & Horak, 2016). The gradual reduction in cognitive resources and motor control that occurs with aging and disease means that it becomes increasingly difficult to respond effectively to obstacles that are encountered while walking. Indeed, falls associated with stumbling or tripping over objects represent a critical factor in the increased mortality rates that are seen for elderly and neurological patients (Kovacs, 2005; Tinetti et al., 1988; Weerdesteyn et al., 2006). Given the complexity and fragility of the processes involved in walking, it is clearly important to identify the neural processes supporting cognitive control during walking and obstacle avoidance, generating new targets for clinical practice (Alexander & Hausdorff, 2008; Peterson et al., 2016). Over the last decade, growing research interest in human ambulation has led to the extensive recording of EEG (the electroencephalogram) during active walking on treadmills (Petersen et al., 2012; Severens et al., 2012; Gwin et al., 2010; Gwin et al., 2011; Gramann et al., 2011; Wagner et al., 2012; Wagner et al., 2016; Wagner et al., 2019; Seeber et al., 2014; Seeber et al., 2015). Recorded from electrodes placed on the scalp, EEG provides a non-invasive representation of oscillatory brain activity produced during task performance, allowing the identification of functionally dissociable cortical mechanisms that drive human behaviour (Buzsáki & Draguhn, 2004). To date, EEG studies of walking have revealed the activation of several ‘prefrontal’ brain signals that are activated during the approach to an obstacle, explained as the recruitment of additional cognitive resources. For example, Haefeli et al. (2011) recorded EEG while participants walked on a treadmill, finding increased activity over frontal areas in response to an acoustic signal that warned of upcoming obstacles. Similar findings have been reported using mobile functional near-infrared spectroscopy (fNIRS).

For example, Maidan et al. (2018) reported a higher hemodynamic response in the prefrontal cortex when participants had to prepare to step over unanticipated obstacles (compared to hemodynamic responses during normal walking), independent of the size of the objects. These findings have been extended by a recent EEG investigation of walking on a treadmill (Nordin et al., 2019). Nordin et al. reported increased power in low-frequency oscillations (ranging from 3 to 13 Hz, i.e., delta, theta and alpha) while participants walked at different speeds and stepped over foam obstacles (appearing from behind a curtain placed at the front of the treadmill). These oscillatory brain changes were widespread across the scalp, with source localisation suggesting the engagement of a distributed cortical network (i.e., supplementary motor, premotor and posterior parietal areas). Furthermore, on the basis of timing information, Nordin et al. (2019) argued that obstacle avoidance involved identifying the obstacle and interrupting the gait cycle (associated with early engagement of premotor and supplementary motor areas) and then planning the foot placements required to cross the obstacle (associated with later activation of posterior parietal cortex). Wider interest in the processes involved in goal-directed behaviour have led to the development of theoretical models of cognitive control—and these models provide a framework for understanding ambulatory control. Notably, studies of cognitive control by Braver (Braver, 2012; see also Pezzulo & Ognibene, 2012) have characterised two broad stages of control processing. First, when a behaviour is planned, proactive control processes are employed to respond to potential sources of interference, allowing the original goal to be reached. Importantly, in theory, proactive control processes can occur at different times, reflecting either early selection or late adaptation of planned behaviour. Second, after an unexpected event has occurred, reactive control processes are employed to allow recovery from the interference and return to the original goal. Markedly similar distinctions between proactive and reactive control mechanisms have also emerged from studies on human balance (Bhatt et al., 2018; Horak, 2006; Shumway-Cook & Woollacott, 2007). Proactive strategies are used to anticipate the loss of balance (due to some source of interference), when the body has enough space and time to predict the upcoming interference and adjust motor plans. By contrast, reactive strategies involve compensatory adjustments to restore postural control and balance after unexpected events. Although the theoretical distinction between proactive and reactive control strategies was not developed in relation to ambulatory control per se, the distinction is nonetheless clearly relevant for understanding the processes supporting obstacle avoidance during walking. Indeed, the neural signals observed in studies of treadmill walking can be readily interpreted within this ‘dual mode’ framework (Dual Mechanisms of Control, Braver, 2012). For example, Nordin et al. (2019) reported modulation of low-frequency oscillations linked to supplementary motor cortex and posterior parietal cortex. Both signals occurred before unexpected obstacles, consistent with the operation of a proactive control mechanism that allows planned behaviour to be refined. Moreover, the timing of the posterior parietal signal suggests that the adjustment was made shortly before the obstacle was encountered, which is suggestive of a late adaptation form of proactive control. To our knowledge there is no equivalent evidence of EEG markers of reactive control during obstacle avoidance. However, there is wide evidence for reactive control mechanisms after movement. For example, EEG studies have revealed post-movement increases in beta power (13–30 Hz), described as the beta rebound, a marker of reactive control (Liebrand et al., 2017). Evidence from the wider literature on movement control reveals that beta power over sensory motor regions is enhanced when the predictions of an incoming stimulus are violated (Arnal et al., 2011) and after forcibly interrupted movements (Alegre et al., 2008; Heinrichs-Graham et al., 2017), suggesting a mechanism that re-calibrates the motor system after a movement (Engel & Fries, 2010; Kilavik et al., 2013; Pfurtscheller et al., 1996a). Thus, although reactive control mechanisms have not been demonstrated during obstacle avoidance, changes in beta power may index the operation of such mechanisms. The recent emergence of mobile EEG (Gramann et al., 2011, 2014; Ladouce et al., 2017; Makeig et al., 2009) represents a particularly important development for researchers interested in walking, not least because mobile techniques significantly extend the range of contexts in which brain signals can be studied (e.g. see Park et al., 2018; Park et al., 2015). Critically, using mobile EEG technology makes it possible to monitor the brain while participants navigate natural environments, taking walking research away from the use of treadmills and out of the laboratory (see Ladouce et al., 2019; Park & Donaldson, 2019, for recent examples). As a result, the neuro-cognitive processes supporting walking can now be studied in the real world, offering an entirely new embodied perspective to the understanding of human behaviour and motor impairments (which had been previously limited to non-ecological settings and fairly uninformative tasks; cf. Ladouce et al., 2017; McFadyen et al., 2017). Furthermore, the high temporal resolution of EEG (i.e., millisecond accuracy), combined with wireless portability, makes mobile EEG ideally suited to capturing the rapid cortical responses that occur in response to dynamic stimuli (Makeig et al., 2009). As far as we are aware, currently there is no direct evidence for EEG markers of proactive and reactive control processes during real world ambulatory obstacle avoidance. Thus, our primary aim in the current study is to ask whether it is possible to identify neural signals of proactive and reactive control during real world obstacle avoidance. To address this issue, we recorded EEG while participants walked freely along a

10-m-long path. Critically, we manipulated the presentation of obstacles across trials, providing participants with more or less time and space to prepare for a response to the obstacle. Obstacles were absent, always present at the start of the action, or appeared up ahead after a short or long delay. In addition, we manipulated the available time and space that participants had to adjust their gait when negotiating the environment, while allowing the walking task to remain as natural as possible. Based on the literature reviewed above, and as a test of the dual-mode framework (Braver, 2012), we predicted that distinct proactive and reactive control mechanisms should be identifiable based on their temporal dynamics. As well as demonstrating that neural markers of movement control can be identified during natural walking, we also examined two specific hypotheses. First, by varying the time and space that participants had to prepare for an obstacle we were able to arbitrate between early selection and late adaptation mechanisms of proactive control. Current evidence (cf. Nordin et al., 2019) is not sufficient to differentiate between early and late proactive control mechanisms before an obstacle is overcome. Here, we predict that proactive control processes will operate as soon as information about an upcoming obstacle becomes available (i.e., early selection). Put simply, the high temporal resolution of EEG data should allow us to reveal the precise temporal dynamics of proactive control during walking. Second, by varying the opportunity to anticipate and prepare before adjusting to an obstacle, we aimed to test whether reactive control processes during walking are indexed by changes in beta power (the so-called beta rebound). That is, we tested whether reactive control processes are specifically associated with recovery after a change in a motor plan, in order to reset the previous state. As we show below, mobile EEG does indeed capture and characterise the dynamic engagement of proactive and reactive control processes during real world ambulatory obstacle avoidance.

2.2. Materials and methods

This study was approved by the local ethics committee and conformed to standards set by the Declaration of Helsinki. Thirty-two healthy participants (21 females and 11 males; age range = 19–65; mean age = 32.1 years, SD = 11.6 years) took part in the experiment. All participants were right-handed (self-reported) and gave their written informed consent before the experiment. The experimental design involved four conditions (as depicted in Figure 2.1) in which participants walked along a 10-m-long carpet, passing through a series of infrared laser beams that recorded their location and controlled the presentation of obstacles (visible as a coloured patch projected onto the floor that had to be stepped over).

In the “no adjustment” condition, no obstacle was presented, and participants simply walked across the room. In the “preset adjustment” condition, obstacles were present at the start of each trial, placed at a fixed location 250 cm from the first laser beam. In the “immediate adjustment” condition, walking through the laser beam would trigger the presentation of an obstacle, displayed 160 cm in front of the participant. Finally, in the “delayed adjustment” condition, walking through the laser beam once again triggered the presentation of an obstacle, presented 310 cm in front of the participant. The participants were always instructed to walk straight across the room, to maintain a comfortable pace and to step over any obstacle presented in front of them. Each crossing of the room corresponded to an individual trial, and on reaching the end of the carpet participants were asked to turn around and walk back across the room in the same way. The video projector and laser beams were arranged to allow data collection in both directions. Participants completed a total of 240 trials divided into six experimental blocks. Each block lasted around 5 min. All conditions were presented with equal probability. Participants were given 5–10 min breaks between each experimental block, and were encouraged to request additional breaks during each block should they need this. Any systematic influence of fatigue on the data was further minimised through randomisation of condition order across participants. The overall experimental session lasted approximately 90 min, including preparation, recording and breaks between experimental blocks.

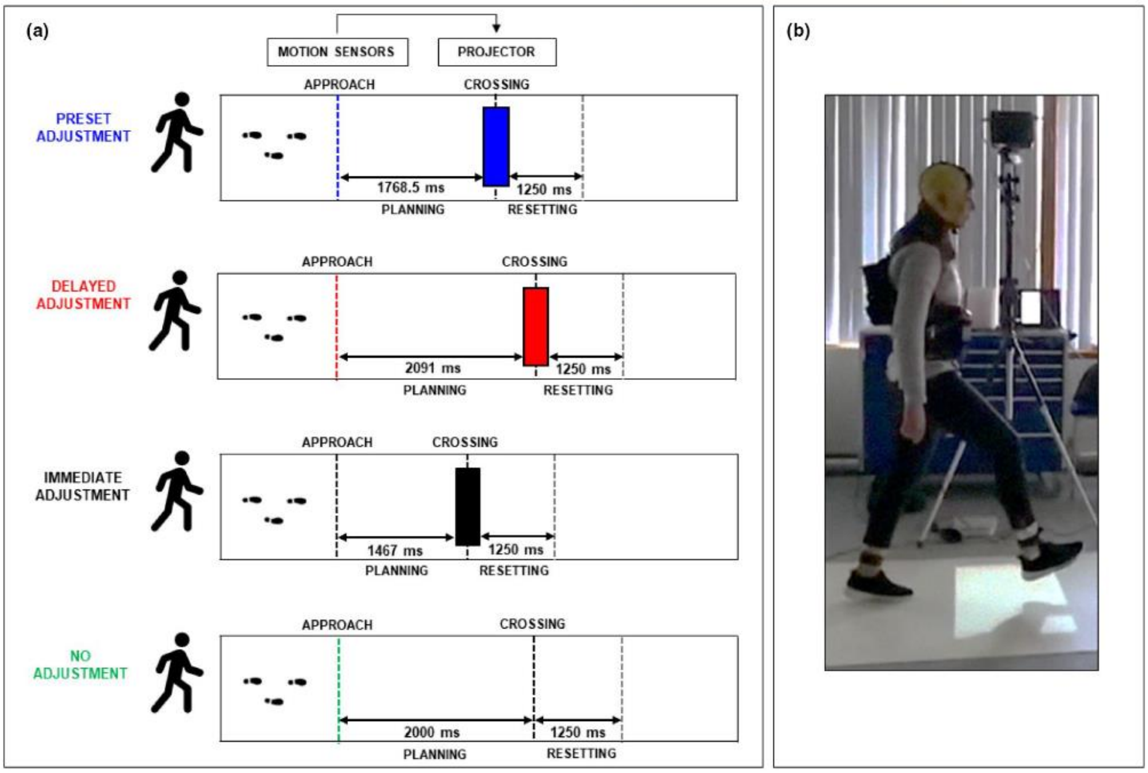

Figure 2.1. Panel a) Representation of the experimental conditions, indicated with different colors (from top to bottom, respectively: blue, preset adjustment; red, delayed adjustment; black, immediate adjustment; green, no adjustment). For each condition, the median duration (in ms) of the planning phase (between participants) is reported inside each path between the approach and the crossing dashed lines. Panel b) Photograph of a participant, wearing the mobile EEG equipment, as they cross an obstacle.

The obstacle was presented as a white stripe (40x80cm) projected on a 10-m-long carpet. The obstacle presentation was controlled with a system interfacing two fixed motion sensors, placed at 230 cm from both ends of the carpet (directing infrared laser beams across the room, through which participants would pass). Stimulus presentation was controlled using E-prime 3.0 software (Psychology Software Tools) and a projector. The motion sensors were designed to send an input signal to the stimulus presentation software running on a laptop, using the Auxiliary I/O port of a Chronos response device (Psychology Software Tools). The laptop was connected to a projector placed at the side of the carpet. The presence and location of the obstacle presented varied on a trial-by-trial basis, depending on the experimental condition. During each trial, the experimenter manually marked two main events (as illustrated in Figure 2.1): the moment that the participant crossed the beam (‘Approach’) and the moment when the participant was over the obstacle (‘Crossing’). These two points provided temporal markers for use within the analysis of the EEG data that identified a planning phase (before the obstacle was encountered) and a resetting phase (after the obstacle was encountered). Participants also wore foot sensor insoles (Pedar-x System, novel.de), a bluetooth pressure distribution measuring system for monitoring local loads between the foot and the shoe. The data of gait parameters were not recorded in all participants of this study and are not reported here.

2.2.1. EEG acquisition and analysis

EEG data were recorded from 32 Ag/AgCl electrodes connected to a portable amplifier (ANT-neuro, Enschede, The Netherlands). Electrodes were positioned according to the International 10–20 system (FP1, FPz, FP2, F7, F3, Fz, F4, F8, FC5, FC1, FC2, FC6, M1, T7, C3, Cz, C4, T8, M2, CP5, CP1, CP2, CP6, P7, P3, Pz, P4, P8, POz, O1, Oz, O2) with AFz electrode as ground and CPz electrode as reference. The electrode impedances were reduced below 5 kΩ before the recording. During recording EEG data were sampled at 500 Hz and bandpass filtered at 0.01–250 Hz. EEG data analyses were performed using custom scripts written in MATLAB 2019a (The MathWorks) incorporating EEGLAB toolbox (Delorme & Makeig, 2004). Data from the mastoid channels (M1 and M2) were removed from the analysis, and all remaining EEG data were filtered using a 0.1 to 40 Hz bandpass filter. EEG channels with prominent artefacts were automatically selected (kurtosis > 5 SDs) and interpolated, and all channels were then re-referenced to the average. An extended infomax Independent Component Analysis (ICA, Makeig et al., 1996) was performed to identify and remove non-brain signals. Artifactual ICs scalp maps were selected through SASICA (Semi-Automated Selection of Independent Components of the electroencephalogram for Artifact Correction, Chaumon et al., 2015) combined with the ADJUST (Automatic EEG artefact Detection based on the Joint Use Of Spatial and Temporal features, Mognon et al., 2011) and MARA (Multiple Artifact Rejection Algorithm, Winkler et al., 2011) plugins. These methods provide objective means of evaluating artifactual signals that, due to their multi-dimensionality and heterogeneity, can be difficult to interpret and identify in raw EEG. Consequently, we used the following measures: Autocorrelation, Focal Components, Signal-to-Noise Ratio, Dipole Fit Residual Variance, Correlation with other channel(s), ADJUST and MARA. Detailed descriptions of each of these methods are available in the wider literature, however, for clarity here we briefly describe what each procedure achieves, highlighting any parameter settings employed. The 'Autocorrelation' measure detects noisy components with weak autocorrelation (e.g. muscle artefacts) with a threshold of 2 SDs and a lag of 20 ms. The 'Focal Components' measure detects components that are too focal and thus unlikely to correspond to neural activity (e.g. bad channels or muscle artefacts) with a threshold of 2

SDs. The ‘Signal-to-Noise Ratio’ measure (0-Inf, -Inf 0, threshold ratio = 1) is used to identify components with weak signal-to-noise ratio that occur between the baseline and the time window of interest. The ‘Dipole Fit Residual Variance’ measure (threshold = 15%) detects components with high residual variance after subtraction of the forward dipole model. The ‘Correlation with other channel(s)’ measure detects components whose time course correlates with any channel(s), with a threshold of 4 SDs. The ADJUST (Mognon et al., 2011) and MARA (Winkler et al., 2011) plugins automatically compute spatial and temporal features (using pre-set parameters) to classify components as artefacts. The resulting ICs scalp maps (or topographies) were further visually inspected to identify ICs with low residual variance (<15%). Across conditions an average (mean ± *SD*) of 5.85 ± 1.97 of non-artifactual ICs were retained for analysis. After artefacts were removed, the remaining data were segmented into epochs relative to the step over the obstacle (i.e. the ‘Crossing’ event, which was defined as time 0), producing a −3,500 ms to 2,000 ms time window. Since the latency of different trials was affected by a great deal of variability within and between participants, single-trial spectrograms were time warped to the median latency (across participants) of the ‘Approach’ event using linear interpolation. In order to have the same number of trials, 40 trials were randomly selected for each condition. Epochs that exceeded the bounding values within the epochs, that is, in which the latency of the ‘Approach’ event exceeded the limit of −2,500 ms from the ‘Crossing’, were excluded (i.e. trials in which the participant was very slow to walk along the carpet). Epochs were further visually inspected to identify trials that still appeared to be contaminated by prominent muscular artefacts and these were manually removed. Across conditions, an average (mean ± *SD*) of 37 ± 2.07 epochs were included in the subsequent analysis, resulting in 7.5% of trials being excluded. Event Related Spectral Perturbations (ERSPs) were obtained by computing the mean difference between single-trial log spectrograms for each channel, for each participant, relative to the mean baseline spectrum (from −3,000 ms preceding to 1,500 ms following the obstacle stepping).

2.2.2. Statistical analysis

Midline single-channel spectrograms (Fc, Cz and POz; Figure 2.2) were visually inspected to identify prominent changes in the spectral power across conditions. Informed by our hypothesis and visual inspection of the topographic maps of theta (Figures 2.3 and 2.4) and beta (Figure 2,5) power, we identified frontal (FC1, Fz and FC2 channels), central (CP1, Cz and CP2) and parietal (P3, POz and P4) locations that captured the effects of interest. Finally, in order to examine the time course of spectral changes before and after the obstacle, the planning (from −1,750 ms to −250 ms) and the resetting (from 250 ms to 1,250 ms) periods were divided into a series of successive 500 ms time windows. Three different repeated measures ANOVAs with three within factors (Experimental Condition, Time Window and Scalp Location) were performed to examine the power modulation across the planning and the resetting phases for each frequency band. Significance level was set at $p < .05$ and, where the sphericity assumption was violated, the Greenhouse-Geisser method was used to correct the degrees of freedom. Post-hoc paired samples *t*-tests were adjusted for multiple comparisons using Bonferroni correction.

2.3. Results

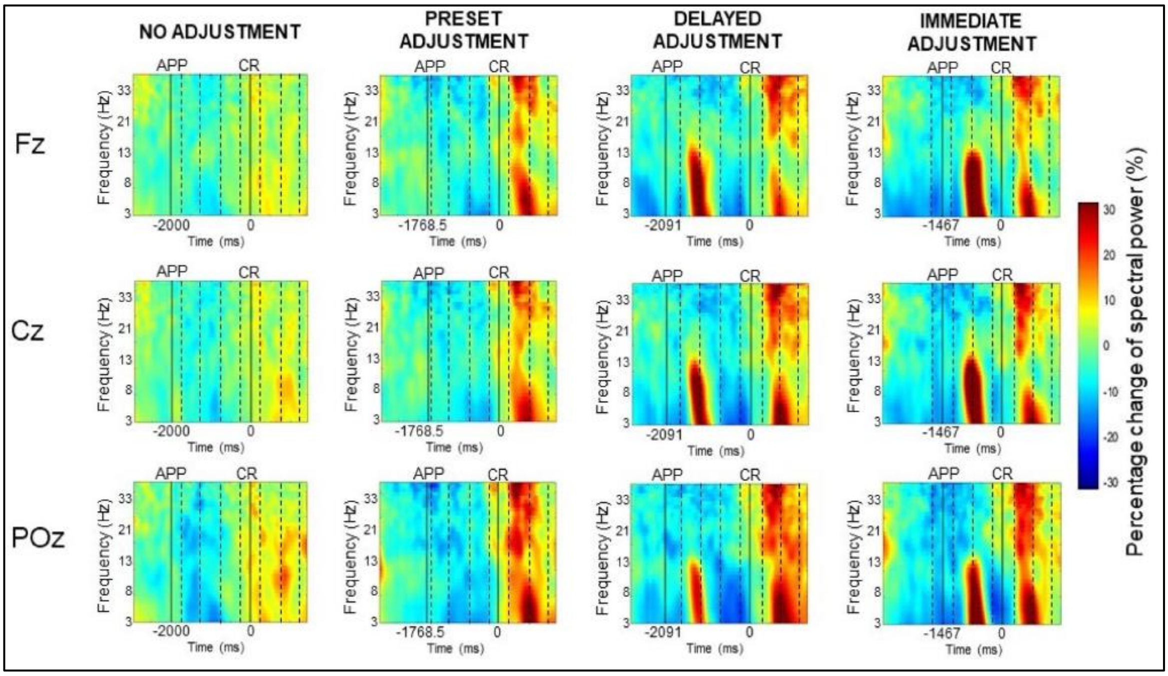

Figure 2.2. Time warped spectrograms at electrodes Fz, Cz, and POz for each experimental condition. Vertical solid black lines represent the 'Approach' (APP) and the 'Crossing' (CR, time 0) events, respectively. Vertical dashed lines represent time windows included in the analysis. On the x- axis (time in ms), the median latencies of the timing of the Approach point are reported for each condition. The lowest frequency shown is 3 Hz, the highest is 35 Hz. Colors indicate the relative change of power from the baseline (%). Blue colors represent decrease of power; red colors indicate increase of power

Midline time warped spectrograms (Figure 2.2) revealed a transient change in the spectral power of theta (4–7 Hz) and beta (13–35 Hz) frequency bands, occurring after the 'Approach' and before 'Crossing' and differently distributed across conditions. Below the results for each frequency band are presented separately for the planning and the resetting phases.

2.3.1. Planning

2.3.2. Theta

The ANOVA indicated that changes in the theta spectral power were significantly different across experimental conditions [F(1,31) = 14.645, p < .001, η_p^2 = 0.321]. Post-hoc paired sample t-tests revealed that the theta increase was significantly stronger both in the immediate adjustment [immediate vs. no adjustment: t(31) = 6.150, p < .001; immediate vs. pre-set: t(31) = 5.374, p < .001; immediate vs. delayed: t(31) = 2.142, p < .05] and in the delayed adjustment condition [delayed vs. no adjustment: t(31) = −4.235, p < .001; delayed vs. pre-set: t(31) = −2.811, p < .01], but similar in the pre-set adjustment and no adjustment conditions (p = .375).

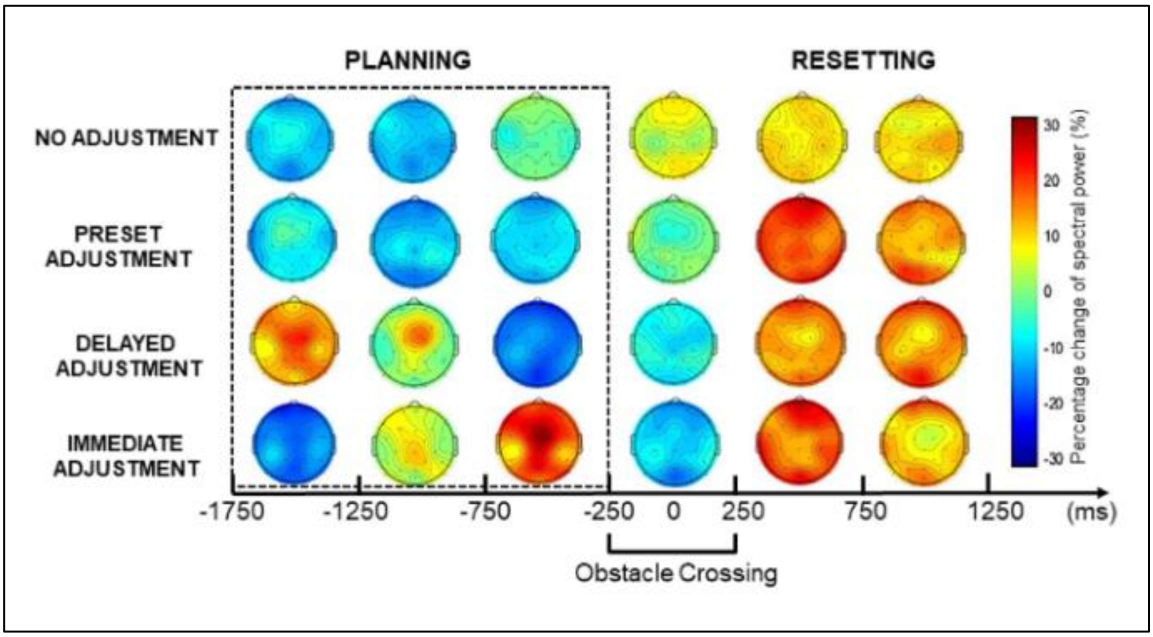

Figure 2.3. Topographic maps illustrating the temporal dynamics of theta power across conditions and time windows. The dashed rectangle around the scalp maps before time 0, indicates the time windows included in the planning phase

A main effect of Scalp Location [F(1,31) = 8.302, p < .001, η_p^2 = 0.211] revealed that the theta increase was more pronounced at frontal compared to parietal [t(31) = 3.733, p < .001] and central [t(31) = −2.154, p < .05] electrodes, and decreased strongly in parietal compared to central [t(31) = 2.138, p < .05] electrodes. A significant interaction between Experimental Condition and Time Window [F(1,31) = 37.313, p < .001, η_p^2 = 0.546; Figures 2.2 and 2.3] confirmed that the timing of the increase in theta power was consistent with the appearance of the obstacle in the immediate and delayed adjustment conditions. As shown in Figure 2.3, a significantly stronger theta increase occurred firstly in the delayed adjustment after the obstacle appeared [−1,750 ms to −1,250 ms; delayed vs. no adjustment: $t(31) = -6.007$, $p < .001$; delayed vs. pre-set: $t(31) = -4.150$, $p < .001$; delayed vs. immediate: $t(31) = -5.598$, $p < .001$] and decreased more in the immediate compared to pre-set adjustment condition [$t(31) = -3.248$, $p < .01$]. In the following time window (−1,250 ms to −750 ms), the theta increase became stronger in the immediate adjustment condition [immediate vs. no adjustment: $t(31) = 4.922$, $p < .001$; immediate vs. pre-set: $t(31) = 4.432$, $p < .001$] but was still present in the delayed adjustment condition [delayed vs. no adjustment: $t(31) = -6.052$, $p < .001$; delayed vs. pre-set: $t(31) = -3.345$, $p < .01$]. In the last time window the theta increase was stronger in the immediate adjustment condition [immediate vs. no adjustment: $t(31) = 5.902$, $p < .001$; immediate vs. pre-set: $t(31) = 6.904$, $p < .001$; immediate vs. delayed: $t(31) = 10.882$, $p < .001$], but the decrease was stronger in the delayed adjustment condition [delayed vs. no adjustment: $t(31) = 7.586$, $p < .001$; delayed vs. pre-set: $t(31) = 2.163$, $p < .05$] and in the pre-set adjustment conditions [pre-set vs. no adjustment: $t(31) = 3.602$, $p < .001$]. Post-hoc t-tests revealed no statistical differences between pre-set adjustment and no adjustment conditions during the first two time windows ($p > .05$) of the planning phase. No other main effect or interaction reached statistical significance ($p > .05$).

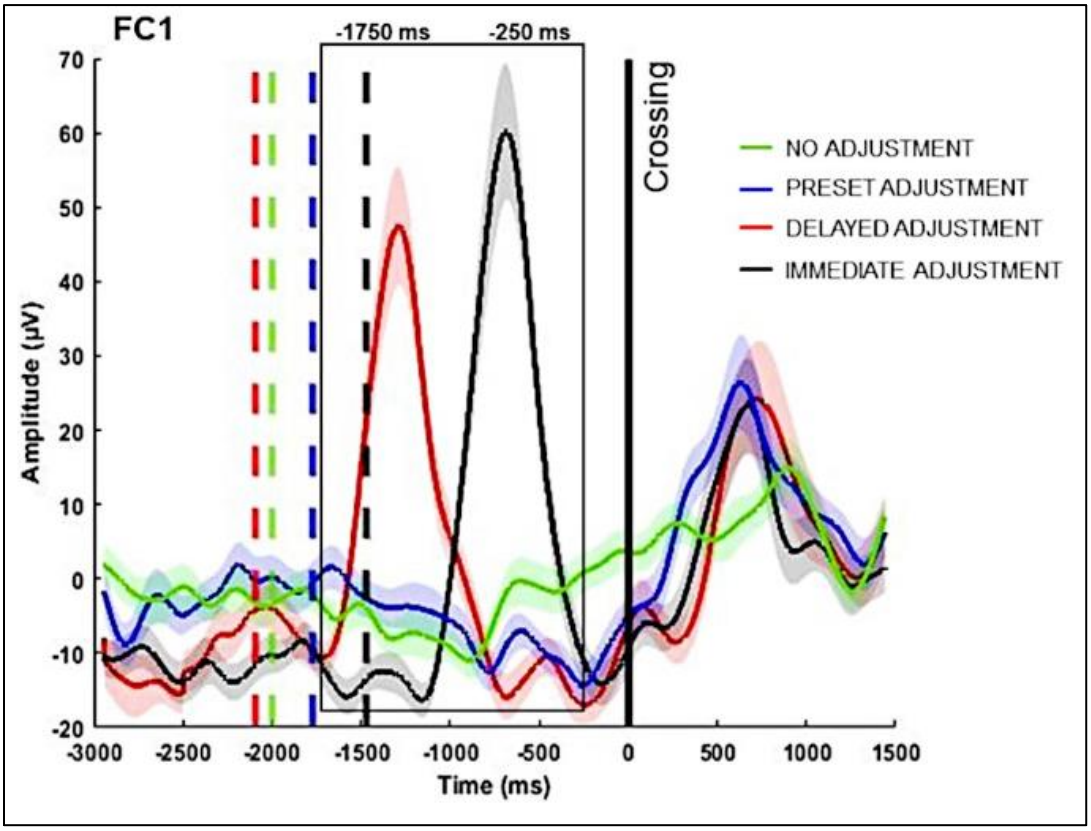

Figure 2.4. The time course of percentage changes from the baseline in theta power across the experimental conditions (group mean, with standard errors indicated by shading) shown for a representative electrode (FC1). Dashed lines represent the median latency of the 'Approach' event, that matches the same color of the conditions indicated by the key. Solid vertical black line indicates the 'Crossing' event (time 0). The black rectangle indicates the time windows included in the analysis of the planning phase

2.3.3. Beta

Although the ANOVA did not show a main effect of Experimental Condition, the decrease in beta power was stronger in the immediate adjustment condition (mean = −9.69 ± 7.09 µV), followed by the delayed adjustment condition (mean = −9.08 ± 6.73 µV), the pre-set adjustment condition (mean = −8.34 ± 6.72 µV) and no adjustment condition (mean = −5.43 ± 7.28 µV). A main effect of Scalp Location [F(1,31) = 4.183, p < .05, η_p^2 = 0.119] revealed that a stronger decrease in beta power occurred in central (mean = −8.43 ± 4.66 µV) and parietal (mean = −8.80 ± 5.03 µV) electrodes compared to frontal (mean = −7.19 ± 4.82 µV) electrodes, although post-hoc paired sample t-tests showed only one statistically significant difference [parietal vs. frontal: t(31) = 2.589, p < .05]. A significant interaction between Time Windows and Experimental Condition [F(1,31) = 2.919, p < .05, η_p^2 = 0.086; Figure 2.6] showed that beta decrease was significantly stronger in all obstacle conditions compared to no adjustment in the last time window [−750 to −250 ms; no adjustment vs. immediate:

t(31) = −2.876, p < .01; no adjustment vs. delayed: t(31) = 4.997, p < .001; no adjustment vs. pre-set: t(31) = 3.742, p < .001]. A significant interaction between Scalp Location and Time Window [F(1,31) = 4,595, p < .01, $\eta_p^2 = 0.129$] revealed that beta decrease was initially stronger in parietal electrodes [time −1,750 to −1,250 ms; parietal vs. frontal: t(31) = 2.219, p < .05] but later (−750 to −250 ms) when the participants were approaching the obstacle became stronger in central electrodes compared to frontal [t(31) = −3.395, p < .01] and parietal [t(31) = −3.475, p < .01] electrodes. No other main effect or interaction reached statistical significance (p > .05).

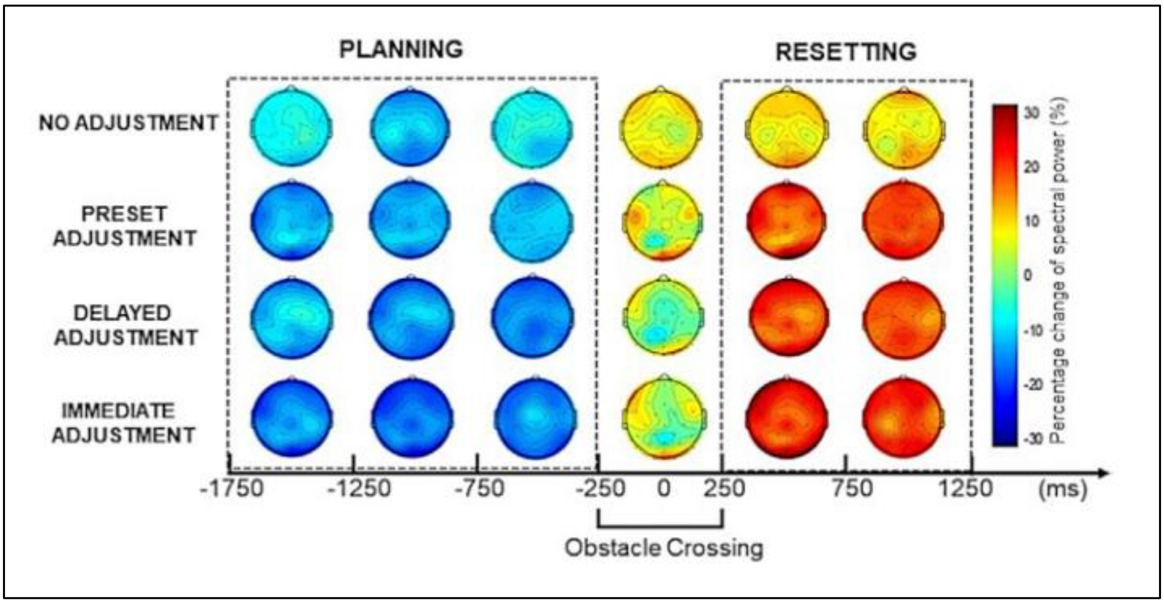

Figure 2.5. Topographic maps illustrating the temporal dynamics of beta power across conditions and time windows. The dashed rectangles around the scalp maps before and after time 0, indicates the time windows included in the planning and in the resetting phase respectively

2.3.4. Resetting phase

2.3.5. Beta

The ANOVA revealed a main effect of Experimental Condition [F(1,31) = 9.912, p < .001, $\eta_p^2 = 0.242$] on beta modulation during the resetting phase. The increase in beta power was stronger in the all obstacle conditions compared to no adjustment condition [no adjustment vs. immediate: t(31) = 4.525, p < .001; no adjustment vs. delayed: t(31) = −5.113, p < .001; no adjustment vs. pre-set: t(31) = −4.062, p < .001]. Additionally, the beta increase was stronger in the delayed adjustment condition compared to the immediate adjustment condition [t(31) = −2.461, p < .05] but not compared to pre-set adjustment condition [immediate vs. pre-set: p = .839; delayed vs. pre-set: p = .258]. A main effect of Scalp

Location [$F(1,31) = 4.028$, $p < .05$, $\eta_p^2 = 0.115$] revealed that the beta increase was stronger in parietal compared to central [$t(31) = -2.143$, $p < .05$] and frontal [$t(31) = -2.143$, $p < .01$] electrodes. No other main effect or interaction reached statistical significance ($p > .05$).

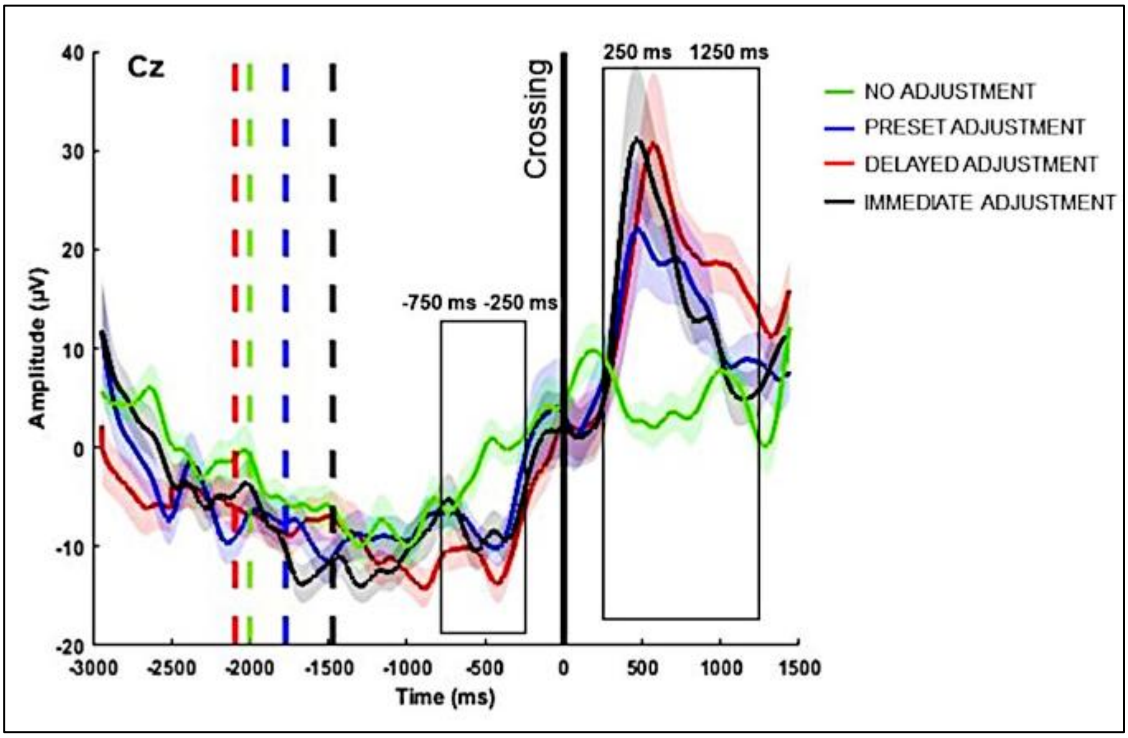

Figure 2.6. The time course of percentage changes from the baseline in beta power across the experimental conditions (group mean, with standard errors indicated by shading) shown for a representative electrode (Cz). Solid vertical black line indicates the 'Crossing' event (time 0). The black rectangles indicate the time windows in which we found significant differences between conditions (−750 ms to −250 ms and 250 ms to 1,250 ms respectively)

2.4. Discussion

To our knowledge, this is the first mobile EEG investigation of real world ambulatory obstacle avoidance. Our primary aim was to assess whether neural signals associated with proactive and reactive forms of cognitive control could be detected during naturalistic movements, using the temporal dynamics of the neural response to dissociate the cognitive processes involved. In short, the results revealed distinct neural markers of proactive and reactive control, distinguishable in frequency (i.e. in theta or beta, respectively) and in time (i.e. present before or after the obstacle, respectively). This neural dissociation is, to our knowledge, the first evidence in support of the dual-mode account of cognitive control (cf. Braver, 2012) during real world walking. Furthermore, the temporal dynamics of the neural response observed while participants approached an obstacle revealed that, within the cognitive process of proactive control, selection is made early. These data are therefore unique in identifying a specific time point at which movement preparation processes occur, a finding that has implications for continuous models of proactive motor control (e.g. Pezzulo & Ognibene, 2012). Below we discuss the implications of these findings for the understanding of each of these control processes, as well as considering technical and practical implications, limitations and recommendations for future studies.

We start by focusing on proactive control mechanisms. As predicted, the analysis revealed a clear neural marker of proactive control: transient increases in theta power over frontal scalp locations during the planning phase, consistent with the timing of the unexpected obstacles' appearance on the path. Analysis of the spectral EEG data revealed that the increase in theta power was largest when participants had less time and space available to change their gait before stepping over an obstacle (i.e. in the immediate adjustment condition). By contrast, this modulation was substantially absent when participants walked without encountering any obstacle (i.e. in the no adjustment condition) or when they could see the obstacle in advance (i.e. in the pre-set adjustment condition). Taken together, therefore, the pattern across conditions strongly suggests that increases in frontal theta observed during walking mark a proactive cognitive control mechanism that is engaged in response to unexpected obstacles.

More importantly, the temporal dynamics of theta showed that the increase in power was linked to the appearance of the obstacle, suggesting an early selection mechanism is at play (Braver, 2012) within proactive control (Pezzulo & Ognibene, 2012). Nordin et al. (2019) investigated the brain dynamics during obstacle avoidance, and concluded that changes in posterior parietal alpha, theta and delta power (i.e. 3–13 Hz) occurred just two steps before the obstacle, providing support for a late adaptation model of control. Analogous oscillatory changes were found by Nordin and colleagues in premotor and supplementary motor areas that preceded posterior parietal cortex activation. However, the limited length of the treadmill belt in the study by Nordin et al. (2019) prevents safe conclusions from being drawn regarding the timing of these changes in relation to crossing the obstacle. By contrast, the present study clearly demonstrates that increases in frontal theta are not related to the time that an obstacle is overcome, but instead to the time that the walker becomes aware of an obstacle. Thus, the present results provide clear evidence in favour of an early selection mechanism underlying proactive control. According to dual-mode theory, proactive control operates through mechanisms which actively maintain relevant information until the behaviour is accomplished (Braver, 2012). In theory, therefore, the continuous maintenance of goal-relevant information supporting complex behaviour in the real world must require the recruitment of substantial cognitive resources. In situations where a planned action needs to be maintained rather than performed immediately, proactive control must operate in a flexible and cost-efficient manner, updating relevant information to ensure that the appropriate action can take place at the right time (Pezzulo & Ognibene, 2012). As noted above, however, in the context of negotiating unexpected obstacles, our mobile EEG findings pinpoint the specific timing of frontal theta in relation to the appearance of the to-be- avoided obstacle revealing an early selection mechanism within proactive control. Support for our account of proactive control can be found in the task switching literature (Cooper et al., 2015, 2017, 2019), where cognitive control has been divided into two stages: an early component, which ensures the preparation and the updating of relevant information facing the change, and a later component that reflects response readiness (Cooper et al., 2015, 2017, 2019). Cooper and colleagues found that, in the context of task switching, frontal theta reflects an early cognitive control mechanism. Taken together, therefore, evidence suggests that increases in frontal theta power index an ‘early’ proactive mechanism, associated with preparing for an upcoming change, regardless of when the action is to be executed.

Having discussed changes in theta power and the timing of proactive control that occurs before an obstacle is encountered, we now turn to changes in beta power that occur as the obstacle is reached. During the planning phase, a greater decrease in beta power was observed at electrodes over sensorimotor areas when the participants had to step over obstacles, compared to when there was no obstacle to avoid. As unobstructed walking involves a more basic negotiation of one's environment compared to obstacle avoidance, the greater decrease in beta band power

likely reflects a state of increased motor readiness, which is needed in order to negotiate the obstacle without interrupting the walking cycle. Furthermore, the magnitude of the decrease in beta power was larger over parietal scalp locations during the earlier stages of movement, but larger at central electrodes when the participants approached the obstacle.

Decreases in parietal beta power have previously been observed during visually guided step adjustments (Wagner et al., 2012) and motor preparation of finger movements (Mars et al., 2007). Central beta power decreases have previously been observed in humans during active walking (Presacco et al., 2011; Seeber et al., 2014; Wagner et al., 2012; Wieser et al., 2010) and cycling (Jain et al., 2013; Storzer et al., 2016). It is well established that changes in beta power over sensorimotor brain regions index motor activation, thought to reflect the planning and the execution of voluntary movements (Neuper et al., 2006; Pfurtscheller & Berghold, 1989; Pfurtscheller & Lopes da Silva, 1999).

Consequently, the temporal evolution of beta power in the present study points towards the operation of a sequential mechanism, which initially recruits sensorimotor integration and spatial representation processes and, at a later stage, movement planning processes. Moreover, neither the temporal evolution nor magnitude of the decrease in beta power were notably different when gait adjustments were present or were triggered by the presentation of unexpected obstacles. This aspect of the data likely reflects the relatively low difficulty of stepping over obstacles in the present study. In addition, however, it also suggests that the updating of motor plans, presumably reflected in theta increases, is not necessarily reflected in greater primary sensorimotor activity.

We now turn to consideration of processes that occur once an obstacle has been negotiated. During the resetting phase we observed robust transient power changes in beta (the so-called post-movement beta rebound; cf. Jurkiewicz et al., 2006; Pfurtscheller et al., 2005; Pfurtscheller & Solis-Escalante, 2009). The beta rebound is typically observed over sensorimotor areas after motor execution or motor imagery (Pfurtscheller et al., 2005; Pfurtscheller & Solis-Escalante, 2009) and it is believed to reflect an active recalibration process that takes place after a change in the state of the motor system (Engel & Fries, 2010; Kilavik et al., 2013; Pfurtscheller et al., 1996a). Notably, studies of cognitive control (e.g. during task switching and go/no-go paradigms; see Cooper et al., 2019 and Liebrand et al., 2017, respectively) suggest the beta rebound seen over prefrontal and sensorimotor areas is an index of reactive control (cf. Liebrand et al., 2017). Accordingly, the presence of the beta rebound in the current study suggests that reactive control processes are also engaged during naturalistic walking, to restore the motor system to its previous state. Critically, and consistent with our hypothesis, increases in beta power were present only when gait adjustments were required (in order to step over the obstacle), but were absent when there was no obstacle to avoid.

The current study design also allowed us to explore whether the beta rebound was modulated by the amount of time participants had to adjust their gait. As such, the beta rebound may be modulated by the motor demands placed when adapting gait. Although the beta rebound was clearly present after negotiating the obstacle, this index of recovery was not more pronounced when obstacles appeared while walking compared to when the obstacle was present at the start of the journey. Modulation was also evident when obstacles appeared while walking: the beta rebound was stronger when the participants had more time to adjust their gait before stepping over the obstacle. Visual inspection of the shape of the beta rebound waveform suggests, however, that this effect may be due to the fact that the beta rebound was prolonged when participants had more time. A recent study has suggested that the duration of the beta rebound is increased after temporally protracted movements (Fry et al., 2016). Accordingly, the modulation of beta rebound appears to signify the longer engagement of the motor system when an unexpected obstacle appeared at a great distance from the participants.

2.4.1. Practical implications, technical considerations and future directions

The overarching objective of the present study was to demonstrate the relevance and utility of using mobile EEG in real world investigations, in particular for detecting neural correlates of natural behaviour that cannot be captured in traditional laboratory settings (Gramann et al., 2011, 2014; Ladouce et al., 2017; Makeig et al., 2009). Despite extensive development of new hardware solutions (i.e. dry electrodes, Lopez-Gordo et al., 2014, or dual-layer EEG caps, Nordin et al., 2019) and tools for signal processing (i.e. independent component analysis, Makeig et al., 1996), to date mobile technologies have not typically been used to test cognitive theories (Ladouce et al., 2017). Here, by revealing neuro-cognitive indices of proactive and reactive control, we show that mobile EEG can be used to characterise the complex pattern of processes that are engaged when humans encounter obstacles while walking. The technical challenges of reducing motion artefacts during natural movements, and the need to integrate the information from multiple devices, differentiate the mobile EEG approach from traditional laboratory-based EEG. A further obvious difference lies in the number of channels employed: here, we used 32 mobile EEG channels, rather than the 64 or 128 channels commonly used in laboratory-based systems.

Inevitably, the methodological constraints associated with mobile EEG have implications for data processing, analysis and interpretation. For example, the use of fewer electrodes results in the extraction of fewer independent components during the pre-processing stage than in equivalent laboratory-based studies. Equally, the use of a restricted electrode montage also precludes using EEG to identify the neural sources of the recorded signal, preventing any strong conclusions about the specific brain regions responsible. More importantly, mobile EEG data tend to be “noisier” in terms of movement and muscle artefact than traditional laboratory-based EEG data, making it more difficult to identify brain signals. To address this issue, we relied heavily on automatic artefact rejection procedures to provide an objective evaluation of brain and non-brain signals. Despite the limitations associated with mobile data collection, the present experiment clearly demonstrates that cognitive processing can be assessed during real world behaviour.

Another challenge for mobile EEG research lies in the presentation and manipulation of real world stimuli within the context of a structured experimental design. For example, in the present study, “obstacles” were images projected onto the floor, which allowed us to easily manipulate the position and predictability of the objects while maintaining a naturalistic and safe environment for participants. Although our paradigm was not entirely natural, lights projected onto the floor have previously been used in behavioural studies of obstacle avoidance (Chen et al., 1996; Salazar-Varas et al., 2015). In addition, the use of 2D (rather than 3D) obstacles could potentially interfere with natural leg mechanics while walking. Critically, however, our aim was to identify the cognitive processes relating to overcoming expected and unexpected obstacles, rather than to explore gait patterns per se. It is nevertheless of interest for future studies to examine whether the introduction of real 3D obstacles significantly influences the engagement of control processes. Similarly, future studies will need to examine the impact of variability in the temporal-spatial features of walking (i.e. changes in speed, acceleration or direction) and the participants’ performance (i.e. successful vs. unsuccessful obstacle avoidance) in order to identify any links between brain cortical dynamics and gait patterns. To fully investigate all of the factors that influence walking would, of course, require a more complex paradigm than was employed here, for example, via the introduction of routes that allow walkers to turn repeatedly. Other developments will require the use of additional sensors, for example, to allow EEG recordings to be time-stamped based on the pattern and timing of heel strikes that are made during walking. Even without additional technical and methodological development, the present findings highlight the exciting opportunities that now exist for studying neurodegenerative and developmental disorders (such as Parkinson's disease and dyspraxia, respectively), where understanding real world behaviours is critical. Negotiating obstacles in the real world requires us to allocate attention, detect relevant constraints and flexibly adapt motor behaviours, which is challenging for elderly or Parkinson's disease patients who often experience gait impairments that increase the risk of falls and mortality (Kovacs, 2005; Tinetti et al., 1988; Weerdesteyn et al., 2006). Studies that aimed to identify neural markers of Parkinson's disease and gait dynamics are presently limited, being restricted to simple tasks (i.e. finger tapping, Stegemöller et al., 2016, 2017) or indirect methods such as kinematics recording (Galna et al., 2010; Vitorio et al., 2010). By contrast, mobile EEG can provide direct insight into the neural and cognitive processes that are affected by disorders, addressing the actual real world situations that are problematic for patients.

For rehabilitation of motor disorders following brain injury or as a consequence of neurodegenerative diseases such as Parkinson's disease, it is particularly important to have an understanding of the cognitive processes involved in the complex, dynamic, modality integrated reality of real world behaviour. As such, identifiable neural markers of real world behaviour offer novel pathways towards tailored neuro-rehabilitation approaches for motor disorders in particular. Such evidence-based cognitive rehabilitation strategies could, for example, use neurofeedback or non-invasive brain stimulation and the online acquisition of cognitive neural markers in offering tailored and ecological diagnostics and rehabilitation processes for patients affected by various neurological aetiologies.

2.5. Conclusion

Our study demonstrates that mobile EEG can be used to capture the dynamic oscillatory responses associated with the neuro-cognitive processes of that are engaged while negotiating real world environments. We demonstrated that naturalistic obstacle avoidance is mediated by proactive and reactive cognitive control processes, reflected in the dynamics of theta and beta oscillations. In particular, the temporal brain dynamics of frontal theta revealed that proactive control during unexpected obstacle avoidance is associated with an early selection mechanism. Furthermore, we showed that motor readiness is mediated by beta power decreases which were evident when pre-set or externally triggered gait adjustments were needed in order to step over an obstacle. With regards to reactive control, we identified a robust beta rebound after obstacles were crossed, demonstrating that real world negotiation of the environment requires finely tuned resetting of the motor system. Taken together, these mobile EEG data provide a new way to examine the neuro-cognitive processes supporting walking in particular, and of applying an embodied mobile cognition perspective to the understanding of human behaviour in general. The findings are also relevant towards a better understanding of motor impairments in more naturalistic contexts and should inform the development of novel neuro-rehabilitation approaches.

Chapter 3: The neural correlates of the imagery and execution in real world dynamic behaviour: evidence for neural overlap but distinct cognitive processes

3.1. Introduction

The term motor imagery has been used in literature to indicate the visual and kinaesthetic imagination of a movement without execution (Decety, 1996a; Jeannerod, 1994, 2001; Mulder, 2007). Since the first seminal studies in the 1930s (Sackett, 1934, 1935), a large amount of evidence has shown that motor imagery and actual execution of movements share similar cognitive processes and neural activation features. For example, the time taken to execute and to mentally imagine a movement has been shown to be similar (Decety & Michel, 1989; Sirigu et al., 1995) suggesting that imagery is based on actual movement cognitive representations. Similarly, execution and motor imagery adhere to Fitts' law whereby the time to execute or imagine a movement is moderated by accuracy demands (Decety & Jeannerod, 1995; Macuga et al., 2012; Macuga & Frey, 2012). According to the so called 'functional equivalence hypothesis' following Jeannerod's motor simulation theory (Jeannerod, 1994, 2001), similarities between actual execution and motor imagery emerge from shared motor-cognitive processes, allowing for the imagined rehearsal of movement using cognitive motor planning processes (Jeannerod, 2001).

The functional equivalence hypothesis has received large support, primarily from brain imaging studies which have demonstrated that motor imagery and actual motor execution involve activation of similar brain areas (Grèzes & Decety, 2001; Porro et al, 1996; Sharma & Baron, 2013). These brain activations include a distributed premotor-parietal network, involving several subcortical structures, such as the putamen and cerebellum (Grezes & Decety, 2001; Hardwick et al., 2018). Further indirect evidence for equivalence comes from sport (Guillot & Collet, 2008; Williams et al., 2015) and clinical literature, which have shown that the mental practice of movement through motor imagery (i.e., the repetitive exposure to motor imagery of movements) can be effective for learning motor skills (Dijkerman et al., 2010; Barclay et al., 2020). The potential efficacy of mental practice in sport training and in motor rehabilitation is supported by findings which demonstrated that motor imagery practice can induce plastic changes in motor networks (for a review see Ruffino et al., 2017).

Despite evidence for neural similarities, there remains an open debate about the effective equivalence of cognitive processes underlying motor imagery and action execution (i.e., what is the correspondence mechanism?). Indeed, the functional equivalence hypothesis has been challenged by the evidence of substantial temporal and neural differences between action execution and motor imagery (see Glover & Baran, 2017). The behavioural similarities show variance, with for example, time to mentally simulate a movement sometimes taking longer than actual execution (Decety et al., 1989; Louis et al., 2011) especially when participants have to perform novel complex tasks (Calmels et al., 2006; Cerritelli et al., 2020). In a recent meta-analysis, Hardwick et al. (2018) showed a relatively small overlap between brain activations during action execution and motor imagery, which likely indicates a discrete mechanism of equivalence that is not reflected by the majority of the findings. Whereas action execution involves more specific areas involved in motor functions such as the primary motor cortex and the cerebellum, motor imagery involves areas involved in visuomotor control and motor planning, such as the premotor and the parietal areas (Hetu et al., 2013; Hardwick et al., 2018). These findings suggest that cognitive mechanisms underlying motor imagery are yet to be understood (cf. O'Shea & Moran, 2017) and that the functional equivalence between action execution and motor imagery has been probably overstated (Hardwick et al., 2018).

Drawbacks for the effective demonstration of functional equivalence between action execution and motor imagery include confounding factors such as whether some of the neural activity observed during motor imagery represents inhibition of action responses (see Chong & Stinear, 2017; Angelini et al., 2015; Solodkin et al., 2004; Lotze et al., 1999). As during motor imagery no motor response is actually produced, it has been suggested that underlying cognitive mechanisms involve inhibitory processes, preventing the activation of neural descending pathways (Jeannerod, 1994). In line with these hypotheses, different studies have shown that neural areas for inhibitory control of overt motor responses, such as the supplementary motor areas and right inferior frontal gyrus (Angelini et al., 2015), the cerebellum (Lotze et al., 1999) and the parietal areas (Solodkin et al., 2004), are recruited during motor imagery. In particular, Angelini et al. (2015) showed a partial overlap between motor inhibition occurring during motor imagery and the voluntary withholding of motor response during NoGo trials, demonstrating that the inhibitory circuits are recruited in different temporal sequences in overt and covert behaviours. This suggests that inhibition is automatically and involuntarily included in the cognitive mechanisms underlying motor imagery (Angelini et al., 2015).

Likewise, methodological constraints make measures of motor imagery extremely challenging for researchers, even in experimentally controlled settings. This is primarily due to the covert nature of motor imagery tasks and difficulties to demonstrate with evidence that covert imagery (which typically cannot be systematically manipulated and measured) influences performance. Furthermore, without comparison to actual execution, it is not always clear what is being measured by recording brain activations during motor imagery. The assessment of the quality of movement imagery is further called into question through the evaluation of individual participants' imagery ability, which mostly has been evaluated with subjective self-reported questionnaires and scales (Gregg et al., 2010; Mizuguchi et al., 2015; for a review see MacIntyre et al., 2018). Another constraint is related to brain imaging technologies, which usually require participants to lie down in a scanner and imagine movements normally performed when upright, or to sit during EEG recordings while for example imagining walking. This incongruence between body posture and imagined action is an issue because the compatibility of the body position has been shown to affect motor imagery performance. For example, the time it takes to perform a movement mentally has been found to be more similar to the actual execution when participants are in a congruent posture to the imagined movement, compared to incongruent conditions (Parsons et al., 1994; de Lange et al., 2006; Conson et al., 2011; Saimpont et al., 2012). In sum, although the laboratory gives the advantage of studying human cognitive processes in highly controlled settings, the research is far from providing a clear and univocal explanation of neural substrate and cognitive processes underlying motor imagery (Barton & Pretty, 2010; Menicucci et al., 2020), and their equivalence to action execution processes.

The use of mobile electroencephalogram (EEG) technology solves many of the constraints discussed in the previous paragraphs. EEG recordings allow a characterization of highly accurate temporal dynamics of brain rhythms thought to reflect cognitive processing, which overcomes the limitations of functional scanning. A common finding of EEG investigations is that during motor imagery, there is a decrease/suppression and an increase in the spectral power, often termed event related desynchronization and synchronization, respectively. These are more often found in the alpha (8-12 Hz) and beta (13-35 Hz) frequency bands, occurring over sensorimotor (Pfurtscheller & Neuper, 1997; Neuper & Pfurtscheller, 2001; Pfurtscheller et al., 1997) and parietal-occipital (Salenius et al., 1995; Xie et al., 2020) brain areas. Generally, it is widely accepted that power suppression in the alpha and beta frequency bands is related to the activation of relevant brain areas during a given task, whereas power increase is associated with inhibition (Pfurtscheller et al., 1999; Klimesch, 2012). Although

EEG investigations have provided evidence of the engagement of sensorimotor brain areas during action execution and motor imagery, research has typically focused on upper limb movements, while participants were sitting, performing hand or finger movements. EEG measures of lower limb movements and of whole body dynamics such as locomotion have been given little attention. Studies of lower limb imagery were mostly limited to imagery of only minimal movement, such as the dorsiflexion of the foot (Pfurtscheller et al., 2006b; Neuper et al., 1996; Hashimoto et al., 2013; Solis-Escalante et al., 2008, 2012; Muller-Putz et al., 2010) or stepping in place (Hsu et al., 2017; Liu et al., 2019). These investigations mainly aimed to identify reliable signals for brain-computer interface (BCI) control, which connect the oscillatory activity of the brain to a computer (Wolpaw et al., 2002) in order to drive external devices, such as prostheses (Leeb et al., 2007; Pfurtscheller et al., 2003). Indeed, commonly in these studies, recordings were obtained with a limited number of channels and cognitive aspects were less explored. However, lower limb natural movements, such as walking, involve much more complex kinematics than movements such as the dorsiflexion of the feet. Walking is a whole body dynamic action, which involves postural control, coordination of limb kinematics while integrating multisensory information from the body with information from the external environment. Indeed, la Fougere et al. (2010) in a PET/fMRI study showed that the neural activation during execution and motor imagery of walking are substantially different. Whereas actual walking involves primary motor cortex and somatosensory activation, motor imagery involves the activation of the supplementary motor area and the basal ganglia (la Fougere et al., 2010). However, motor imagery in fMRI requires participants to lay supine, which is fundamentally different from the upright position during locomotion. To the best of our knowledge, the neural correlates of motor imagery of whole body dynamic movements have not yet been investigated.

Therefore, in the current study we investigated the similarities and differences of neural activations associated with action execution and motor imagery of whole body walking movements using a mobile EEG approach. We asked participants to walk or (in a standing position) to imagine walking at a natural pace along a path. To enhance the sensorimotor experience, we asked participants to perform the imagery straight after walking, using a first-person perspective and focussing on the kinaesthetic experience (feeling the sensations as if actually walking), which has been shown to elicit greater motor activation compared to visual motor imagery from a third person perspective (Lorey et al., 2009; Mizuguchi et al., 2017). Furthermore, we used a mental counting task as a non-motor control condition. According to the functional equivalence hypothesis of motor simulation theory (Jeannerod, 1994, 2001), we expected that motor imagery and actual execution would elicit similar EEG profiles compared to mental counting, i.e., power spectral changes of alpha and beta frequency bands, which might index similar cognitive mechanisms underlying execution and motor imagery.

3.2. Methods

3.2.1. Participants

Twenty-four healthy participants (23 female and 1 male; age range = 18-44 years; mean age = 22.16 years, SD = 6.8 years) took part in the experiment. The data from three participants were excluded due to the presence of prominent artifacts in EEG recordings. The remaining data of twenty-one participants (20 female and 1 male; age range = 18-44 years; mean age = 21.43 years, SD = 5.5 years) were used in the reported analyses. Height (169.05 ± 8.02 cm), weight (67.5 ± 15.39 Kg) and walking speed (5.29 ± 0.56 Km/h) were also recorded for each participant. All the participants had no history of neurological disorders and were right-handed (self-reported). Before starting the experiment, all the participants gave their informed consent. Ethical approval was provided by the General University Ethics Panel of the University of Stirling.

3.2.2. Material and procedure

In the original design, participants were asked to complete four experimental conditions: i) Actual walking, ii) Motor Imagery of walking, iii) Mental Counting and iv) Observation of walking. In this study, we focus on the comparisons between Motor Imagery, Actual Execution and Mental Counting. Action observation data were part of a separate study and analysed in relation to other hypothesis and parameters (see Chapter 4). They are therefore not included in this Chapter. Participants completed a total of 120 trials (40 trials for each condition) divided in 6 experimental blocks of 20 trials each. During the mental counting (MC) condition, participants were standing and instructed to listen to 6 consecutive tones (107 dB, interval of 600 ms), and then to mentally count up to six at the same frequency. They were asked to say out loud ‘six’ when they finished the mental count. During the execution of walking (EXE) condition, participants were instructed to take 6 steps on a 6 m long carpet, to turn and continue walking without stopping. During the motor imagery of walking (MI) condition, participants were instructed to take 6 steps, stop at the beginning of the 6 m carpet and to ‘imagine feeling as if they were walking on the carpet performing a further 6 steps and arriving to the end of the path’ using the first person’s perspective (kinaesthetic imagery). They were asked to say out loud ‘stop’ when they finished the sixth step of the mental walking task. In order to ensure the success of the task, participants were first trained for several minutes. During training, participants were first introduced to the kinaesthetic imagery perspective, in order to ensure that they understood the task. Secondly, they were told to concentrate their attention on the movement of their legs, and the ‘feeling’ of pushing the foot on the ground, focusing on the sensation coming from the different muscles of the lower limbs. They were asked to try for several minutes before starting the block of MI, until they were certain that they would be able to perform the task. Depending on the condition, a trial was defined as the time period from when the participants started to mentally count until they said ‘six’ (MC condition), from when they started to walk until the end of the path (EXE condition) and from when they started the imagery of walking until they said ‘stop’ (MI condition). The order of conditions and experimental blocks was randomized across participants.

3.2.3. EEG recording and processing

EEG data were recorded from 32 Ag/AgCl electrodes connected to a portable amplifier (ANT-neuro, Enschede, The Netherlands). Electrodes were positioned according to the International 10-20 system: FP1, FPz, FP2, F7, F3, Fz, F4, F8, FC5, FC1, FC2, FC6, M1, T7, C3, Cz, C4, T8, M2, CP5, CP1, CP2, CP6, P7, P3, Pz, P4, P8, POz, O1, Oz, O2. AFz electrode was used as ground and CPz electrode was used as reference. The electrode impedances were reduced below 5 kΩ before the recording. During recording, EEG data were sampled at 500 Hz and bandpass filtered at 0.01-250 Hz. EEG data analyses were performed using custom scripts written in MATLAB 2019a (The MathWorks) incorporating EEGLAB toolbox (Delorme and Makeig, 2004). Data from the mastoid channels (M1 and M2) were removed from the analysis, and all remaining EEG data were filtered using a 0.1 Hz to 40 Hz bandpass filter. EEG channels with prominent artifacts were automatically selected (kurtosis > 5 SDs) and interpolated, and all channels were then re-referenced to the average. Data were downsampled to 250 Hz and an extended infomax Independent Component Analysis (ICA, Makeig et al., 1996) was performed to identify and remove non-brain signals. Brain-related-ICs were identified using the IClabel plugin (Pion-Tonachini et al., 2019). Components exceeding a 90% probability of being eye, muscle, heart, line noise, and channel noise were rejected. Only brain ICs with dipoles located inside the head and a residual variance lower than 15% were kept. An average of (mean ± SD) 6.65 ± 0.81 ICs across conditions was retained for the analysis.

3.2.4. EEG Analysis

In order to investigate the cortical dynamics during the overall length of trials across conditions, EEG data were segmented in epochs of 8500 ms. An epoch lasted from -7000 ms before and 1500 ms after time 0, which corresponded to the end of each trial. Single channel spectrograms were time warped to the median latency of the start of the trial (-3960 ms) across participants for each condition. Event related spectral perturbation (ERSPs) was computed using a Fast Fourier Transform (FFT), and computed as the mean difference between single trial log spectrograms for each channel and each participant across conditions and the mean baseline (-3960 ms before to 1320 ms after time 0). The window of the ERSP computation was sent at 3 cycles in the *newtimef* function and frequencies ranging from 3 to 40 Hz were computed at 2500 time points distributed in the time warped epochs for each trial, channel, participant and condition. Single channel time frequency spectrograms were visually inspected to identify relevant changes in the spectral power in the a priori defined frequency bands of interest: alpha (8-12 Hz) and beta (13-35 Hz). Topographical scalp maps in the frequency bands of alpha and beta (Figure 3.1 and 3.2, panel A) were further visually inspected to identify relevant regions of interest (ROI). We identified a central (FC1, FC2, C3, C4, CZ), a parietal (CP1, CP2, P3, P4, PZ channels) and an occipital (O1, O2, OZ, POZ) ROI.

3.2.5. Statistical analysis

Topographic scalp maps (Figure 3.1 and Figure 3.2, panel A) showed prominent changes in the spectral power in the alpha and in the beta frequency bands across conditions. In order to capture relevant spectral changes, we divided the time window of interest in 4 separate time windows: more specifically [-3960, -2640]ms, [-2640, -1320]ms, [-1320,0]ms, [0,1320]ms. Two separate repeated measures 3x4x3 ANOVAs with factors Condition (Mental counting (MC); Execution (EXE); Motor Imagery (MI)), Time Window (Time 1, Time 2, Time 3, Time 4) and ROIs (central, parietal, occipital) were performed for alpha and beta frequency bands. The Greenhouse – Geisser correction was applied whenever the sphericity assumption was violated and post-hoc paired sample t-tests adjusted using Bonferroni correction, were performed to further investigate significant main effects and interactions.

3.3. Results

3.3.1. Beta oscillations

The ANOVA revealed a main effect of Condition [F(1, 20) = 28.875, p = .000, η_p^2 = .591] showing an overall smaller amplitude in the beta frequency band during EXE compared to MC [t(20) = 8.365, p = .000] and MI [t(20) = 5.585, p = .000]. A main effect of Time Window [F(1, 20) = 36.173, p = .000, η_p^2 = .644] revealed that there was a decrease of beta power in Time Windows 1 and 2 whereas there was an increase of beta power in Time Windows 3 and 4.

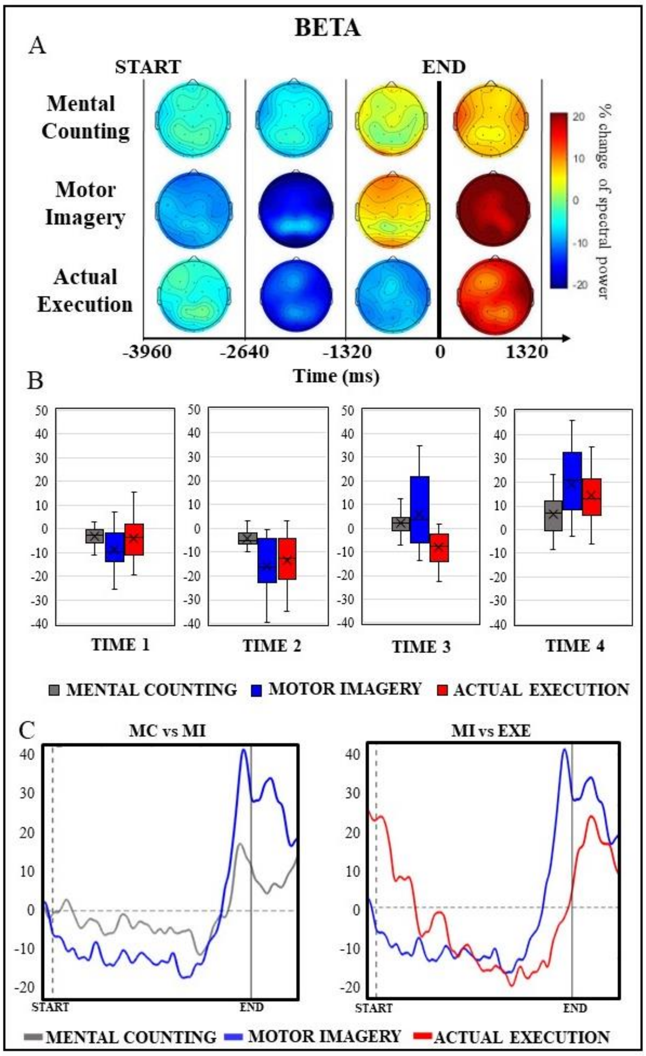

Figure 3.1. (A) Scalp maps topography of beta (13-25 Hz) spectral power across conditions and time windows. **(B)** Averaged beta percentage change of power from baseline across conditions in each time window. **(C)** Averaged waveforms comparison between MC vs MI (left) and EXE vs MI (right) in beta frequency band over parietal areas

Importantly, there was a significant interaction between Condition and Time Window [F(1, 20) = 8.059, p = .000, η_p^2 = .287]. As illustrated in Figure 3.1C, there was a sustained beta power decrease during motor imagery and execution, which was evidently different to the modulation of beta power during mental counting. Post-hoc paired t-tests confirmed that the decrease in beta power was significantly stronger during MI compared to MC in Time Window 1 [t(20) = 2.634, p = .048] and Time Window 2 [t(20) = 4.679, p = .000]. In addition, the increase in beta power in Time Window 4 was significantly stronger during MI compared to MC [t(20) = 3.236, p = .048]. With regard to the comparison between MI and EXE there was only a significant difference in Time Window 3 [t(20) = 4.262, p = .000], due to a faster increase in power in motor imagery.

There was a significant interaction between ROI and Time Window [F(1, 20) = 9.610, p = .000, η_p^2 = .325]. Beta power decrease was stronger in the central ROI compared to the parietal ROI in Time Window 1 [t(20) = 3.752, p = .012] and Time Window 2 [t(20) = 3.828, p = .012]. In Time Window 2 there were also significant differences between the occipital and central [t(20) = 4.019, p = .012] and parietal [t(20) = 6.149, p = .000] ROIs. In addition, there was a stronger increase of beta power in the parietal ROI compared to the occipital ROI [t(20) = 3.336, p = .048] in Time Window 3.

There was a significant interaction between Condition and ROI [F(1, 20) = 3.749, p = .031, η_p^2 = .153]. Post-hoc paired t-tests revealed larger amplitudes of beta power in MI compared to EXE in the central [t(20) = 5.274, p = .000], parietal [t(20) = 6.103, p = .000] and occipital [t(20) = 3.702, p = .012] ROIs. With regard to MC, the beta power amplitude was larger in MI only over parietal areas [t(20) = 2.401, p = .048].

A significant 3-way interaction [F(1, 20) = 2.990, p = .033, η_p^2 = .130] was investigated for each ROI separately. In the central ROI, there was a stronger decrease of beta power in MI compared to MC in Time Window 1 [t(20) = 2.764, p = .048] and Time Window 2 [t(20) = 3.403, p = .048]. In Time Window 3, the beta power increased in relation to the baseline in MI, whereas there was still a beta power decrease in EXE; this difference was significantly different [t(20) = 4.547, p = .000]. Similarly in the parietal ROI, there was a stronger decrease of beta power in MI compared to MC in Time Window 1 [t(20) =2.794, p = .036] and Time Window 2 [t(20) = 3.759, p = .012]. In addition, there was a stronger decrease of beta power in Time Window 2 in MI compared to EXE [t(20) = 2.554, p = .048]. In Time Window 3, the beta power increased in relation to the baseline in MI, whereas there was still a beta decrease in EXE; this difference was significantly different [t(20) = 3.979, p = .012]. In the occipital

ROI, there was a stronger decrease of beta power in Time Window 2 in MI compared to MC [t(20) =6.226, p = .000], whereas there was a stronger increase of beta power in Time Window 4 [t(20) =3.397, p = .036]. In addition, in Time Window 3, the beta power increased in relation to the baseline in MI, whereas there was still a beta decrease in EXE; this difference was significantly different [t(20) = 3.770, p = .012].

3.3.2. Alpha oscillations

The ANOVA revealed a main effect of Condition [F(1, 20) = 57.871, p = .000, η_p^2 = .743]. Post-hoc paired sample t-tests showed an overall smaller amplitude during EXE compared to MC [t(20) = 8.675, p = .000] and MI [t(20) = 9.645, p < .001] but no differences between MI and MC (p > .05). A main effect of Time Window [F(1, 20) = 27.328, p = .000, η_p^2 = .577] revealed that there was a decrease of alpha power in Time Windows 1 and 2 whereas there was an increase of alpha power in Time Windows 3 and 4.

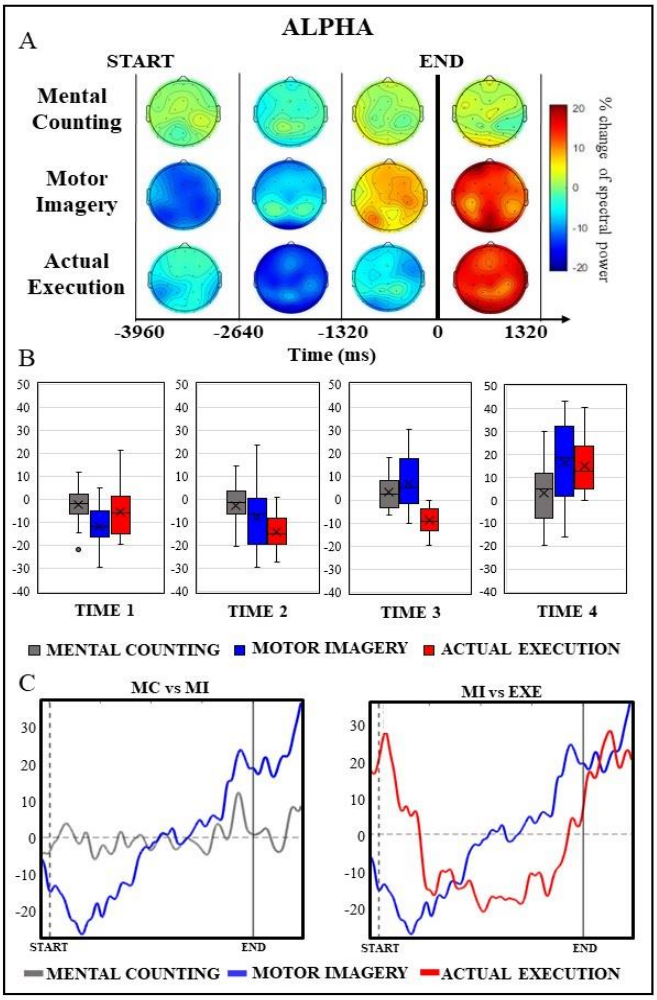

Figure 3.2. (A) Scalp maps topography of alpha (8-12 Hz) spectral power across conditions and time windows. **(B)** Averaged alpha percentage change of power from baseline across conditions in each

time window. **(C)** Averaged waveforms comparison between MC vs MI (left) and EXE vs MI (right) in alpha frequency band over parietal areas

As illustrated in Figure 3.2, the modulation of alpha power was similar to the modulation of beta power only in EXE. There was practically no modulation in MC, whereas there was a sharp and relatively short-lived power decrease at the early stages of MI. This was confirmed by a significant 2-way interaction between Condition and Time Window [F(1, 20) = 7.901, p = .000, η_p^2 = .283]. Post-hoc paired t-tests showed that there was a greater alpha power decrease in MI compared to MC in Time Window 1 [t(20) = 3.53, p = .024], and a greater alpha power increase in MI compared to MC in Time Window 4 [t(20) = 2.910, p = .036]. In addition, in Time Window 3, the alpha power increased in relation to the baseline in MI, whereas there was still a beta decrease in EXE; this difference was significantly different [t(20) = 7.327, p = .000].

A significant interaction between ROI and Time Window [F(1, 20) = 12.005, p = .000, η_p^2 = .375] revealed a stronger decrease of alpha power in the occipital ROI compared to the central [t(20) = 3.4.546, p = .000] and the parietal [t(20) = 4.794, p = .000] ROI in Time Window 2. Similarly, a stronger decrease of alpha power occurred over occipital ROI compared to the central [t(20) = 3.790, p = .012] and the parietal [t(20) = 2.34, p = .000] ROI. In Time Window 4, a stronger increase of alpha power occurred over the occipital compared to the central [t(20) = 3.799, p = .012] and the parietal [t(20) = 3.496, p = .024] ROI.

There was a significant interaction between Condition and ROI [F(1, 20) = 5.756, p = .003, η_p^2 = .223]. The amplitude of alpha power was larger in MI compared to MC in the parietal ROI [t(20) = 2.922, p = .036]. In addition, the amplitude of alpha power was larger in MI compared to EXE in the central [t(20) = 6.823, p = .000], parietal [t(20) = 10.924, p = .000] and occipital ROIs [t(20) = 6.610, p = .000].

A significant 3-way interaction [F(1, 20) = 3.254, p = .016, η_p^2 = .140] was further investigated by each ROI. In the central ROI, there was a stronger decrease of alpha power in MI compared to MC in Time Window 1 [t(20) = 4.234, p = .000] and a stronger increase of alpha power in Time Window 4 [t(20) =2.322, p = .048]. In addition, In Time Window 3, the alpha power increased in relation to the baseline in MI, whereas there was still an alpha decrease in EXE; this difference was significantly different [t(20) = 5.753, p = .000]. Similarly in the parietal ROI, there was a stronger decrease of alpha power in MI compared to MC in Time Window 1 [t(20) = 4.000, p = .012] and a stronger increase of alpha power in Time Window 4 [t(20) =2.818, p = .036]. In addition, In Time Window 3, the alpha power increased in relation to the baseline in MI, whereas there was still an alpha decrease in EXE; this difference was significantly different [t(20) = 4.468, p = .000]. In the occipital ROI, the significant difference between MI and MC appeared later compared to the central parietal ROIs; the analysis revealed a stronger decrease of alpha power in Time Window 2 [t(20) = 3.283, p = .024]. Similar to the other two ROIs, there was a stronger increase of alpha power in Time Window 4 [t(20) =2.623, p = .048]. In addition, In Time Window 3, the alpha power increased in relation to the baseline in MI, whereas there was still an alpha decrease in EXE; this difference was significantly different [t(20) = 8.662, p = .000].

3.4. Discussion

The present study demonstrated an overlap between the oscillatory brain activity related to motor imagery and actual execution of walking, which was significantly different from the mental counting condition. This confirmed that participants were engaged in the motor imagery task, and that they were not only mentally counting the steps. The results showed a general match between the power decrease-increase dynamics in the beta frequency band when participants were performing the actual movement of walking or the motor imagery of walking, and such correspondence did not emerge when participants were mentally counting. However, the data also indicated interesting differences between the action execution and motor imagery conditions. Furthermore, the data indicated a different beta power amplitude over brain areas during motor imagery, which was associated with larger amplitude of beta power over central and posterior electrodes, compared to actual walking. We also found that oscillatory activity in the alpha frequency band was characterised by a stronger power suppression at the beginning of the motor imagery compared to the actual execution and mental counting conditions, which rapidly dissipated during the performance of the task. The alpha power suppression was instead sustained during the actual execution of walking, whereas no modulation was evident when participants had to mentally count.

Consistently with the functional equivalence hypothesis, our results demonstrated that the pattern of power suppression in the beta frequency band is similar in the first two time windows of the actual execution and motor imagery of walking. This is further supported by differences in beta power suppression between the motor imagery and mental counting conditions, suggesting that participants did not just count the steps mentally in the motor imagery condition. Typically, power suppression in the beta frequency band over the central cortical areas is visible during the preparation (Rhodes et al., 2018; Tzagarakis et al., 2010) and the execution of movements (Pfurtscheller & Berghold, 1989; Kaiser et al., 2003; Stančák et al., 1997; Cassim et al., 2000; Kilavik et al., 2013). This pattern of beta band activity has also been reported during the kinaesthetic imagery of movement of body parts, i.e., hand, foot and tongue motor imagery (Pfurtscheller & Neuper, 1997; Neuper & Pfurtscheller, 1998; 1999; Pfurtscheller et al., 2006a, 2006b) and for motor imagery of skilled movements over sensorimotor areas (Nakagawa et al., 2011; Pfurtscheller et al., 2002; Di Nota et al., 2017). The role of beta suppression over the sensorimotor areas has been regarded as the index of a mechanism that recruits necessary units required to generate a motor output (Rhodes et al., 2018). In line with this account, our data showed that both motor imagery and execution of walking elicited a stronger beta power suppression, specifically during the first two time windows of the tasks, compared to mental counting. The suppression of beta oscillations might signal the recruitment of neural circuits underlying the activation of the relevant motor information related to the action representation of walking, which possibly resemble typical cognitive mechanisms occurring during motor planning of overt motor responses (see Glover & Baran, 2017).

However, the data also indicate relevant differences between beta power modulation during motor imagery and actual execution of walking. As shown in Figure 3.1, after the first two time windows of the motor imagery task, the beta power suppression rapidly faded away, whereas it was continuously sustained during actual execution of walking. This is likely due to a greater recruitment of motor units during overt motor outputs compared to covert actions. Furthermore, the power suppression in the beta band during motor imagery occurred over central, parietal and occipital electrodes. This finding would suggest the involvement of a complex cognitive substrate and distributed neural network for motor imagery (Solodikin et al., 2004). Indeed, suggestions for a multi-dimensional account of motor imagery are gaining consensus (Kraeutner et al., 2020; Cumming & Eaves, 2018; Dahm, 2019). According to this view, the generation of an action representation not only involves motor specific information related to the movement to be executed or imagined, but also its visual and sensory features (Munzert et al., 2009). Moreover, in order to maintain an action representation active in one’s mind, the visuomotor processing of the movement to be imagined requires additional cognitive resources compared to that needed for execution. Indeed, according to the recent motor cognitive model (Glover & Baran, 2017), motor imagery involves a greater engagement of executive functions compared to actual execution (Glover et al., 2020). In our study, participants were required to imagine walking down a room and to indicate the completion of the path. This condition requires the maintenance of the simulation of action active as well as a dynamic integration of visual and kinaesthetic sensory information associated with the motor imagery of one's body moving in the environment (Kruger et al., 2020). This suggests that motor imagery involves cognitive mechanisms that go beyond the mere encoding of motor information, and that the investigation of real world complex behaviour might have a critical role in revealing the multidimensional nature of these processes. Furthermore, the present study suggests that motor imagery of dynamic whole body movements might represent a window into the understanding of the neural and cognitive similarities with actual execution, but also the differences between the two behaviours.

The results of the present study also showed an increase of power in the beta frequency band toward the end of the walking movement in all three experimental conditions, but overall stronger in the motor imagery condition. The increase in the beta frequency band, also known as beta 'rebound', is typically observed over premotor and sensorimotor areas in the post movement phase (Jurkiewicz et al., 2006; Pfurtscheller et al., 2005; Pfurtscheller & Solis-Escalante, 2009). The beta rebound has been related to a possible resetting mechanism or to an 'idling state' occurring at the end of a movement (Engel & Fries, 2010; Kilavik et al., 2013). In the present study, the beta power increase was apparent at different times across the three experimental conditions, with two peaks occurring during the last two time windows in the motor imagery conditions. From these two peaks, the first coincided with the beta peak in the mental counting condition and the second with the beta peak in the actual execution condition. This possibly suggests two different mechanisms occurring at the end of the motor imagery trials: a first - early - increase of beta power which might indicate the end of the mental counting of the steps, occurring at the same time of the mental counting condition, and a second - delayed - increase of beta power related to the reset of the motor representation, occurring at the same time of the end of walking execution. The distinct patterns of the beta rebound would also indicate a different temporal recruitment of neural circuits related to the reset (Engel & Fries, 2010) or alternatively to inhibition (Salmelin et al., 1995). This evidence is furthermore in line with the study of Angelini et al. (2015), which showed that inhibitory processes are temporally distinct in motor imagery and action execution, suggesting that inhibition is automatically included in the cognitive processes underlying motor imagery (Angelini et al., 2015). Our data support such an account, showing an earlier activation of the beta rebound during motor imagery compared to actual execution of walking, likely indicating that inhibition is anticipated during the rehearsal of the action representation during covert motor behaviour. This data also shows that inhibition processes might be included in the multidimensional cognitive substrate of motor imagery.

Alpha power modulation followed a different pattern across the three experimental conditions. It is well known that during movement preparation and execution, a power desynchronization in the alpha and beta frequency bands occurs over sensorimotor areas (Leocani et al., 2001; Pfurtscheller & Berghold, 1989; Kaiser et al., 2003). This pattern has also been observed during motor imagery and movement observation, suggesting an association with action simulation mechanisms (Pfurtscheller & Lopes da Silva, 1999; Jurkiewicz et al., 2006; de Lange et al., 2008). In the present study, we found a continuous alpha desynchronization during actual execution, consistent with previous findings on walking (Gwin et al., 2011; Bradford et al., 2016; Bulea et al., 2015). Our results showed a prominent suppression of alpha power in the motor imagery condition, but only at the beginning of the imagined walking, whereas there was no evident modulation during the mental counting condition. The strong alpha desynchronization occurring at the beginning of motor imagery could indicate the initial allocation of attention towards relevant features of the task at hand, as the participants were instructed to actually walk for six steps, and then to start the motor imagery, focusing on the feeling and the sensation of ‘mentally’ moving the muscles. Our participants were furthermore asked to keep their eyes open during the motor imagery condition, in which they had to imagine walking down the path and to say ‘stop’ when they mentally reached the end of it. Therefore, it is likely that the large alpha power suppression at the beginning of the task indexed the allocation of attention towards the relevant aspects of the task, such as the visual input coming from the external environment. This is in line with previous literature (Foxe & Snyder, 2011; Brinkman et al., 2014) suggesting that the role of alpha decrease of power might be related to the allocation of attention toward relevant task-related information, such as visual information or changes in arousal (Brinkman et al., 2014). In our study, we also found a larger alpha suppression over central and posterior electrodes compared to actual execution. This result suggests the engagement of a wide range of brain areas involved during motor imagery, possibly indicating the processing of kinaesthetic and visual information related to the action to imagine. The activation of central and parietal areas has been reported to be prominent for kinaesthetic imagery, and occipital brain activation has been found to be stronger for visual imagery tasks (Guillot et al., 2009). Our results may suggest that the alpha decrease of power observed over central, parietal and occipital electrodes indexes the integration of visual and motor information related to action representation (Babiloni et al., 2002). This would indicate that during the imagery of whole body movement in the environment, the processing of multiple visual and motor information is required.

Overall, the present results indicate that motor imagery and actual execution of movements share common neural features, as predicted by the functional equivalence hypothesis. However, the results also highlighted imagery-related differences, which might play a crucial role in the understanding of cognitive mechanisms underlying motor imagery. The shared features occur during the early stages of walking action execution and motor imagery, possibly reflecting the initiation of an action plan representation (Glover & Baran, 2017). Furthermore, the beta rebound occurs similarly for walking action execution and motor imagery at the end of the action, possibly indicating the resetting of motor processes (Engel & Fries, 2010). The differences likely indicate the superior volume of cognitive processes and resources needed to sustain and integrate over a planned imagined walking movement, making the imagined movement an independent cognitive process to executed action, but nevertheless using some of the same areas of the brain as those used for action execution (Glover & Baran, 2017; Van der Lubbe et al., 2021). This suggests that functional equivalence has precise and general similarities. A precise similarity is the exact use of a specific cognitive mechanism for an objective. From the data here, it seems that the cognitive mechanism used for initiation of a plan and termination of an action plan is the same for both action execution and motor imagery. However, our data also suggest that while the imagination of movement uses sensory motor areas of the brain, the activity might not represent the activation of specific mechanisms used for action execution, and possibly reflects an independent cognitive process that is born out of the motor execution cell assembly (Keysers & Gazzola, 2014; see also Cooper et al., 2013). In these terms, during motor imagery, different information related to the action to imagine, which are stored and coded by multiple sensorimotor areas of the brain, are triggered and activated. This chain of cognitive events might require not only a mere static associative process that activates motor information, but a dynamic mechanism, as it might involve the processing of both past sensorimotor experience and online updating of sensorimotor input coming from the external environment (Keyers & Gazzola, 2014). That is to say that motor imagery uses some of the same cognitive apparatus as that used for action execution, but the cognitive processes for imagery and execution are independent; equivalent, but not functionally equivalent (not a common function).

Taken together, our data demonstrate that the high temporal accuracy of the EEG offers the possibility to disentangle cognitive processes occurring during motor imagery and action execution. It is crucial to investigate the neural correlates of these processes also considering the growing applications of motor imagery in clinical settings. Indeed, motor imagery of movements represents one of the main cognitive tools being used within the BCI approach, as it can be applied in absence of physical involvement and can be employed as a self-regulatory control signal of motor brain areas. The principle of the BCI approach is to detect neural signals in order to control external devices, such as exoskeletons or wheelchairs (Choi & Cichocki, 2008; Lafleur et al., 2013; Leeb et al., 2007). It is therefore important to understand which are the neural correlates of walking imagery as they can be used as self-regulatory signals for motor learning and recovery in patients with gait impairments (Malouin & Richards, 2010; Kranczioch et al., 2014; Daeglau et al., 2020).

In conclusion, the present results highlight the need to shed a new light on the previous assumptions of the functional equivalence hypothesis. This can be achieved using more ecological paradigms and employing tasks involving whole body movements, which have not received attention by previous literature. A new methodological approach such as the one used in the present study, might reveal critical differences in the stages of cognitive processes taking place during motor imagery and action execution.

Chapter 4. The neural response is heightened when watching a person approaching compared to walking away: evidence of dynamic social neuroscience

4.1. Introduction

In face-to-face daily social interactions, we constantly decipher and predict others' behaviour in order to produce appropriate responses. Research over the past 30 years has identified the neural substrates supporting the processing of actions performed by other individuals in a wide sensorimotor brain network including the occipital-temporal, parietal and premotor cortex, known as the action observation network (Grafton et al., 1996; Cross et al., 2009; Buccino et al., 2001; Caspers et al., 2010; Hari et al., 1998; Rizzolatti & Sinigaglia, 2010; Cattaneo & Rizzolatti, 2009; Hari & Kujala, 2009; Decety & Grèzes, 2006; Gallese et al., 2004). This action observation network represents observed action in the motor system of the observer (Rizzolatti et al., 2001; Sinigaglia, 2013). According to the theory of motor perception (Rizzolatti & Craighero, 2004), the implicit knowledge about motor principles of movement is obtained through representing the observed action in the same areas of the brain as those used for motor execution. However, the overlap between motor brain areas activated during both action observation and real execution does not only concern the kinematics of a given action, but also includes the goal of the action (Rizzolatti & Fogassi, 2014). Indeed, action observation has been proposed to play a key role in predicting others' action intentions or goals, and in the understanding of actions performed by other individuals (Schippers & Keysers, 2011; Hamilton, 2013; Buccino et al., 2001, 2004; Wheaton et al., 2004; Rizzolatti & Fogassi, 2014).

One aspect that we need to evaluate when interacting with others is whether the observed action is directed towards or away from us, allowing for cooperative interaction (for a review see Rizzolatti & Fogassi, 2014). In these terms, the perspective of the observer with respect to the observed action, becomes critically relevant. Indeed, previous research has shown that the visual perspective of an observer modulates the activation of the action observation network (Koski et al., 2003; Vogt et al., 2003). First-person perspective action observation seems to elicit stronger activity in sensorimotor areas compared to third-person perspective action observation (Maeda et al., 2002; Jackson et al., 2006; Angelini et al., 2018). For example, using TMS, Maeda et al. (2000) showed that corticospinal excitability increased during action observation of hand movements placed in a natural orientation (i.e., an egocentric perspective relative to the observer) compared to an unnatural orientation (i.e., an allocentric perspective relative to the observer). In a functional MRI study, Jackson et al. (2006) showed that participants were faster when they were required to imitate an action observed from the first-person than third-person perspective, and that first-person perspective action observation elicited stronger activation over the sensory motor cortex, compared to the third-person perspective action observation. Recently, Angelini et al. (2018) using electroencephalography (EEG), compared the cortical activity during action observation of hand movements from four different points of view (i.e., first-person, third-person and lateral left/right perspectives). They showed a stronger suppression of mu rhythm alpha (8-13 Hz) and beta (14-25 Hz) frequency band components, commonly considered as cortical markers of action observation. These suppressions occurred over sensorimotor areas during action observation of first-person perspective action, compared to the other points of view. As suggested by Maeda et al. (2002), the first-person perspective seems more similar to the 'self' perspective, which likely induces a facilitation of sensorimotor integration processes in the observer.

Aside from the perspective of the observer, another feature that might play a relevant role during the observation of others' actions, is the position in space of a moving agent with respect to the observer. Indeed, research with monkeys has shown that action observation network activation is differently modulated by the distance of the observed moving agent, and that 'mirror' neurons are selectively activated when the observed action is performed in the monkey's peripersonal space (Caggiano et al., 2009; Bonini et al., 2014). Generally, peripersonal space designates the immediate space surrounding the body, in which we can directly interact with objects or other agents, whereas extrapersonal personal space designates the space beyond our reach (Holmes & Spence, 2004; Rizzolatti et al., 1997; di Pellegrino & Làdavas, 2015). To date, studies on peripersonal and extrapersonal space in humans have focused mainly on cognitive processes related to the perception of manipulable objects (Culham et al., 2008; Proverbio, 2012). Few studies have considered the 'social' aspect of the proximity of other conspecifics to our peripersonal space (for a recent review see Bogdanova et al., 2021). For example, Teneggi et al. (2013) showed that the mere presence of another individual, but not of an artificial stimulus (i.e., a mannequin) in the extrapersonal space, narrows the boundary of the peripersonal space, suggesting that the boundary of one's peripersonal space representation can be shaped by the presence of others in social interactions. Additionally, Teneggi and colleagues showed that when participants interacted cooperatively (compared to a condition in which they were interacting non-cooperatively), the peripersonal space of the self, merged with the other's peripersonal space, suggesting that the representation of the peripersonal space is not only influenced by the presence of other individuals, but also by the valence of the social interaction.

As far as we are aware, to date no studies have shown how the perspective and the distance of an observer from an active agent might modulate the cortical activity during action observation. One reason for this is that action observation neuroimaging studies tend to use videos, rather than live actions, and hence the effect of proximity of the observed agent could not be studied. Thus, the objective of the present study was to investigate whether the perspective and distance of a passive observer with respect to a natural model moving towards and away from the observer would modulate the cortical mu rhythms commonly associated with action observation (alpha 8-12 Hz and beta 13-25 Hz oscillations). Previous studies showed that during action observation, event-related desynchronization or suppression of spectral power occurs over areas included in the action observation network; occipital, parietal, and sensorimotor brain areas (Arnstein et al., 2011; Avanzini et al., 2012; Muthukumaraswamy et al., 2004; Babiloni et al., 1999). Consequently, here we predicted that alpha and beta oscillations recorded during live whole body action observation would be modulated by the perspective of the observer, and that the condition of action observation of walking away (i.e., first person perspective), would elicit stronger suppression of alpha and beta frequency bands (Angelini et al., 2018), which has been reported as the cortical markers of the mental simulation occurring during action observation (Eaves et al., 2016; Muthukumaraswamy et al., 2004). Additionally, we expected that oscillations in the alpha and beta frequency bands would be modulated by the distance of the model from the observer, with a stronger suppression when the moving agent is close to the observer compared to when they are far away from the observer. Such modulation would indicate that the action observation network in the brain is particularly sensitive to the proximity of the observed agent.

In the present study we used a natural walking task, which in this case meant that participants observed a human model walking towards or away from them. As pointed out by Angelini et al. (2018), a general bias of action observation investigations has focussed on upper limb body effector actions, whereas lower limbs movements have been typically less explored. This is perhaps not surprising considering that the direct evidence for the mirror neuron network is largely based on reaching and grasping movements. The focus on upper limb movements may have arisen due to an assessment bias, caused by the inadequacy of methodologies for measuring dynamic executed actions of people moving around compared to observed lower limb actions. However, as discussed above, observation of movements that involve the other approaching or walking away from the observer are critically relevant for perceiving the impending interaction with others (e.g., Rizzolatti & Fogassi, 2014), akin to the basic survival principle of working out whether the lion is a threat walking towards you or is walking away. As far as we are aware, where previous studies of action observation have involved walking, the paradigms involved videos (Cochin et al., 1998) or animated pictures (Ulloa & Pineda, 2007; Zarka et al., 2014), rather than the observation of actual walking made by an agent present in the same room as the observer. As suggested by previous literature (for a review see Cevallos et al., 2015), ecological features (e.g., the dynamics of live action) might have an important role in action perception mechanisms and that brain responses during action observation of videos may be less consistent compared to live actions (Rizzolatti & Fogassi, 2014).

To date, only one recent study examined action observation of live-action walking (Kaneko et al., 2021). However, in that study, the model walked on a treadmill and only one observer point of view (lateral third person perspective) was investigated. By contrast, in the present study, we investigate how action observation network activity is modulated by the natural observation of an agent walking towards and away from the observer. In Kaneko et al.'s treadmill study (2021), it was found that that action observation of walking did modulate both alpha and beta oscillations over sensorimotor areas, but only when participants were requested to observe and simultaneously imagine the movement (kinaesthetic motor imagery), compared to passive observation. These modulations were found to be coupled with the observed gait cycle phases. Therefore, in the present study we also investigated whether coupling between the observed gait cycle and mu rhythms is dependent on the perspective of the observer.

4.2. Methods

4.2.1. Participants

Twenty healthy participants (18 female; age range = 18-44 years; mean age = 21.4 years, SD = 5.6 years) took part in the study. Due to the presence of prominent artifacts in EEG recordings, the data of two participants were excluded. The remaining data of eighteen subjects (18 female; age range = 18-44 years; mean age = 21.67 years, SD = 5.9 years) were used in the analysis reported. All the participants had no history of neurological disorder. Before starting the experiment, all the participants gave their written informed consent. Ethical approval was provided by the Research Ethics Panel of the University of Stirling.

4.2.2. Material and procedure

EEG data were continuously recorded using a 32 channels mobile EEG amplifier (ANT-neuro, Enschede, The Netherlands). Participants completed 40 trials for each condition. During the observation of walking conditions, participants stood 1 m away at the head of a carpet, watching the walking actions of a model walking up and down the carpet. The observed model was a female (M.M.) and walked in two directions: towards the participant and away, performing six steps on the 6 m carpet in each trial for a total of 80 trials divided in two blocks. The model wore the insoles of the Pedar-x System (novel.de, Munich, Germany), a bluetooth pressure distribution measuring system for monitoring local loads between the foot and the shoe, which allowed the extraction of temporal parameters of gait for this study. Each insole was connected to a controller-box attached to the model's waist with a belt. An Arduino board connected to the TTL port of the EEG amplifier and to the sync-box of the Pedar-x was used to synchronize the recording of the two devices, so that the EEG signal and gait can be integrated. At the beginning of each recording, a pulse was sent from the Pedar-x to the EEG in order to temporally align the two recordings. Trials in which the model walked towards the observer (AO of walking Towards condition, 40 trials) were separated offline from trials in which the model walked away and the observer viewed the back of the model (AO of walking Away condition, 40 trials) in order to compare the two perspectives in the following analysis. Figure 4.1 shows this study's two experimental conditions.

The conditions of this study were nested and counterbalanced with the conditions of another study, reported elsewhere, and included the following other conditions: Actual Execution of walking (in which the participant themselves walked up and down the carpet), Motor Imagery of walking (in which the participant imagined walking up and down the carpet) and Mental Counting (in which the participant counted to six paced by a metronome). None of these other conditions can be analysis with regards to the parameters on interest in this study (distance and perspective) and are therefore not included in this manuscript.

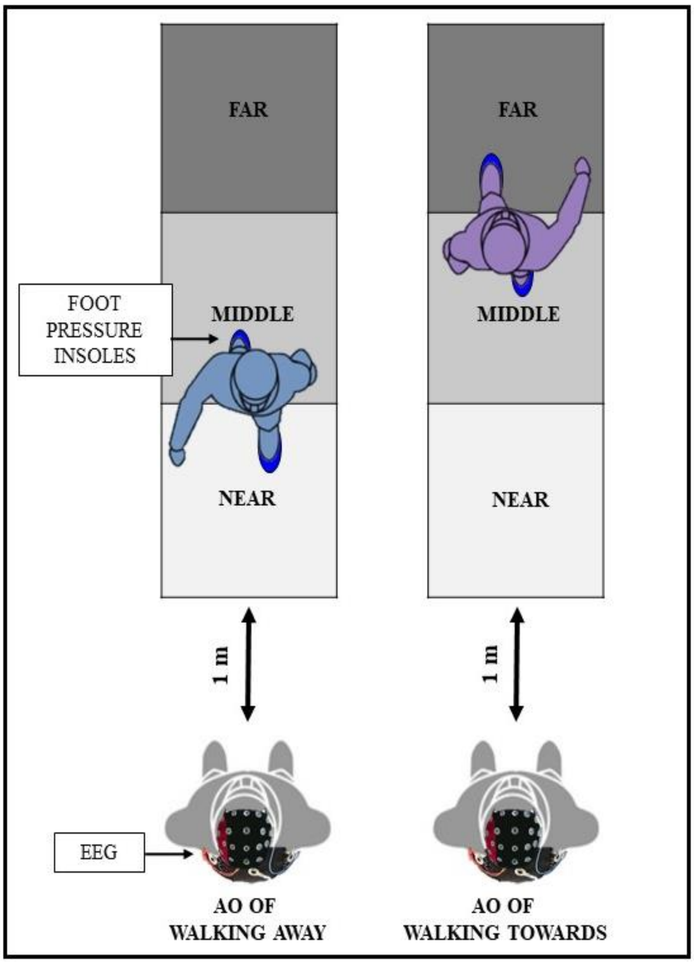

Figure 4.1. Representation of the two experimental conditions.

4.2.3. EEG acquisition and processing

EEG data was continuously recorded from 32 Ag/AgCl electrodes caps connected to a portable amplifier (ANT-neuro, Enschede, The Netherlands) at a sampling rate of 500 Hz and bandpass filtered at 0.01-250 Hz. Electrodes were positioned according to the International 10-20 system: FP1, FPz, FP2, F7, F3, Fz, F4, F8, FC5, FC1, FC2, FC6, M1, T7, C3, Cz, C4, T8, M2, CP5, CP1, CP2, CP6, P7, P3, Pz, P4, P8, POz, O1, Oz, O2, with AFz electrode as ground and CPz electrode as reference. The electrode impedances were reduced below 5 kΩ before the recording. EEG data analyses were performed using custom scripts written in MATLAB 2019a (The MathWorks) incorporating the EEGLAB toolbox (Delorme and Makeig, 2004). Data from the mastoid channels (M1 and M2) were removed from the analysis, and all remaining EEG data was filtered using a 0.1 Hz to 40 Hz bandpass filter. EEG channels with prominent artifacts were automatically selected (kurtosis > 5 SDs) and interpolated, and all channels were then re-referenced to the average. Data were downsampled to 250 Hz and an extended infomax Independent Component Analysis (ICA, Makeig et al., 1996) was performed to identify and remove non-brain signals. Brain-related-ICs were identified using the IClabel plugin (Pion-Tonachini et al., 2019). Components exceeding a 90% probability of being eye, muscle, heart, line noise, and channel noise were rejected. Only brain ICs with dipoles located inside the head and a residual variance lower than 15% were kept. An average of (mean ± SD) 7.19 ± 1.6 ICs across conditions was retained for the analysis.

4.2.4. Event related spectral perturbation (ERSP) analysis

EEG data were segmented in 4.5s epochs from -500 ms before and 4000 ms after the start of the trial (time 0). Single channel spectrograms were time warped to the median latency of the end of the trial across participants for each condition. Event related spectral perturbation (ERSP) was computed as the mean difference between single trial log spectrograms for each channel and each participant across conditions and the mean baseline of the overall trial (from 0 to 4000 ms). Middle line single channel time frequency spectrograms (Cz, Pz, POz, Oz; Figure 4.2) were visually inspected to identify relevant changes in the spectral power. In a data-driven manner, plots suggested two main spectral changes from baseline (event related desynchronization and event related synchronization) occurring in a range from 8 to 25 Hz. We defined the two frequency bands of interest namely alpha (8-12 Hz) and beta (13-25 Hz).

4.2.5. Statistical analyses

Alpha and beta oscillations were analysed by pooling the activity of neighbouring electrodes in relevant regions of interest (ROI) over sensorimotor (FC1, FC2, C3, C4, CZ, CP1, CP2) and parietal-occipital (P3, P4, PZ, O1, O2, OZ, POZ) areas. Both AO conditions were examined in two separate statistical analyses, described below.

(a) Effect of perspective and distance. In order to investigate the effect of both the perspective of the observer and the distance of the model from the observer on cortical activation in the mu rhythm subcomponents (alpha and beta) during AO, the overall length of each time-warped epoch was divided in 3 distances: the near, the middle and the far distances. Significant changes in the spectral power were assessed with 2x3x2 Repeated Measures ANOVAs with Condition (AO of walking Away, AO of walking Towards), Distance (near, middle, far) and ROIs (central, parietal-occipital) as within subject factors, separately for each frequency band.

(b) Cortical modulation depending on gait phases. In order to investigate whether cortical activation during AO is modulated by the gait phases, the model's heel strike latencies were extracted from the Pedar-x step analysis output and were used to analyse the EEG data of the participants (observers). To explore whether alpha and beta modulations were related to the perspective of gait phases, a gait cycle performed by the model (i.e., 3 consecutive heel strikes) was selected during the first time window of AO conditions (i.e., at the beginning of the trial). EEG data were segmented into epochs relative to the observed first heel strike (time 0) and single trial spectrograms were time warped to the median of the second and the third consecutive heel strike. Each gait cycle was then divided in percentage following the standard division of Perry & Davis (1992): stance phase (0-60%) and swing phase (60-100%). These phases were subdivided into: loading response (0-10%), mid-stance (10-30%), terminal stance (30-50%) and pre-swing (50-60%) for the stance phase; and initial swing (60-73%), mid-swing (73-87%) and terminal swing (87-100%) for the swing phase. ERSP was computed for each gait phase as the difference between each log spectrogram and the mean of the baseline (mean activity of the overall gait cycle) for each channel and participant within each condition. We assessed through two separate 2x7x2 Repeated Measures ANOVAs with Condition (AO of walking Away and AO of walking Towards), Gait Phase (loading response, mid-stance, terminal stance, pre-swing, initial swing, mid-swing, terminal swing) and ROIs (central, parietal-occipital) as within subject factors, separately for each frequency band.

For all the analyses, the Greenhouse – Geisser correction was applied whenever the sphericity assumption was violated and post-hoc sample t-tests adjusted using Bonferroni correction were performed to investigate significant main effects and interactions.

4.3. Results

As can be seen in Figure 4.2, which illustrates the time frequency spectrograms of Cz, Pz, POz, Oz channels, the two AO conditions showed a distinct pattern of power decrease and increase. The main differences appear to be confined to the extremities of the epoch (areas highlighted in the black rectangles in Figure 4.2) in which the model was near or far from the observer, indicating an effect related to the proximity of the moving agent. Furthermore, the two patterns appear to be reversed depending on the perspective (highlighted in the black rectangles in the plots in Figure 4.2).

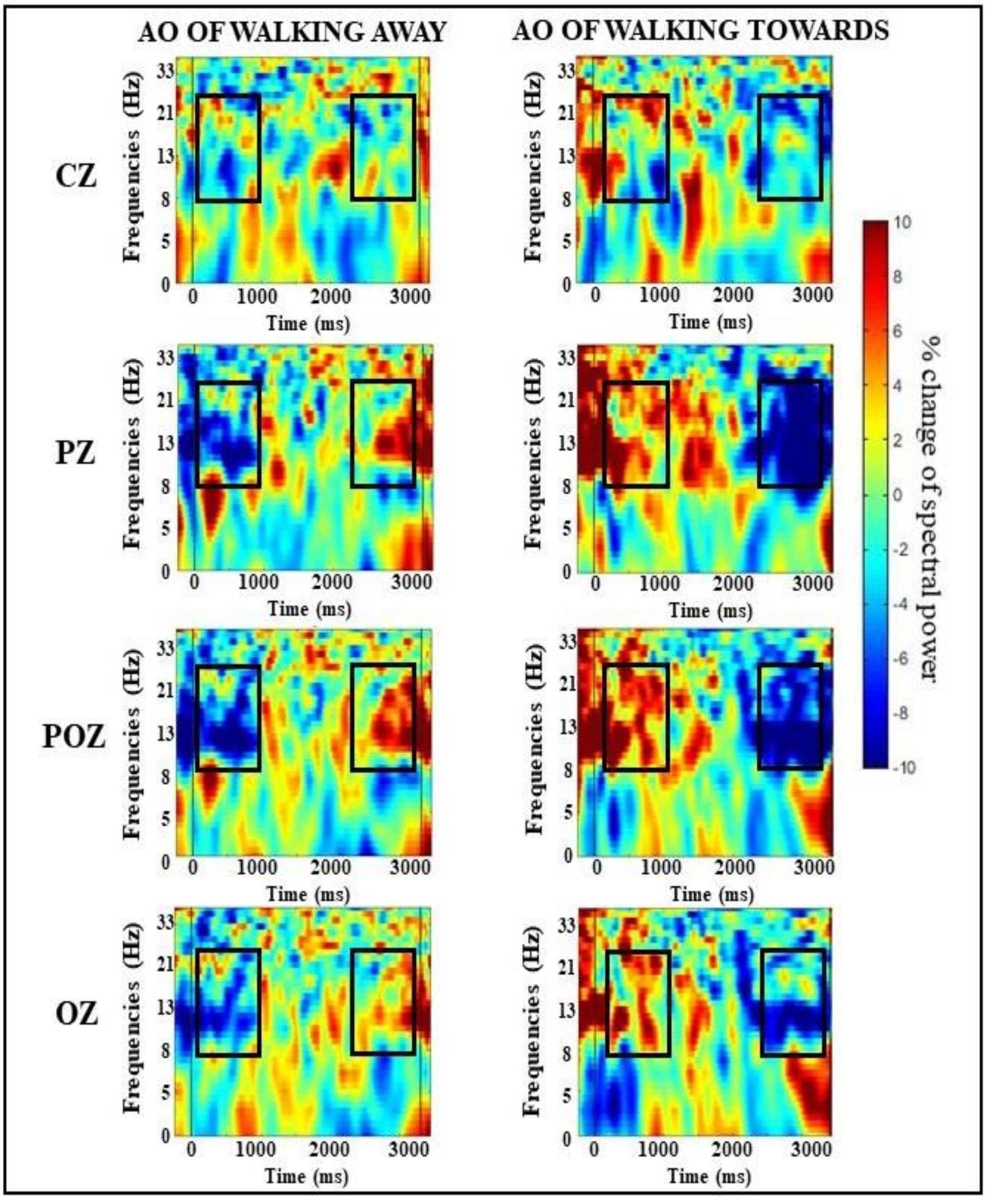

Figure 4.2. Time-frequency spectrograms of midline channels (in order Cz, Pz, POz, Oz) across conditions for the whole epoch. The onset of the trial is at 0 ms.

4.3.1. Effect of perspective and distance

4.3.2. Alpha

The ANOVA revealed a main effect of Distance [F(1, 17) = 4.859, p < .05, η_p^2 = .222] with an overall stronger decrease of alpha power when the observer was near to the model compared to when the model was in the middle of the walk (t(17) = 2.855, p = .033) and a marginally significant difference when the model was near compared to far (t(17) = 2.855, p = .066). There was no significant difference in alpha modulation between the middle and far distance (p>.05).

A main effect of ROIs [F(1, 17) = 6.139, p < .05, η_p^2 = .209] showed an overall stronger decrease of alpha power over parietal-occipital areas compared to central brain areas.

A significant interaction between ROIs and Distance [F(1, 17) = 4.383, p < .05, η_p^2 = .205, see Figure 4.3, panel (a)] showed a significantly stronger decrease of alpha power over parietal-occipital compared to central areas when the model was near to the observer (t(17) = 3.382, p = .012), but showed no significant differences for the middle and far distances (p > .05).

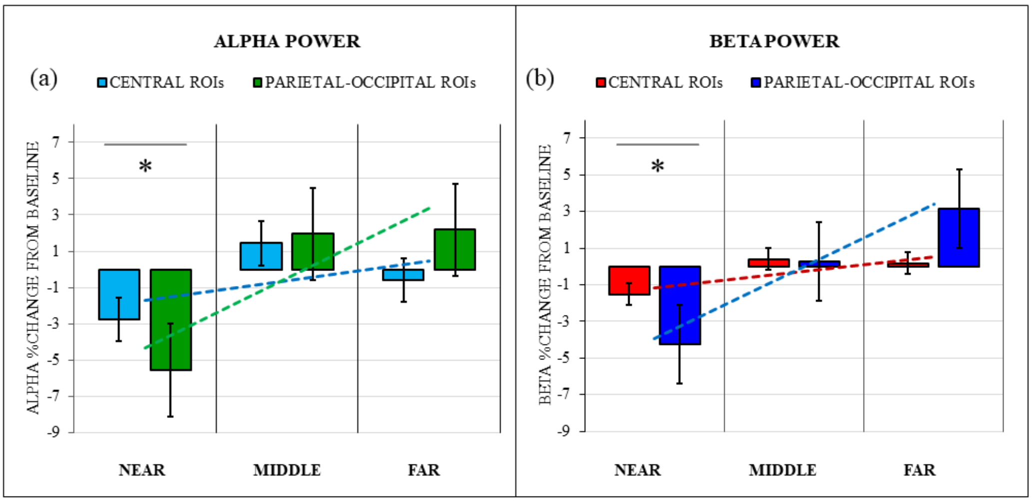

Figure 4.3. (a) Alpha percentage change from the baseline across ROIs and Distance (with relative standard error bars and dashed linear trendline). **(b)** Beta percentage change from the baseline across ROIs and Distance (with relative standard error bars and dashed linear trendline).

4.3.3. Beta

The ANOVA revealed a main effect of Distance [F(1, 17) = 9.293, p < .01, η_p^2 = .353] with an overall stronger decrease of beta power when the model was near to the observer compared to when the model was in the middle (t(17) = 3.415, p = .009) and far from the observer (t(17) = 4.056, p = .003). There was no significant difference in beta modulation between the middle and the far distance (p > .05) (see Figure 4.3, panel (b)).

A significant interaction between Condition and Distance [F(1, 17) = 5.103, p < .05, η_p^2 = .231, see Figure 4.4] showed that a stronger decrease of beta power occurred when the model was near and walking towards the observer (i.e., the model facing the observer) compared to when the model was near and walking away from the observer (i.e., the model showing her back to the observer), (t(17) = 2.713, p = .035).

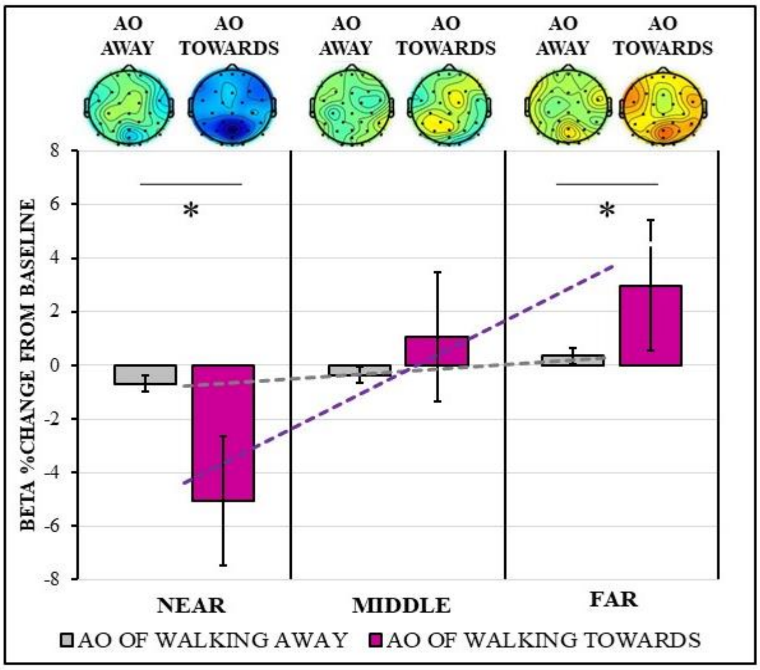

Figure 4.4. Beta percentage change from the baseline across Conditions and Distance (with relative standard error and dashed linear trendline). Scalp topographies of beta activity for each condition (AO of walking Away; AO of walking Towards) across distances (near, middle, far) are shown on top of the relative bars. As can be seen from the trendlines, there was a weak modulation of beta power when the model was moving away from the observers. On the contrary, there was a strong modulation when the model moved towards the observer, approaching them.

A significant interaction between Condition and ROIs [F(1, 17) = 8.424, $p < .05$, $\eta_p^2 = .331$] showed a significant stronger decrease of beta power over parietal-occipital areas when the model was walking towards the participants compared to the condition in which the model was walking away (t(17) = 2.189, p = .043). In contrast, in the condition of AO of walking Away, there was a stronger decrease in beta power over central areas compared to parietal-occipital areas (t(17) = 2.816, p = .012).

A significant interaction between ROIs and Distance [F(1, 17) = 10.083, $p < .01$, $\eta_p^2 = .372$, see Figure 4.3, panel (b)] showed a significant stronger decrease of beta power over parietal-occipital areas compared to central when the model was near to the observer (t(17) = 3.539, p = .009) and a stronger decrease over central areas compared to parietal-occipital areas when the model was far from the observer (t(17) = 3.539, p = .015). There was no significant difference in beta modulation over central and parietal-occipital areas when the model was in the middle distance ($p > .05$).

4.3.4. Cortical modulation depending on the perspective of gait phases/cycle

4.3.5. Alpha

Figure 4.5 shows alpha modulation during the gait cycle across the two different conditions. As we can see from the graph, alpha modulation presents an inverse pattern depending on the perspective of the observer with respect to the direction of the gait cycle of the model. Furthermore, the graph indicates that alpha modulation is stronger in the condition in which the model was walking towards the observer. Indeed, the ANOVA did not reveal any significant main effect (p > .05). A significant interaction between Condition and Gait Phases [F(1, 17) = 3.206, p < .05, η_p^2 = .159] indicated that differences in alpha modulation occurred during the first gait cycle of both AO conditions. Paired-sample post-hoc t-tests showed a significantly stronger decrease of alpha power in AO of walking Towards compared to AO of walking Away during the mid-stance, just before the second heel contact (t(17) = 2.823 , p = .035). During the pre-swing and initial swing (just after the second heel contact) a significantly stronger decrease of alpha power occurred in AO of walking Away compared to AO of walking Towards (pre-swing: t(17) = 2.679, p = .042; initial swing: t(17) = 2.504 , p = .028).

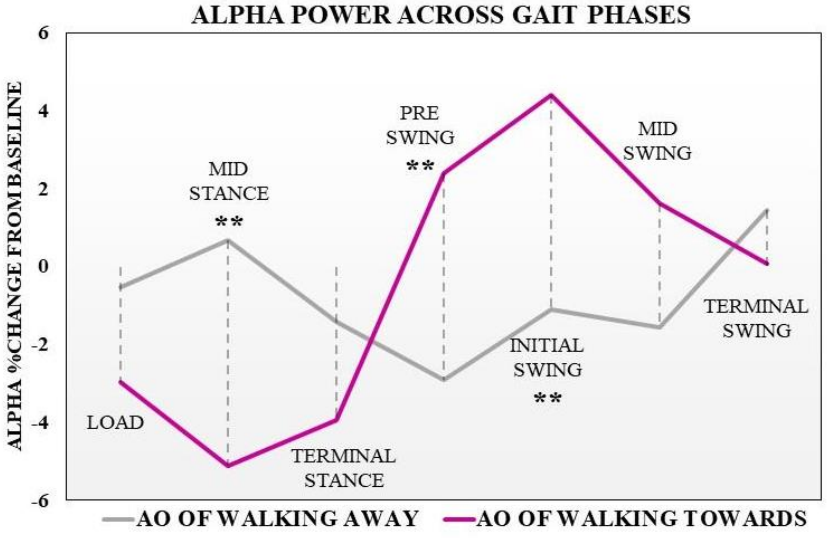

Figure 5. Alpha percentage change from the baseline averaged across central and parietal-occipital ROIs, across AO conditions and gait phase. Dashed lines represent the alignment between time points of the different gait phases across two conditions, respectively defined: load (0-10%), mid-stance (10-30%), terminal stance (30-50%), pre-swing (50-60%), initial swing (60-73%), mid-swing (73-87%) and terminal swing (87-100%).

4.3.6. Beta

The ANOVA did not reveal any significant main effect or interaction ($p > .05$).

4.4. Discussion

This study uniquely establishes that during the observation of a live agent walking away or towards the observer, the action observation network is sensitive to both the perspective and the distance of the observer relative to the moving agent. By examining the time course and distribution of the cortical activation associated with action observation, we revealed distinct patterns of modulation in the alpha and the beta frequency bands depending on the distance and perspective of the observed action. This dissociation between the two frequencies demonstrates that alpha is tuned to visual information, such as a person's proximity, but that beta, as this study shows for the first time, reveals tuning of the action observation network to those situations compatible with impending social interaction between the observer and the agent.

The analysis revealed that alpha frequency was modulated only by the distance of the model from the observer, demonstrated by a stronger decrease of power over parietal-occipital brain areas when the model was 'near' to the observer compared to 'far', regardless of perspective. Previous primate research has shown that mirror neurons of the brain area F5 responded selectively to object-directed actions performed in the peripersonal space of the monkey (Caggiano et al., 2009; Bonini et al., 2014). Similarly, human EEG studies, investigating peripersonal and extrapersonal space, reveal alpha suppression of power over parietal areas when participants estimate the reachability of manipulable objects placed within - compared to outside - their peripersonal space (without making overt action) (Wamain et al., 2016). Taken together these previous findings suggest that motor activation is moderated by the location of an object in the space relative to the subject, and enhanced when the object is within peripersonal space and the subject can directly interact with the object (Wamain et al., 2016). Building on these earlier data, the present research findings provide the first demonstration that the proximity of a moving agent approaching the peripersonal space of an observer moderates neural activity within the action observation network.

One important outcome of the current study is further clarification of the circumstances under which the action observation network operates. In the present study design, the movement of the model did not imply the use of any object or any explicit goal-directed behaviour towards the subject, thus our results suggest that even in the absence of an object or an explicit intention of an interaction, alpha and beta oscillations over parietal-occipital areas are selectively modulated by the proximity of others. As previously shown by a large body of evidence, the parietal-occipital cortex is part of the action observation network involved in the representation of space for action (Colby & Goldberg, 1999; Husain & Nachev, 2007), in motor planning (Andersen et al., 1997; Andersen & Cui, 2009; Buneo & Andersen, 2006; Busan et al., 2009), in the action observation of object and non-object directed actions (Iacoboni et al., 2004; Evangeliou et al., 2009; Buccino et al., 2001) and in processing social information during action observation (Tunik et al., 2007; Pobric & Hamilton, 2006). The present data furthermore suggest that when the model is far away, an increase of power occurs both in the alpha and in the beta bands, suggesting a reverse oscillatory pattern compared to when the model is near to the observer. We speculate that this ~~distinctive~~ pattern of activity suggests the involvement of attentional processes, visible in the relative increase of alpha spectral power when the agent is farther away from the perceiver, when attentional demands are more likely be reduced (Foxe & Snyder, 2011; Talsma et al., 2010). These results are consistent with the accounts that suggest alpha power is inversely related to effortful attentional processing, such that increased power reflects a reduction in cognitive load (Foxe et al., 1998; Vanni et al., 1997; Van Diepen et al., 2019). At least in part, however, the apparent increase in alpha power visible during the moment in which the model is farther away from the perceiver might also reflect the fact that the baseline was computed over the entire epoch. As can be seen in Figure 3, alpha power values relative to the baseline are negative when the model is near the observer and positive when the model is farther away from the observer. Regardless, our results support the view that alpha oscillations over parietal-occipital areas reflect a mechanism which underlies the processing of relevant visual and spatial information of the observed action, such as the distance of another agent from the observer.

Crucially, the results revealed that differently from alpha, oscillations in the beta frequency band are modulated not only by distance, but also by perspective. The analysis revealed a stronger decrease of beta spectral power over parietal-occipital brain areas when the model was facing the participant (AO of walking towards) compared to when observed walking from the back (AO of walking away). Furthermore, beta power suppression was more prominent during approach when the model was near and walking towards the participant. Sensorimotor beta oscillations have previously been shown to be an index of the activity of the action observation network in humans (Cochin et al., 1998; Hari et al., 1998). Perspective (but not distance) was previously considered in an EEG study of action observation of video recorded meaningless hand gestures by Kilner and colleagues, which showed beta (Kilner et al., 2009) but also alpha (Kilner et al., 2006) were modulated by the direction of the model in respect to the observer (Kilner et al., 2009). Indeed, Kilner and colleagues (2009) found a stronger beta power suppression over sensorimotor areas contralateral to the side of the screen in which the gesture was performed, but only when the model was facing the participant, compared to the condition in which the model was facing away. This finding has been interpreted as a modulation in visuospatial attention driven by the social relevance of the observed action. Kilner et al. (2006) described a similar pattern in the alpha frequency band, suggesting that both alpha and beta cortical rhythms could be related to a mechanism that filters socially relevant information of an observed action within the action observation network (Kilner et al., 2006). Critically, our results showed a clear dissociation in which only oscillations in the beta (and not alpha) frequency band were modulated by the perspective of the observer.

The current finding is furthermore important because it demonstrates that the two cortical rhythms have partially distinct roles within the action observation network. In a further dissociation, we found that only oscillations in the alpha, but not in the beta frequency band, were modulated by the gait phases of the observed model. It has been shown that cortical activity in the alpha and in the beta frequency bands over the sensorimotor cortex is locked to the gait phases (Gwin et al., 2011; Seeber et al., 2014; Wagner et al., 2012). A similar modulation has been reported during the simultaneous observation and imagination of treadmill walking (Kaneko et al., 2021; to our knowledge the only other study that integrated brain signals of the observer with the live movements of the observed). Indeed, in their recent study Kaneko et al. (2021) reported beta power suppression at the stance and mid-swing phases, and alpha and beta power increases at the terminal stance, when participants were required to imagine walking and observe a model walking on a treadmill from the lateral perspective. By contrast, in the present study we found that alpha, but not beta, was modulated by the gait phases during action observation, and that this modulation depended on the perspective of the observer.

4.5. Implications and conclusion of the present study

Due to the novelty of both a dynamic (mobile) brain imaging method and a novel experimental design, the findings of this study mean a significant move forward in the understanding of the cognitive and neural processes supporting observation of real world action. The live presence of the moving agent meant that, for the first time, we could examine the neural correlates of the dynamic features of action observation, where the moving agent was closer or further away from the observer. We showed that mu rhythms (alpha and beta) suppression was stronger when actions were performed near to the observer - close to the participant's peripersonal space - compared to actions performed far away from the observer. It is significant that earlier studies in non-human primates have shown that the action observation network is activated when the observed action is performed in the peripersonal compared to extrapersonal space (Caggiano et al., 2009; Bonini et al., 2014), providing support for the claim that the present results relate to impending social interaction between the observer and the agent.

Furthermore, our data showed that in real world action observation of walking, motor activation is not necessarily facilitated by first person perspective of the observer, as previously suggested (Maeda et al., 2000; Jackson et al., 2006; Angelini et al., 2018), as we found a stronger beta suppression of power over parietal-occipital brain areas when the model is facing the participant. Previously, action observation investigations used only videos, not live actions, and furthermore showed only part of the body when displaying movements usually of the upper limb. Here we used a live action involving the actual presence (and therefore whole body) of the moving agent, typical of real-life social interactions. The fact that we found that in live action observation the action observation network responds to perspective and proximity, highlights the need to examine the kinds of real-life interaction that have been neglected due to technological constraints. This suggests that in daily life action observation, the observer has to monitor and assess multiple sources of information from the observed action, such as the orientation of the agent moving towards the observer and the decreasing distance between the observer and the approaching agent.

Finally, our study suggests that alpha and beta oscillations are dissociable, playing distinct roles during action observation. Previous studies have not typically separated the two bands, describing mu rhythms together as the index of a general mechanism involved in the regulation of inhibition/activation of cortical visual, somatosensory, and sensorimotor brain areas (Pfurtscheller & Lopes da Silva, 1999). However, recent evidence points towards different functional and topographical distribution for alpha and beta activities (Stolk et al., 2019). Indeed, alpha rhythm has been proposed to signal the allocation of attention toward relevant task-related information (Foxe & Snyder, 2011; Brinkman et al., 2014; Babiloni et al., 2006), while beta oscillations are thought to be related to motor activation (Ronqvist et al., 2013). Our results do indeed support these accounts (e.g., see Kilner et al., 2009) and demonstrate that whereas alpha oscillations signal the brain response to salient visual aspects of an observed action (i.e. the presence of an agent near to our peripersonal space), beta oscillations might instead reflect a specific process which filters and discriminates between relevant social motor information of action performed by others (i.e., the direction of the interaction).

Overall, the findings in our study provide neural evidence for the significance of interactions between people, and highlights that in order to understand social interactions we need to investigate dynamic real world behaviour. To do this, it is necessary to employ methodological approaches suited to a new dynamic social neuroscience, such as mobile neuroimaging techniques, bringing experimentation into the real world.

Chapter 5. General discussion

5.1. Summary of findings

The findings of the studies reported in the present thesis demonstrate the feasibility of the mobile EEG approach to investigate neural correlates of action representation in real world locomotor behaviour. An important aspect highlighted throughout the three studies is that the distinct pattern of neural activity in the theta, alpha and beta frequency bands over cortical areas were modulated by the task performed and by the incoming sensory information from the surrounding environment. The findings demonstrated cognitive processes underlying the monitoring, updating and maintenance of an internal model of behaviour during online gait adaptations and motor imagery of walking, and how these processes are modulated by relevant social cues when observing other people' movements. More importantly, the findings of this thesis suggest the embodied nature of cognitive processes underlying action representation.

The study described in Chapter 2, support the 'Dual Mechanism of Control' framework (Braver, 2012). According to this model, cognitive control can be dissociated in two forms of control, the proactive form of control and the reactive form of control. The proactive form of control is a strategy which detects possible interference, updates the action representation and its goal accordingly, and maintains them active until the effective implementation of the action. The findings indeed demonstrate that a proactive control mechanism is involved when we face unexpected changes in the environment, such as the appearance of an unexpected obstacle to overcome. More specifically, when participants had to avoid unexpected obstacles, a power increase in theta frequency band occurred over frontal brain areas. This change in spectral power was not visible both when participants had to avoid predictable objects, already visible from the beginning of the walk, and when they had to walk without any obstruction. The frontal theta is furthermore temporally aligned with the presentation of the unpredictable obstacle in the two alternative distances, near and far from the participants, and it occurs stronger when the motor adjustment requires more effort, i.e., when the object suddenly appeared closer to the participants compared to when it was projected farther away. This would also indicate that cognitive demand associated to the task is reflected in the power spectral increase of theta oscillations.

The brain area that plays a crucial role proactive control of behaviour is the prefrontal cortex (Braver, 2012). Due to its broad connections, the prefrontal cortex processes the information associated with both internal mental states and external inputs (Miller & Cohen, 2001). Indeed, the prefrontal cortex receives inputs from temporal, occipital and parietal areas, which are responsible for processing multimodal sensory information, such as visual, somatosensory, and auditory information. The main output connections of the prefrontal cortex include the motor cortex, cerebellum, limbic structures, and the basal ganglia. Therefore, it represents a hub for the integration of sensory and motor information, which makes it suitable to exert a general top-down control over different cognitive process (Miller & Cohen, 2001). A widely accepted hypothesis suggests that the prefrontal cortex is responsible for activating higher level representations and maintaining them online until the goal is achieved (Miller & Cohen, 2001; Braver, 2012). However, the prefrontal cortex also updates representations when a change is detected, such as the appearance of an unexpected obstacle, ensuring a switch in the motor plan and providing the flexibility needed depending on the cognitive demands (Miller & Cohen, 2001; Braver, 2012).

Although the Dual Mechanism of Control framework provides useful insights to understand cognitive control mechanisms underlying human behaviour, it might be suggestive of a highly disadvantageous system (Braver, 2012). For example, when the implementation of a response to an interference needs to be delayed in time – i.e., not implemented immediately – the information related to the action plan should be maintained active in the brain until the response is completed, involving a considerable cognitive cost. Indeed, the data reported in Chapter 2 showed in theta power increase a possible marker of proactive control when unexpected obstacles appear while walking. However, encountering objects on the floor, regardless of their expectation, also elicited a beta power suppression, which was visible just before crossing the obstacle but not when participants freely walked the path. This temporal dissociation suggest that the implementation of the motor adaptation is triggered just before performing it, with no need to maintain the information active in the brain until the response is required. This aspect of cognitive-motor control is not explained by the Dual Mechanism of Control (Braver, 2012). A theoretical model which provides a possible explanation is the proactive model of action preparation, which has been proposed by Pezzulo & Ognibene (2012). According to this model, proactive and reactive control strategies lay on a continuum, rather than being two independent and separate processes as suggested by the Dual Mechanism of Control framework (Braver, 2012). Consequently, the proactive form of control monitors the internal model which drives the motor plan to accomplish a certain goal, but this representation is not continuously maintained active in the brain, as the appropriate action can be triggered at the right time. The results of the first study presented in Chapter 2, support both accounts, as they suggest a distinction between proactive and reactive stages of cognitive control in line with the Dual Mechanism of Control framework (Braver, 2012). However, the findings also suggest the involvement of a 'late' component of proactive control mechanism, likely reflected in the power suppression in the beta frequency band, which occurred significantly stronger when participants had to step over obstacles, but only before crossing the object, regardless of the expectations (i.e., both for predictable and unpredictable conditions), compared to the condition in which no obstacle appeared. This 'late' component would support the account of a continuous proactive process that trigger the right response at the right time (Pezzulo & Ognibene, 2012), indicating the activation of sensorimotor processes related to the execution of the motor adaptation only when required by the task.

At the end of the motor adaptation a clear beta rebound was found over parietal areas, possibly corresponding to the reactive control mechanism indicated by Braver in his Dual Model of Control (2012). According to the model, the reactive form of control is activated after the detection and the resolution of an external interference (Braver, 2012). The beta rebound over sensorimotor areas has been previously reported as an index of reactive control (Liebrand et al., 2017) and it has been associated with a resetting mechanisms that recalibrate the state of the motor system after a change (Engel & fries, 2010). According to these different perspectives, the beta rebound after crossing an obstacle regardless of the expectations, but not when walking without obstructions, might represent a resetting mechanism, which restore the motor system to its previous state after implementing a change in a typical pattern of behaviour.

The second study, reported in Chapter 3 of the present thesis, concerned the investigation of the neural correlates of action representation during motor imagery of walking. The results of this study showed an overlap between brain activity during motor imagery and actual execution of walking, which were reflected in the modulation of alpha and beta frequency bands. However, the temporal dynamics of alpha and beta frequency range, differed between the two conditions. The data indeed showed an alpha power suppression occurring both in motor imagery and in actual execution of walking; however, in motor imagery, the suppression of alpha power rapidly faded away, whereas it was sustained during actual execution of walking. The pattern of brain activity recorded in the second study (Chapter 3) during actual performance of walking, is consistent with previous literature reporting alpha power suppression over sensorimotor areas during the planning and the execution of voluntary movements (Leocani et al., 2001; Pfurtscheller & Berghold, 1989; Kaiser et al.,

2003) and during active gait (Gwin et al., 2011; Bulea et al., 2015; Seeber et al., 2014; Wagner et al., 2014). During motor imagery, the alpha suppression was visible only at the beginning of the trials, and occurred over central, parietal, and occipital electrodes, which might reflect the processing not only of motor information related to the activation of the action representation of walking, but possibly also the encoding of spatial features of the environment. Indeed, it is worth noting that the participants were instructed to perform the motor imagery of walking with eyes open in order to enhance the visual representation of the surrounding environments, and to indicate verbally when they mentally reached of the end of the path. The role of occipital alpha in the allocation of attention towards spatial information has been established by previous literature (Foxe et al., 1998; Foxe & Snyder, 2011; Brinkman et al., 2014). Furthermore, the engagement of central and parietal areas has been reported to be more prominent for kinaesthetic imagery compared to visual imagery (Guillot et al., 2009). Conversely, occipital brain activation has been found to be stronger for visual imagery compared to motor imagery (Guillot et al., 2009). The findings of the second study are in line with this evidence, suggesting that alpha suppression during motor imagery of whole body movements in the environment might signal the engagement of different functional brain areas and the processing of visual and motor information related to the action representation.

The results of the second study also indicate similar pattern of beta power modulation during motor imagery and actual execution of walking, which supports the functional equivalence hypothesis assumptions. The similarities are visible in the beta power suppression occurring during the first two seconds of walking execution and motor imagery, which was not evident in the mental counting condition. As already mentioned in this thesis, power suppression in the beta frequency band over sensorimotor areas has been typically observed during the execution of movements (Pfurtscheller & Berghold, 1989; Kaiser et al., 2003; Stančák et al., 1997; Cassim et al., 2000; Kilavik et al., 2013) and during the kinaesthetic imagery of movements (Pfurtscheller & Neuper, 1997; Neuper & Pfurtscheller, 1998; 1999; Pfurtscheller et al., 2006a). This evidence has suggested that beta power suppression over sensorimotor brain areas might signal the activation of neural network necessary to generate a motor output (Rhodes et al., 2018). Therefore, the beta power suppression observed in the second study might reflect the processing of motor information related to the action representation of walking, which is similar to cognitive processes occurring during motor planning of actual execution of movements (Glover & Baran, 2017). Furthermore, a clear beta rebound occurred in at the end of the three experimental conditions, although with differences in its time course. More specifically, the beta rebound was characterized by two prominent peaks in the motor imagery condition: a first peak was apparent towards the end, aligned with the increase of beta power in the mental counting condition and a second peak of beta rebound aligned with the beta rebound in the actual walking condition. The time course of the two peaks in the beta rebound during motor imagery might indicate the involvement of cognitive processes associated with the reset of the motor system (Engel & Fries, 2010) or alternatively with inhibition (Salmelin et al., 1995). Indeed, in an EEG study, Angelini et al. (2015), showed that inhibitory processes are temporally distinct in motor imagery and action execution. The findings of their study showed an earlier activation of neural circuit related to inhibitory control, suggesting that inhibition is automatically recruited when withholding over motor output (Angelini et al., 2015). The findings of the second study are in line with this evidence, showing that the earlier beta rebound occurring during motor imagery might signal the recruitment of inhibitory processes, which might be automatically activated during motor imagery. Taken together, these results provide real world evidence for the functional equivalence hypothesis, suggesting that the activation of the action representation during motor imagery share the encoding of sensory and motor information with action execution. However, they also highlight temporal differences in cognitive and neural processes underlying motor imagery and actual execution of whole body movements in real world environments, which is consistent with the multidimensional account of motor imagery (Kraeutner et al., 2020; Cumming & Eaves, 2018; Dahm, 2019).

The third study, reported in Chapter 4 of the present thesis, concerned the investigation of action observation of whole body motion in the real world. More specifically, we investigated a situation in which an observer watches another person approaching or walking away. In real world interactions, the distance and the perspective of another person is of critical importance to determine the possibility of a social interaction. Therefore, we recorded EEG from participants who observed a ‘model’ walking away and towards them. The data revealed two distinct cognitive processes reflected in the modulation of alpha and beta frequency bands, commonly considered as the index of the activation of the action observation network.

The data showed that a stronger suppression of alpha power over parietal-occipital electrodes occurred only when the model was ‘near’ to the observer, but not when it was ‘far’. This is consistent with previous EEG studies showing alpha suppression of power over parietal areas when participants estimate the reachability of manipulable objects placed within their peripersonal space (Wamain et al., 2016). Furthermore, other investigations showed that parietal-occipital areas are associated with the representation of space and motor preparation

(Colby & Goldberg, 1999; Husain & Nachev, 2007; Andersen et al., 1997; Andersen & Cui, 2009; Buneo & Andersen, 2006; Busan et al., 2009). This suggest that motor activation is greater when an object is placed within the reachable space of the perceiver, i.e., it is possible to directly interact with the object (Wamain et al., 2016). The data of the third study of this thesis are in line with this evidence, suggesting that in real world contexts, alpha oscillations over parietal-occipital electrodes are modulated by the distance of an agent from the observer.

More importantly, the results of the third study revealed that beta frequency band was modulated both by the perspective and the distance. Indeed, the data showed a stronger decrease of beta spectral power over parietal-occipital scalp locations when the model was approaching the observer (facing them) compared to when the model was moving away. Furthermore, beta power suppression was more prominent when the model was near and walking towards the participant. These findings highlighted the role of beta oscillation within the action observation network (Cochin et al., 1998; Hari et al., 1998) and are furthermore in line with previous EEG laboratory-based investigations (Kilner et al., 2009, 2006). Kilner and colleagues (2009) reported a larger beta amplitude over sensorimotor areas contralateral to the side of the screen in which the gesture was performed, but only when the model was facing the participant, compared to the condition in which the model was facing away. This finding suggests that beta oscillations might be associated to the encoding of socially relevant information of an observed action, such as the perspective of the model with respect to the observer (Kilner et al., 2009).

Taken together, the results of this thesis highlight the importance of studying neural correlates of action representation in real world environments using a naturalistic approach, revealing the complexity of cognitive mechanisms behind human behaviour. The data furthermore demonstrate that mobile EEG is a feasible and reliable method to dissociate and understand cognitive processes occurring during both overt and covert behavioural responses. In the following sections, implications of the findings will be discussed in relation to the theoretical framework of embodied cognition. A section regarding the relevance of mobile approach will illustrate potential applications and technical challenges of real world investigations of human locomotion. In addition, this discussion will cover the use of mobile approach in clinical settings and the recent development of neurofeedback and BCI systems, which are promising tools for the treatment of motor disorders and gait impairments.

5.2. Embodied nature of action representation

The findings reported in the present thesis provide evidence for the embodied nature of human cognition, which depends on the interaction between the body and the surrounding environment. A unifying theoretical framework that highlights the embodied nature of action representation during overt and covert behaviour, is the so-called emulation account (Grush, 2004, 2007; Ptak et al., 2017), which incorporates the assumptions of theories of action control, human information processing and the embodied cognition perspectives (Ptak et al., 2017).

According to the emulation account, the brain is functionally organised in different neural circuits on the basis of sensorimotor experience, which create internal models that guide behaviour (Grush, 2004). The functional complexity of neural networks increases dynamically throughout life, by replacing and integrating existing models with new behavioural responses, along with the acquisition of new skills (Ptak et al., 2017). These models represent patterns of interaction between the body and the environment and include different information about action plans, such as high levels information associated to the action goals, and the kinematic aspects of the specific movements (Ptak et al., 2017). In other words, the emulation account posits similarly to motor control theories, that the brain creates an action representation which acts as a feedforward model, guiding motor planning during overt behaviour and predicting sensory outcome in order to produce a successful performance (Wolpert, 1997; Wolpert & Kawato, 1998). According to this view, action representation is not a static model of behaviour, but it is dynamically updated during the interaction between the body and the environment and it needs to be monitored and adapted depending on the circumstances. This means that the emulation model also assumes the need for control processes, which monitor online the behaviour and adjust the internal model accordingly (Ptak et al., 2017). The findings of the first study, reported in Chapter 2, support this perspective, showing that oscillations in the theta frequency band might reflect control mechanisms associated with the updating and the monitoring of action representations when facing unexpected changes in the environment. This is also in line with evidence suggesting that midline theta may be an index of the need for increased cognitive adaptive control in contexts of uncertainty (Cavanagh & Frank, 2014) and an online action monitoring mechanism, which ensures a successful behavioural outcome (Luu et al., 2004).

Furthermore, the emulation account provides a general embodied framework for the findings of the second study, reported in Chapter 3, regarding motor imagery of walking. As mentioned above, sensorimotor experience during life allows to create models of the interaction between the body and the environment. Action representation can then be used unintentionally or intentionally offline, in order to produce the imagination of movements (Grush, 2004). According to this view, motor imagery reflects the emulation of an action plan, which can be dynamically manipulated, transformed, and mentally maintained (Grush, 2004; Ptak et al., 2017). The emulation account also predicts that action execution and motor imagery rely on the same action representations and share similar cognitive mechanisms, which are used to simulate the behavioural outcome during motor planning. The brain areas that play a crucial role in the emulation model are collectively referred to as the dorsal frontoparietal network (see Ptak et al., 2017). This neural network supports different cognitive functions, such as cognitive control, action planning, working memory and motor imagery (Ptak et al., 2017). These mechanisms are structured in hierarchies, which develop throughout life from a 'general purpose-function' to more specific operations, emerging from a combination of more elementary processes. However, as suggested by Ptak et al. (2017) although these processes share some basic functions and patterns of brain activations, they have been investigated in isolation, preventing a full understanding of complex cognition behind overt and covert human behaviour. Thus, in order to understand human cognitive processes, is necessary to analyse overlapping mechanisms between different behaviours.

In line with this perspective, our data showed that execution of walking and its motor imagery elicit similar patterns of cortical oscillations, although with notable differences primarily with regards to their time course. This is suggestive of overlapping basic cognitive mechanisms between execution of movements and motor imagery, but also of differences in the temporal dynamics of the cortical modulation associated with cognitive processes. In these terms, the similarities might involve the encoding of kinaesthetic information associated with the mental rehearsal of action representation of walking, which are likely reflected in the similar modulation of beta frequency band (Nauta et al., 2002). However, the data also suggest that other mechanisms are involved in motor imagery of walking, such as a possible automatically triggered inhibitory process – supported by a prominent beta rebound at the end of motor imagery. These findings provide evidence for a multidimensional nature of motor imagery and support the emulation account, for which action execution and motor imagery do share core cognitive mechanisms, which is also in line with the predictions of the functional equivalence hypothesis (Jeannerod, 1994, 2001).

The embodied perspective was also supported by the findings reported in Chapter 4. In this study it was described how in real world action observation, the perspective of the observer and the distance of an agent from an observer, are encoded by oscillations in the alpha and in the beta frequency band over parietal electrodes, which are thought to signal the activation of the human action observation network (Grafton et al., 1996; Cross et al., 2009; Buccino et al., 2001; Caspers et al., 2010; Hari et al., 1998; Rizzolatti & Sinigaglia, 2010; Cattaneo & Rizzolatti, 2009). The action observation network has attracted the attention of different fields of research and it represents one of the main neuroscientific evidence for the embodied cognition framework. The extensive number of investigations on action observation have provided support for a matching mechanism between observed and executed actions, a process that contributes to the understanding of others' intentions (Konorski, 1967). Action observation, however, was an important theme in psychological literature already before the discovery of the mirror neuron system, as it can be seen from observational learning (Bandura et al., 1966) or imitative behaviour (Meltzoff & Moore, 1983) theories. Through the observation of others' actions, the infant can learn and acquire new skills, and build an internal representation of behaviour, which according to the emulation account, is dynamically transformed and updated throughout life. In addition, action observation mediates our knowledge of the external environment, i.e., by observing others' behaviour, we can infer the properties of the surrounding environment and build a representation of the interaction between the body and the external world. Mattar & Gribble (2005) showed that participants learned mechanical properties of the environment by observing other people's movements. In this study, participants were required to execute or to observe and then execute an arm movement in the same or in a different environment, while a robotic device applied a perturbing force in different directions to the arm movement. The results showed that participants performing action observation before the execution, performed better compared to participants that did not observe the movement. Furthermore, participants that performed the movement in the same environment of the video performed better than participants who executed the movement in a different environment. These findings suggest that action observation might play a critical role also in the knowledge of the properties of the environment, guiding the creation of an embodied action representation, which is the product of the interaction between the body and the environment.

In the real world, action observation is shaped by different circumstances and contexts, and happens also when we are interacting with other individuals. Our interactions, indeed, are not always mediated by language, and in such circumstances, we need to select the relevant cues to understand the intentions of others in relation to our own goal. Pezzulo and colleagues (2013, 2019) proposed a theoretical framework, the so-called sensorimotor communication model, which differently from linguistic communication is not mediated by the transmission of an explicit meaning but is related to the encoding of motor signals such as kinematics, sent by other individuals. According to this model, the body posture and the kinematics convey the information without the need of a previous knowledge or a shared communicative system between individuals. Although this perspective implies a communicative intention between co-actors, it also have important implications for action observation. The findings described in Chapter 4 of this thesis provide support for such account. The results showed that during action observation of an agent either approaching or moving away from an observer, contextual and bodily cues, such as the distance and the perspective respectively, modulate differently neural markers of the action observation network, even in the absence of a communicative intention. These dynamics might represent the basic level of analysis in real world interactions that are not mediated by linguistic communications. In such circumstances, bodily cues such as distance and perspective of another individual, embedded in a specific context, are evaluated to establish whether we are required to cooperate or to not interact at all. In these scenarios, the sensorimotor communication represents the principal channel that drives the understanding of the intentions of others during action observation.

5.3. Relevance of real world settings and mobile potentials to study human locomotion

The studies described in this thesis focused on neural correlates of cognitive processes underlying action representation during both overt and covert natural locomotor behaviour. Evolutionary, locomotion certainly represents the most preserved form of movement across different species (Ferreira-Pinto et al., 2018). It might appear as a very intuitive and simple behaviour, due to its ubiquity in daily living. Conversely, control of locomotion depends on a complex interplay between supraspinal brain areas, such as the cortex, basal ganglia, cerebellum, midbrain and hindbrain, and spinal neurons (Kiehn, 2016; Ferreira-Pinto et al., 2018). Locomotion itself is a whole body movement, characterized by automatic rhythmical lower limbs' movements, which can be triggered by external sensory stimuli or in absence of evident external triggers, to accomplish a particular goal. For example, initiation of locomotion can be due to a specific need, such as food or water, but it can be also driven by other goals, such as the need to explore the surrounding environment and reach objects. This would suggest how cognitive decisions might prompt the voluntary control of locomotion (Ferreira-Pinto et al., 2018).

Voluntary control of locomotion develops slowly and represents one of the most critical steps of human psychological development (Anderson et al., 2013). Indeed, it has been demonstrated that acquisition of locomotion plays an important role in the development of psychological functions, such as perception, memory, motor coordination, spatial abilities, and social skills (for a review see Anderson et al., 2013). Early forms of self-motion in infants, such as crawling, provide the opportunity to not depend anymore on others' movements and explore the environment pursuing specific goals, proving the ability to produce changes in the external world (Gibson, 1988). Moving within the environment, allows the acquisition of information that drives the development of psychological and motor skills. However, the importance of locomotion in cognitive development has been considered only recently, due to the dualism between motor and cognitive domains pervading scientific research until the mid-twentieth century (Anderson et al., 2013). It was with the emergence of ecological psychology (Gibson, 1979) and the development of system accounts (Thelen & Smith, 1994) that the close relationship between action, perception and cognition was recognized (Anderson et al., 2013). Indeed, a large body of evidence has shown how locomotion requires both sensory and cognitive resources (Sheridan & Hausdorff, 2007). The cognitive load during walking has been mainly assessed with dual task paradigms (for a review see Al-Yahya et al., 2011), which showed that performing a demanding additional task while walking might interfere with gait parameters, such as speed (Patel et al., 2014).

Remarkably, our knowledge of the neural control of human locomotion is still limited and comes primarily from animal models (Armstrong & Edgley, 1988; Beloozerova & Sirota, 1988; Drew et al., 2002; Drew & Marigold, 2015). Although bipedal locomotion is relevantly different from quadrupeds' ambulatory movements, these investigations allowed the identification of neural circuits of locomotion and highlighted the role of the cortex in the voluntary control of precision stepping tasks and in adaptation during walking (Drew & Marigold, 2015; Marigold and Drew, 2017). Brain activity during locomotion in humans has been traditionally assessed though the recording of MEPs (Schubert et al., 1997; Petersen et al., 1998; Capaday et al., 1999) or in fMRI during motor imagery of walking (Hamacher et al., 2015; Jahn et al., 2004, 2008; Bakker et al., 2008; Malouin et al., 2003; la Fougere et al., 2010). These studies revealed that cortical areas related to cognitive control, are also active during motor imagery of walking (Rosano et al., 2008; Thompson, 2001; Whitman et al., 2001). However, as already highlighted in the General Introduction and in the three studies reported in this thesis, walking in the real world environment requires complex cognitive and motor resources, compared to the mere imagination of walking from a supine position, as specifically revealed by the findings reported in Chapter 3. Additionally, even when in the standing position, locomotion cannot be maintained without sensory feedback from vision, proprioception, and somatosensory information (Horaket al., 1994). A clear example of the amount of information that we need to process when moving around, is the relevant visual flow coming from the external environment. Vision is certainly one of the most relevant channels to guide locomotion, and it represents the interface between the agent and the environment (Gibson, 1954; for a review see Logan et al., 2010). A large body of studies has shown how vision supports spatial navigation and gait adaptations with regards to obstacles (Grasso et al. 1998; McFadyen et al. 2007; Patla & Vickers 1997; Schubert et al. 2003; Warren et al. 2001) and modulates gait parameters, such as speed and stride length (Konczak 1994; Prokop et al. 1997; Mohler et al. 2007). It is thus clear, that the investigation of neural and cognitive control of locomotion implies processes that can be investigated only when individuals actively walk around, rather than lying down in a scanner. Thus, to understand cognitive processes underlying locomotion, it is critical to investigate real world human ambulatory behaviour.

Only recently, along with the development of new portable devices, such as mobile EEG and fNIRS, it has been possible to deepen the understanding of neural circuits for locomotion in humans. fNIRS is used for recording indirect cortical activity through the hemodynamic changes in the brain and it was one of the first techniques to be applied to assess cortical activity during walking (Miyai et al., 2001). Although it has produced useful insights in the study of cortical control of walking, such as during precision stepping tasks (Koenraadt et al., 2014) and obstacle avoidance (Maidan et al., 2018), its application includes several drawbacks (for a review see Vitorio et al., 2017). For example, as reported by Vitorio et al. (2017), fNIRS recordings during walking are characterized by relevant artifacts and noise, which constitute an obstacle for the identification of reliable brain signals. Furthermore, the lag between cortical signals and hemodynamic changes is relevant (4-7 sec, Vitorio et al., 2017), which means that fNIRS is not suitable to detect fast neurophysiological processes in the brain.

The EEG presents many more advantages compared to other non-invasive techniques. With its high temporal accuracy, the EEG can record fast changes in the brain, which are not captured by fNIRS (Delval et al., 2020). Furthermore, the EEG offers the opportunity to correlate the cortical activity with other portable devices for gait measurements, which allows the investigation of natural walking behaviour in the real world environment. Indeed, human locomotion represents one of the main research field for the application of mobile technologies. One of the most important novelties brought by the MoBI approach is the synchronous investigation of brain activity and lower limb kinematics, employing the concurrent recording of the electromyogram (EMG) or mechanical force sensors (foot pressor insoles or motion capture) (Artoni et al., 2017a; Presacco et al., 2012). A major finding of this application regards the coupling between gait patterns and rhythmical oscillatory activity, which elucidated the cortical contribution in the control of locomotion (Gwin et al., 2010, 2011; Gramann et al., 2010; Severens et al., 2012; Bradford et al., 2016; Bulea et al., 2014, 2015; Seeber et al., 2014, 2015; Wagner et al., 2012, 2014). In their seminal study, Gwin and colleagues (2010) analysed brain activity during walking and running on a treadmill. In this investigation, the combined recording of cortical oscillations through the EEG and the measurement of gait parameters, using mechanical force sensors for lower limb movements, was employed. The findings of their study highlighted specific pattern of cortical activity in alpha, beta, and gamma frequency bands over sensorimotor cortex during intra-stride changes. Furthermore, Presacco et al. (2012), showed synchronous activation between beta oscillations in the primary motor cortex and EMG activity of the tibialis anterior during treadmill walking. These findings have been consistently reported in subsequent studies, which showed that cortical changes are associated with specific gait phases during treadmill walking (Seeber et al., 2014, 2015; Bulea et al., 2014, 2015). Furthermore, the MoBI approach has been applied to investigate cycling on stationary bicycle (Jain et al., 2013; Enders et al., 2016), precision stepping tasks (Oliveira et al., 2018), adaptations during walking (Wagner et al., 2016; Yokoyama et al., 2020) and obstacle avoidance (Nordin et al., 2019). These studies showed that an extensive network of frontal, central and parietal areas, typically involved in action planning and cognitive control, are also activated during voluntary control of locomotion, even though cognitive mechanisms remained unexplored in these studies, which was key to the rationale for the work reported in this thesis.

Another field of application of the MoBI approach, is the concurrent recording of EEG activity and gaze behaviour using eye tracking techniques. Gaze dynamics are characterized by patterns of fixations whose role is to guide behaviour in acquiring the relevant visual information to perform a specific task (Land, 1999; 2006). From an evolutionary perspective, the main goal of gaze is to drive actions through the surrounding environment to survive (Land, 1999; 2006). The relevance of vision in guiding actions has been demonstrated in different investigations in real world daily behaviour, such as driving (Land and Lee 1994), sports, such as cricket (Land and McLeod 2000), walking (Patla and Vickers 1997), sandwich making (Hayhoe 2000, Hayhoe et al. 2003) and tea making (Land et al. 1999). The intrinsic relationship between action and vision, make the synchronous application of EEG and eye tracking recordings a compelling method to study embodied cognition (Mele & Federici, 2017). Vision represents an important window into human cognitive processes. Several investigations showed the bidirectional relationship between eye movements and cognitive processes (Grant & Spivey, 2003). Furthermore, it has been showed that eye movements do not only occur in response to external visual inputs, but also to internal 'mental' images, such as visual memories and motor imagery (Richardson & Spivey, 2000; Spivey & Geng, 2001). Indeed, it has been suggested that eye movements might also index the scanning of mental visual images, related both to spatial representation and to the internal model of behaviour within the environment (Richardson & Spivey, 2000; Spivey & Geng, 2001).

Visually guided attention is undoubtedly essential during locomotion, as it allows the exploration of the surrounding environment and more importantly, it supports the detection of possible threats such as obstacles (Foulsham et al., 2011; Franchak & Adolph, 2010). A major theoretical challenge for mobile eye tracking studies is to dissociate between visual and motor systems during spatial navigation in the environment. As part of a complex and intertwined system, locomotion and visual attention are difficult to dissociate (Franchak & Adolph, 2010). Visual attention during locomotion is of particular interest also for obstacle avoidance tasks in the real world, and such a focus would represent a possible future direction for the study described in Chapter 2 of this thesis. Particularly, it would be interesting to understand how visual attention is related to cognitive mechanisms of proactive and reactive cognitive control. Previous laboratory investigations have shown that eye movements are directed toward critical spatial points of the visual scene, and that these movements occur in anticipation of a stimulus, i.e., gaze is used to collect relevant information to plan ahead the action (Ballard et al., 1995; Johansson et al. 2001). This strategy seems to be used in a 'just in time' manner (Ballard et al., 1995), which means that once relevant information is processed, it does not need to be maintained active in the working memory (Mennie et al., 2007). The first study of the present thesis did indeed offer a demonstration of 'just in time' mechanisms at play. The study furthermore showed that proactive control of natural behaviour is a form of cognitive control which updates action representation when an unexpected change in the environment is detected, regardless of when the behavioural adjustment needs to be implemented. Eye movements could offer a critical window into these mechanisms, providing further data about how we process relevant information when we have to implement complex behavioural responses in the real world environments.

5.3.1. Technical challenges of mobile approach

Locomotion represents one of the most relevant research targets of the recent MoBI approach. However, as mentioned in the General Introduction, the combined application of different portable devices opens several problems that need to be addressed in order to provide a reliable recording of brain and body signals. Aside from the online recording strategies, another technical challenge is related to the analysis of the brain signals in real world investigations. In the traditional laboratory experiments, EEG recordings are usually carried out while participants are almost motionless, and motion artifacts are minimised or rejected offline using EMG or ocular activity recordings. Conversely, in real world investigations, where participants can freely move in the surrounding environment, the artifacts generated by body and eye movements and from external sources (e.g. cables or electrodes) are much more prominent, thus enlarging the problem of dissociating non brain-related activity from the neural signals of interest. Several studies have attempted to identify gait related artifacts during natural walking and have highlighted how neck and head movements can cause systematic artifacts, which are more prominent at high walking speed (Jacobsen et al., 2020; Arad et al., 2018; Castermans et al., 2014; Kline et al., 2015).

A very popular method to identify and then remove artifacts in EEG data is based on independent component analysis (ICA, Amari & Cichocki, 1998; Comon, 1994; Hyvärinen, 1999). Recently, the artifacts subspace reconstruction (ASR) has been successfully applied in pre-processing pipeline of EEG data (Chang et al., 2018; Blum et al., 2019). The ICA is a linear decomposition technique, which aims to find maximally independent linear projections or independent components (ICs). In order to differentiate between different ICs, there are several main assumptions in the ICA: the statistical independence of source signal, the linear mixing at the sensor level and the stationarity of the signal (Vigario et al., 2000). In other words, the ICA assumes that independent source signals are fixed, and their number is equal to the number of the applied scalp sensors. The source signals are then selected depending on the linear projection to the head model, also known as single equivalent dipole model (Gramann et al., 2014; Jung et al., 2000; Makeig et al., 2004; Delorme et al., 2012).

Single equivalent dipole model is a source localization technique which works on the assumption that cortical activity recorded by the EEG is determined by metabolic active regions which are related to neuronal assemblies, structured in macrocolumns perpendicular to the cortex (Akalin Acar and Makeig, 2013; Baillet et al. 2001; Lutkenhoner et al. 1995; Baillet and Garnero 1997). The source localization models allow the identification of the location of source signals in the physical space and approximate the location for unknown sources (Gramann et al., 2014). These methods represent important tools in order to identify brain related signals in EEG investigations. However, for mobile EEG recording, the most problematic aspect is represented by the heavy presence of noise and artifacts, which might reduce the amount of brain signals detected by the ICA. This might result in low number of ICs to include in the subsequent analysis, which might inevitably compromise the reliability of the interpretation. As shown in the methods sections of Chapter 2, 3 and 4 of this thesis, the ICA was employed to separate brain related ICs from non-brain ICs. The apparent low number of ICs remaining after removing non-brain ICs in the three studies of this thesis, is partially due to the limited number of electrodes of the mobile EEG employed (32 channels). However, it is noteworthy that the number of brain ICs extracted in the three studies (average± SD: 5.85 ± 1.97 ICs for Chapter 2's study; 6.65 ± 0.81 ICs for Chapter 3's study; 7.19 ± 1.6 ICs for Chapter 4's study) represented more than the 15% of the total ICs extracted. Our data are generally in line with previous observations on the optimal number of ICs that can be extracted by applying the ICA on mobile data. As recently tested by Klug & Gramann (2021) on a 128-channel mobile EEG, the ICA led to a maximum of 12.7 brain related ICs classified, corresponding to approximately to the 10% of the total number of ICs, suggesting that the number of ICs of the three studies presented in this thesis represents a suitable amount of brain-related signal to further analyse.

Artifact subspace reconstruction (ASR; Bulea et al., 2015; Luu et al., 2017; Nordin et al., 2019) is a tool similar to the ICA, which allows the removal of artifacts dividing EEG continuous data in short portions (usually 500 ms) and decomposing them using an unmixing method (Gramann et al., 2014; Jacobsen et al., 2020). The ASR assumes that the presence of artifacts in the EEG data determine a relevant level of variability, which can be identified using a covariance matrix for detecting the deviant statistical values extracted by the principal component analysis (Arad et al., 2018; Plechawska et al., 2019).

These two procedures have been successfully applied to MoBI data in real world EEG investigations. However, a critical issue for offline pre-processing tools such as ICA and

ASR, is that although they dissociate brain signals from artifacts, they do not categorise or dissociate noise and other body signals. A possible solution to this problem is represent by the recently developed tool within the EEGlab framework, the so-called IClabel (Pion-Tonachini et al., 2019). IClabel is an automated method to standardise the categorization of ICs, which has been applied to the studies reported in Chapter 3 and 4 of the present theses. A similar EEGlab tools is SASICA (Semi-Automated Selection of Independent Components of the electroencephalogram for Artifact Correction, Chaumon et al., 2015) which has been used in the study in Chapter 2 of this thesis and it has been replaced by IClabel method in Chapter 3 and 4. This replacement was solely guided by the availability of IClabel plugin, which was released online only recently (Pion-Tonachini et al., 2019). Generally, automated methods for the selection of artifactual ICs in the EEG data allow the assessment of different statistical threshold which are not visible to the human eye, which is the main characteristics of both SASICA and IClabel, which are based on the same parameters. However, compared to SASICA, IClabel can guide more specifically the selection of ICs using a classifier which provide probabilistic labels for each signal source comparing them with a dataset containing over 200,000 ICs from more than 6000 EEG datasets (Pion-Tonachini et al., 2019).

To summarise, the application of semi-automatic methods for the identification of non-brain sources in EEG recordings rely on the computation of spatial and temporal features commonly associated with artifactual signal. The strict criteria employed by these algorithms might affect the number of brain sources selected and used in the analysis, as the resulting brain-related ICs might appear to be lower compared to laboratory EEG recordings. However, using manual and subjective approaches does not facilitate reproducibility of the research. For example, critical features of brain components are not visible to the human eye, but can be computed only using statistical and mathematical functions or thresholds. Considering the heavy presence of noise in mobile EEG data, the semi-automated methods employed in this thesis, represented a more suitable approach to identify brain signals in the EEG data compared to manual approaches. Additionally, the limited number of electrodes used within the frame of this thesis represented a strong limiting factor to the number of neural sources that could be estimated. These constraints associated with mobile EEG, might have critical impact on strategies for data analysis and the interpretation of the results. For example, the use of 32 electrodes montage prevented the precise identification of neural sources of the recorded signal, precluding the interpretation relative to the neural origin of the observed oscillations.

Despite the significant improvements in signal pre-processing tools, currently there is still no agreement on the pipeline for mobile EEG data (Jakobsen et al., 2018). It is critical to propose and assess new approaches to reliably analyse cortical activity during real world behaviour. For example, as suggested by Jacobsen et al. (2020), it might be more relevant to characterise firstly artifacts occurring during gait and focus on the optimization of the online recording. This would allow a better classification of brain signals, reducing the offline operations which might affect the outcomes and the interpretation of the data.

5.4. Action representation as a tool for motor disorders

Locomotion is a crucial skill acquisition for humans, and its progressive loss impacts significantly in aging and in neurological disorders. Falls during walking are the main direct risk to health for neurological and elderly population, and according to the World Health Organization, they represent the second leading cause of deaths or injury worldwide (World Health Organization, 2021). The risk of falls is related to age; indeed, it has been demonstrated that among 85 years old individuals, only 20% of them showed normal gait patterns (Ataullah & De Jesus, 2021; Pirker et al, 2017; Jahn et al., 2010). The strong correlation between locomotion and cognitive decline, suggests a common mechanism for both walking and cognition (Ataullah & De Jesus, 2021; Verghese et al., 2013; Christensen et al., 2001). As demonstrated by the results presented in Chapter 2 and 3 of this thesis, neural control of walking requires also attentional, visual, and cognitive resources, which involve the activation of a broad network of cortical and subcortical neural structures (Holtzer et al., 2014). One of the most reported consequences of gait and cognitive decline is the progressively reduced gait speed (Verghese et al., 2013; Montero-odasso et al., 2014; Y Tseng et al., 2014) and increased gait variability (Boripuntakul et al., 2014; Beauchet et al., 2016). Given the impact of the loss of locomotor abilities on the quality of life, it is important to develop novel rehabilitation treatments in order to improve motor functions in both elderly and neurologic patients. The results of the present thesis represent an important contribution for the understanding of cognitive processes underlying real world locomotor human behaviour. In particular, the data presented in Chapter 3 and 4 regarding neural correlates of motor imagery of walking and action observation of walking, might suggest new insights for rehabilitation techniques. Indeed, both motor imagery and action observation have been commonly applied in clinical settings as effective tools for the recovery of motor impairments. These topics will be further discussed in the following paragraphs.

A critical finding for motor rehabilitation practice, is that the brain can recover its functions after a structural damage, a process that is commonly called neuroplasticity (Pascual-Leone et al., 2005). Neuroplasticity is the product of the intrinsic relationship between the body and the environment, which can induce physiologic, structural, and organizational changes in the brain through experience (Pascual-Leone et al., 2005; Gulyaeva, 2017). The ability of the brain to reorganize itself is crucial throughout human life, as it allows the learning of new skills and the adaption to an everchanging environment (Hallett, 2005; Gulyaeva, 2017). Neuroplastic changes can develop quickly or might take longer and can occur both at the cellular and at neuronal networks levels. The main mechanism that promotes neuroplasticity in the central nervous system is the continuous change of synaptic connections, which represents the principal neural mechanism for the development of memories and learning (Gulyaeva, 2017). A critical consequence of the neuroplastic ability of the brain, is the opportunity to recover and restore functions after both short-term temporary neural damage (Edeline et al. 1993; Brasil-Neto et al. 1993) or after a stroke (Dimyan & Cohen, 2011). Indeed, after a lesion, the brain can reorganize the cortical functions and recover motor functions to some extent.

Physical exercise has been identified as the most important tool to enhance neuroplasticity, improving both motor and cognitive functions (Hotting & Order, 2013). In rehabilitative setting, the physical exercise is the main activity used, as it allows the “rewiring of the brain” (Gulyaeva, 2017). Despite the actual execution of movements, as in physical practice, appears to be the main promoter of cortical reorganization and motor recovery, a large body of evidence have shown that motor imagery (Ruffino et al., 2017) and action observation (Naish et al., 2014) can induce plastic changes in the brain.

As already mentioned, brain areas involved in the actual execution of movements, i.e., the premotor, the supplementary motor, and the parietal cortical areas, but also subcortical structures such as the basal ganglia and the cerebellum, are similarly active also during motor imagery (Hallett et al. 1994; Sirigu et al. 1995; Stephan et al. 1995; Lotze et al. 1999; Gerardin et al. 2000; Grezes & Decety 2001; Jeannerod 2001; Kimberley et al. 2006). As demonstrated by the results reported in Chapter 3, actual execution of walking and motor imagery share similar core cognitive mechanisms which are reflected in modulation of alpha and beta oscillations. The first evidence showing that the repeated use of motor imagery - i.e., the rehearsal of action representation, also called ‘mental practice’- can elicit cortical changes in the brain, was provided by Pascual-Leone and colleagues (1995). In this study, participants had to learn a sequential finger movement either performing it or imagining it in 5 separate sessions. TMS was applied on the contralateral hand area of the primary motor cortex following each session. At the end of the training, both groups showed similar improvements and error rates. Similarly, Avanzino et al. (2015) used a paired associative stimulation (PAS) approach combining TMS and peripheral nerve stimulation, assessing the long-term depression plasticity (LTD) and the long-term potentiation plasticity (LTP) with an interstimulus interval of 25ms and 10ms - which reduce (the LTD) and increase (LTP) corticospinal excitability. In this study participants were required to learn a sequential finger movement by performing it or imagining it. Behavioural results showed similar speed rates after both training in the participants. More importantly, they found that both physical and motor imagery training influenced the excitability of the primary motor cortex, affecting the LTD and the LTP in an opposite way, suggesting an effect of motor imagery on synaptic changes in the brain. Similar findings were reported also in brain imaging studies. Jackson et al. (2003) showed that mental practice of sequential movements, induced similar changes in the activation of the orbitofrontal cortex and the cerebellum, as physical practice of movements.

Although these studies highlight that mental practice might affect cortical plasticity, they also pointed out the different effect in comparison with physical practice. Lacourse et al. (2005) showed that whereas mental practice of sequential movement increased brain activity over the cerebellum, premotor areas and striatal brain areas, physical practice induced decreased activity in the cerebellum and increased activity in striatal brain area. These differences suggest that the absence of sensory feedback in motor imagery might prevent the potentiation of cortical plasticity which need the support of covert motor output occurring in physical practice (Ruffino et al., 2017). Importantly, the data reported in Chapter 3, provide relevant support for this perspective: although neural markers of cognitive mechanisms underlying actual execution and motor imagery share similar features, they also partially differ, suggesting a complex neural substrate underlying motor imagery of real world locomotor behaviour. The novelty of the mobile data reported in Chapter 3 of this thesis, therefore provides an important contribution for the understanding of the nature of motor imagery, with might have relevant impact for rehabilitative contexts in particular in the absence of neural data comparing imagery and actual locomotor behaviour.

The evidence that motor imagery can induce plastic changes in the brain has led to the application of mental practice as a rehabilitation technique (Mulder, 2007; De Vries & Mulder, 2007; Dickstein & Deutsch, 2007). Indeed, mental practice has been used in Parkinson’s disease (Tamir et al., 2007; Brown et al., 2011), low back pain (Fairweather &

Sidaway, 1993) and stroke (Page et al., 2001, 2000; Page et al., 2007; Stevens & Stoykov, 2003; Cho et al., 2013) and has been proposed as effective for gait impairments (Malouin & Richards, 2010). However, despite the promising results obtained from the application of motor imagery practice in rehabilitation, several meta-analyses and reviews suggest to carefully consider the different evidence, mainly for the high heterogeneity that characterizes protocols and studies (Guerra et al., 2017; Hardwick et al., 2017, 2018; Herranz-Gómez et al., 2020). For example, in rehabilitative settings, the different duration of the interventions, the frequency of the treatment, the sample size and the task employed make it very difficult to assess the benefits of motor imagery practice (Barclay et al., 2020; Guerra et al., 2017; Hardwick et al., 2017, 2018; Herranz-Gómez et al., 2020; see also Ietswaart et al., 2011). Additionally, depending on the brain lesions, motor imagery ability can be impaired in neurological populations when critical brain structures are compromised, therefore motor imagery practice might not be always effective (McInnes et al., 2016).

Neural plasticity has been also proposed to occur during action observation, which can induce a facilitation in motor execution (Fadiga et al., 1995; Urgesi et al., 2006; Castiello et al., 2002; Buccino et al., 2001). In a TMS study, Fadiga et al. (1995) showed that action observation of hand-object interaction increased motor excitability in finger muscle involved in the observed movements, suggesting that action observation have an effect in facilitating motor output. Urgesi et al. (2006) measured MEPs recoded from hand muscles involved in observed finger movements in different postures. They found an increased motor excitability when the observed hand posture was compatible with the posture of the observer. Brass et al. (2000) showed that the execution of finger movements was facilitated when participants observed and executed congruent actions but not when the two movements were not the same (i.e., observing a finger lift movement and performing a finger tap). Similarly, Castiello et al. (2000) asked participants to observe and execute incongruent and congruent actions (i.e., observe a grasping action towards a small or a large object) and found that both the speed and the acceleration of the movement were faster for congruent compared to incongruent actions. These findings were further confirmed by investigations on action observation training on motor performance. For example, Porro et al. (2007) found that the repetitive training based on action observation of finger movement produced similar increase in the isometric force of the muscle involved in the movement as physical practice.

According to motor theory, motor learning can happen through the observation of other movements and this would be relevant also for the recovery of motor functions. For example, action observation treatments have been proven to be effective in the rehabilitation of

Parkinson’s disease (Pelosin et al., 2010; Buccino et al., 2011), stroke (Ertelt et al., 2007; Franceschini et al., 2010; Bang et al., 2013) and orthopaedic patients (Belelli et al., 2010). However, it also been shown that the mere observation of movements is not enough to activate neural pathways of the mirror neuron system. Indeed, recently it has been proposed that the combined use of motor imagery and action observation might be more effective than using the two techniques alone (Sakamoto et al., 2009; Lawrence er al., 2013; Taube et al., 2015). EEG investigations reported that cortical activation is less pronounced during mere action observation, when compared to the condition in which participants are required also to simultaneously imagine kinaesthetically the movement (Berends et al., 2013; Eaves et al., 2016a; Kaneko et al., 2021). This suggests that when performed alone, action observation might be less effective in eliciting sensorimotor facilitation, and that using action observation simultaneously with motor imagery might be more effective in clinical treatments based on mental simulation of movements (see Eaves et al., 2016b).

The fast technological development of the past twenty years has signified an important step forward for the conceptualization of rehabilitative techniques in clinical settings. In particular, the EEG has been extensively used to build computerised assisting technology such as neurofeedback and BCI systems. With the emergence of portable devises, these two techniques have been integrated with mobile portability, which will be described in the following section.

5.4.1. Neurofeedback, BCIs and mobile EEG

Brain computer interfaces (also called brain–machine interfaces) use brain signals to control and communicate to external devices without activating peripheral output channels such as muscle and nerves (Wolpaw, 2013). According to Wolpaw & Wolpaw (2012), a BCI can be seen as a system that measures the activity of the central nervous system and translates it into artificial output which replaces the natural output, changing the relationship between the central nervous system and the environment (Wolpaw & Wolpaw, 2012). BCI systems have been used with a large range of acquisition techniques. For example, for locomotor behaviour, fMRI, MEG, electrocorticography (ECoG), LFP, fNIRS and EEG have been employed (McFarland & Wolpaw, 2017; Khan et al., 2021). Although both MEG and fMRI have an excellent temporal and spatial resolution respectively, their basic features requiring the participants to be stationary and motionless, are not compatible for real-time application of BCI on walking behaviour (Khan et al., 2021). Among non-invasive approaches to record brain activity for BCI system during gait, the EEG represents the most popular technique, due to its portability and easy-to-use features (Khan et al., 2021).

The excellent temporal resolution of the EEG makes it ideal for BCI applications. Indeed, an increasing number of investigations have attempted to detect and classify EEG signals related to normal gait (Severens et al., 2012; 2015), attention during gait initiation (Hasan et al., 2020; Choi et al., 2019; Sburlea et al., 2019) and obstacle avoidance (Salazar-Varas et al., 2015; Long et al., 2018) to control external devices, such as exoskeletons, through a BCI system. One of the most robust signals of gait-related brain activity used in EEG-BCI applications is the event related desynchronization in the alpha and beta frequency bands over the sensorimotor cortex (Severens et al., 2012; 2014; Wagner et al., 2012). Other investigations have been focused on attentional mechanisms while walking through the assessment of the P300 potential (Debener et al., 2012; De Vos et al., 2014; see also Ladouce et al., 2019), which is an event related potential (ERP) associated with attentional allocation (Johnson, 1988), context updating (Donchin & Coles, 1988), working memory processes (Polich, 2007) and reactivation of stimulus-response links (Verleger et al., 2017; Verleger 2020). Movement related cortical potentials (MRCPs) have also been used in BCI applications to predict motor intentions (Savic et al., 2014). MRCP also known as Bereitschaftspotential (BP), is a slow negative wave occurring over the primary motor cortex around 1s before movement onset (Shibasaki & Hallett, 2006). This signal has been used to detect the intention of gait initiation as it provides information about the preparation of movement (Savic et al., 2014; Sburlea et al., 2015). Among locomotor tasks used to control BCI systems, obstacle avoidance represents one of the main challenges (Salazar-Varas et al., 2015; Long et al., 2018). For example, Salazar-Varas et al. (2015) investigated brain signals during the detection of expected and unexpected obstacles while participants walked on a treadmill and found increased activity in EEG potentials over frontal and central electrodes compared to rest.

Although these investigations have provided valuable insights in the understanding of cortical signals to drive BCI systems, EEG signals acquisition was mainly carried out while participants walked on a treadmill, which might have an important impact on cortical activity. As mentioned already in the present thesis, real walking in natural environments is the product of a complex interaction between cortical and subcortical structures, which drives the integration of sensory and motor information. The results presented in Chapter 2 of this thesis clearly show the complexity of neural signals while walking in the real world environment and encountering objects to avoid. The specificity of the cortical modulation in relation to unexpected obstacles appearing on the floor, compared to expected obstacles and unobstructed walking, highlights that complex locomotor scenarios require the involvement of different neural processes compared to simple ones. Indeed, it has been showed that brain and body signals during normal and complex gait conditions might differ (Wagner et al., 2014; den Otter et al., 2004). In order to control BCI systems and develop robot assistive technologies, it is therefore important to identify signals associated with real life circumstances that might represent a possible risk for people with gait impairments. Avoiding unexpected obstacles is certainly one of the most challenging situations for elderly and neurologic patients. The findings of the first study, reported in Chapter 2 of this thesis are therefore particularly relevant for this aim, as they provide the evidence for distinct neural signatures of cognitive processes and as such, they might represent a critical contribution to the understanding of signals associated with the detection of potential risks in the environment, i.e., the theta modulation when encountering unexpected obstacles on the floor and the beta modulations when stepping over any obstacle. This also shows that the mobile approach provides the advantage to detect and classify more reliable signals for BCI systems, aimed to support obstacle avoidance during natural walking.

In clinical settings, BCI systems have been mostly applied with individuals with amyotrophic lateral sclerosis (ALS) or spinal cord injuries, however, recently, this technology has been proposed also for other neurologic disorders, such as stroke (McFarland & Wolpaw, 2017). The main idea that drives the application of BCI technique in rehabilitation is to promote neural plasticity and to replace natural motor behaviour with artificial output through an external device interacting with the environment, in order to support the patient autonomy in daily life (Abibullaev et al., 2017). A large number of BCI applications have used neural signals of motor imagery during upper limb tasks (Gomez-Rodriguez et al., 2011; King et al., 2014; Ang et al., 2013) and during gait (Severens et al., 2105; Ferrero et al., 2021; Tang et al., 2018; Choi et al., 2019). However, motor imagery presents several problematic aspects for BCI systems. Firstly, as no motor output is required during motor imagery, it is difficult to assess whether participants are actually performing the task. That is why the neural signature of ambulatory motor imagery identified in the study reported in Chapter 3 is so promising: it offers a way to capture the covert process of motor imagery. Secondly, any other external stimulus such as noise that may distract the participants during the recording, affecting the quality of the data. Finally, neural correlates of motor imagery tasks might present high variability between and within individuals, which is an important issue for the reliability of the signal detected. A possible solution would be enhancing cortical activation by combining motor imagery and action observation, which has been suggested to be more effective compared to the application of the two techniques alone (Marshall et al., 2019; Romano Smith et al., 2019). Abibullaev et al., 2017 recently proposed a combined approach using motor imagery and action observation to drive a fNIRS-BCI system to control a haptic device in real time. The study reached a good accuracy for signal detection compared to previous BCI studies using motor imagery. However, as pointed out by the authors, fNIRS has a low temporal resolution compared to the EEG. Therefore, to increase the reliability of signals for BCI approaches, the EEG might be an ideal solution, offering the temporal accuracy that the fNIRS cannot achieve.

Aside from BCI, another popular technique which is gaining growing attention in technological and clinical settings is neurofeedback. Neurofeedback is a particular type of training by which users learn to control their own cortical activity in order to modify behavioural responses (Kamiya, 1996, 1968; landers et al., 1991). This technique usually employs EEG signals which are represented to the user on a monitor, graphically or by auditory signals. After neurofeedback training, users learn to control their own body signals in order to optimise their behavioural performance. Neurofeedback technique has been applied in different settings, for example in clinical contexts to reduce anxiety (Peniston & Kulkosky, 1991; Raymond et al., 2005), on healthy individuals to improve cognitive performance (Hanslmayr et al., 2005) or physical performance (Hammond, 2007) and in sport (Arns et al., 2008; for a review see Park et al., 2015).

Motor imagery is the most popular paradigm used in neurofeedback investigations. The advantage of motor imagery consists in the potential application of neurofeedback in the natural daily living environment. The possibility of monitoring continuously brain signals might increase attentional focus, but also enhance motivation and compliance to the treatment in patients with neurologic disorders (Kranczioch et al., 2014). Several investigations have shown the relevance of a neurofeedback training based on motor imagery to improve motor rehabilitation (Mihara et al., 2013; Zich et al., 2015). Mihara et al. (2013) employed fNIRS neurofeedback training based on motor imagery in hemiplegic patients with subcortical stroke in addition to motor rehabilitation. They showed that after six repetitive sessions, patients receiving neurofeedback training showed significant improvements in motor recovery compared to patients who did not receive the neurofeedback training. Zich et al. (2015) used a mobile EEG based neurofeedback training in stroke patients moving in natural domestic environments. They showed that brain activity during movements of the affected hand became increasingly more lateralised after practicing motor imagery regularly. These results were accompanied by improvement in motor functions and structural changes that indicated an increased integrity of white matter.

Although previous works on motor imagery-based neurofeedback have provided promising results, the difficulty of finding reliable signals during motor imagery recordings, along with the high variability within and between participants, means that the neural substrate of motor imagery still require further investigations. Furthermore, traditional brain imaging techniques allow the assessment of very poor and elementary movements (Pfurtscheller et al., 2006a, 2006b; Neuper et al., 1996; Hashimoto et al., 2013; Solis-Escalante et al., 2008, 2012; Muller-Putz et al., 2010) preventing the examination of complex real world dynamic actions, which are of critical importance for the development of assistive technology supporting daily life activities. Indeed, how neural activation in imagery and execution compares for naturalistic whole body movements, such as walking, has not been studied due to methodological constraints. The findings reported in Chapter 2 of this thesis represent a window into the complex neural substrate underlying motor imagery of locomotor behaviour, revealing similar patterns of cortical oscillations during actual walking and motor imagery, but also specific differences. These results clarify the neural substrate of motor imagery of complex real world behaviours and represent a critical contribution for the development of motor imagery-based neurofeedback techniques.

Taken together, the findings of previous investigations demonstrate the potential of BCI and neurofeedback applications, which might have important implications for the development of accessible and low-cost rehabilitation techniques. Moreover, mobile technologies have a large range of possible applications, such as sport performance, as they allow to record and detect neural signals while participants are actively engaged in natural behaviour, and they can be transmitted to external devices in real time, enhancing learning and the improvement of motor skills (Park et al., 2015). However, neuroscientific research is still far from the identification of reliable signals, mainly because of the limitation of brain imaging and experimental paradigms. The results presented in three studies of this thesis show that the mobile EEG approach is feasible to capture the complexity of brain signal related to whole body movements in real world environments and furthermore offer distinct neural signatures of the processes involved. As such, these findings offer a relevant insights for the identification neural markers of real world behaviours, which might be used for assistive technologies in clinical settings, in order to support elderly and patients affected by motor disorders in daily life activities.

5.5. Conclusion

The body of works reported in the present thesis contribute to investigate neural correlates of cognitive processes underlying action representation in real world locomotor behaviour, using a mobile approach. A fundamental aspect highlighted across the three studies is the embodied nature of internal models of behaviour, which are the product of sensorimotor experience of the body moving in the surrounding environment. The brain processes information and guides behaviour through internal representations, which are dynamically updated during voluntary control of locomotion depending on external circumstances (investigated in Chapter 2). The brain also activates and rehearses the action representation during covert behaviour, such as during motor imagery (investigated in Chapter 3), which includes not only the kinematic information of the action, that replace the covert motor output, but also spatial information about the environment in which the imagined action is embedded. The dynamic interaction between body and context is also visible when we have to observe others' behaviour (investigated in Chapter 4) in which relevant bodily cues are processed in order to encode possible goals of another person's actions, even without a communicative intention. These results provide novel insights in complex cognitive processes underlying real world human behaviour, and strong evidence for theoretical models of cognitive control, action emulation and simulative processes, which share significant core components.

Across the three studies, it was illustrated how neural markers underlying cognitive processes related to action representation are distinct, flexible, and modulated by the task at hand in real world environments. At the same time, it was also possible to identify some core functions of brain oscillations in covert and overt human behaviour. As it was demonstrated in Chapter 2, theta oscillations over frontal brain areas were associated with cognitive proactive control, which updates the internal representation of the body in relation to unexpected changes in the environment. Alpha oscillations were associated with visual and spatial information during the rehearsal of action representation (Chapter 3) and also with the encoding of relevant spatial information relative to an observed moving agent (Chapter 4). Beta oscillations were associated with the adaptation of the motor plans (Chapter 2), with the kinaesthetic aspects of action representation (Chapter 3) and with the encoding of relevant bodily cues such as distance and perspective of another person (Chapter 4), reflecting a role in sensorimotor processing, in line with the broad previous literature.

The novelty of the experimental paradigms employed in the present thesis signify an important step forward for the mobile cognition framework (Gramann et al., 2011; Ladouce et al., 2017). The three studies demonstrate the feasibility of mobile EEG in capturing neural markers of cognitive mechanisms during real world overt and covert behaviour, which have never been investigated in real world contexts. Furthermore, the technical aspects of the setup of the studies described in Chapter 2 and Chapter 4 of the present thesis, offers new potentials solutions to the issue related to real world recordings, both during online recordings and in the offline processing pipeline. Nonetheless, the mobile approach still requires the development of new solutions to improve the reliability of both online recordings and offline analysis tools. Although there is still much to work on, the mobile approach represents one of the most promising tools for clinical applications, as demonstrated by the increasing number of investigations on BCI and neurofeedback systems, which have the potential of being non-invasive, feasible to use in home environment and at low cost.

References

Abibullaev, B., An, J., Lee, S. H., & Moon, J. I. (2017). Design and evaluation of action observation and motor imagery based BCIs using near-infrared spectroscopy. *Measurement, 98*, 250-261.

Acar, Z. A., & Makeig, S. (2013). Effects of forward model errors on EEG source localization. *Brain topography, 26*(3), 378-396.

Adrian, E. D., & Matthews, B. H. (1934). The Berger rhythm: potential changes from the occipital lobes in man. *Brain, 57*(4), 355-385.

Aftanas, L. I., & Golocheikine, S. A. (2001). Human anterior and frontal midline theta and lower alpha reflect emotionally positive state and internalized attention: high-resolution EEG investigation of meditation. *Neuroscience letters, 310*(1), 57-60.

Ahn, M., Cho, H., Ahn, S., & Jun, S. C. (2013). High theta and low alpha powers may be indicative of BCI-illiteracy in motor imagery. *PloS one, 8*(11), e80886.

Alegre, M., Alvarez-Gerriko, I., Valencia, M., Iriarte, J., & Artieda, J. (2008). Oscillatory changes related to the forced termination of a movement. *Clinical Neurophysiology, 119*(2), 290-300.

Alexander, N. B., & Hausdorff, J. M. (2008). Guest editorial: linking thinking, walking, and falling. *The Journals of Gerontology Series A: Biological sciences and medical sciences*, *63*(12), 1325-1328.

Allen, D. P., & MacKinnon, C. D. (2010). Time–frequency analysis of movement-related spectral power in EEG during repetitive movements: A comparison of methods. *Journal of neuroscience methods*, *186*(1), 107-115.

Al-Yahya, E., Dawes, H., Smith, L., Dennis, A., Howells, K., & Cockburn, J. (2011). Cognitive motor interference while walking: a systematic review and meta-analysis. *Neuroscience & Biobehavioral Reviews, 35*(3), 715-728.

Amari, S. I., & Cichocki, A. (1998). Adaptive blind signal processing-neural network approaches. *Proceedings of the IEEE, 86*(10), 2026-2048.

Andersen, R. A., & Cui, H. (2009) Intention, action planning, and decision making in parietal-frontal circuits. *Neuron, 63*(5), 568-583.

Andersen, R. A., Snyder, L. H., Bradley, D. C., & Xing, J. (1997). Multimodal representation of space in the posterior parietal cortex and its use in planning movements. *Annual review of neuroscience, 20*(1), 303-330.

Anderson, D. I., Campos, J. J., Witherington, D. C., Dahl, A., Rivera, M., He, M., Uchiyama, I., & Barbu-Roth, M. (2013). The role of locomotion in psychological development. *Frontiers in psychology, 4,* 440.

Androulidakis, A. G., Doyle, L. M., Gilbertson, T. P., & Brown, P. (2006). Corrective movements in response to displacements in visual feedback are more effective during periods of 13–35 Hz oscillatory synchrony in the human corticospinal system. *European Journal of Neuroscience, 24*(11), 3299-3304.

Ang, K. K., & Guan, C. (2013). Brain-computer interface in stroke rehabilitation. *Journal of Computing Science and Engineering, 7*(2), 139-146.

Angelini, M., Calbi, M., Ferrari, A., Sbriscia-Fioretti, B., Franca, M., Gallese, V., & Umiltà, M. A. (2015). Motor inhibition during overt and covert actions: an electrical neuroimaging study. *PloS one, 10*(5), e0126800.

Angelini, M., Fabbri-Destro, M., Lopomo, N. F., Gobbo, M., Rizzolatti, G., & Avanzini, P. (2018). Perspective-dependent reactivity of sensorimotor mu rhythm in alpha and beta ranges during action observation: an EEG study. *Scientific reports, 8*(1), 1-11.

Anguera, J. A., Seidler, R. D., & Gehring, W. J. (2009). Changes in performance monitoring during sensorimotor adaptation. *Journal of neurophysiology, 102*(3), 1868-1879.

Annett, J. (1995). Motor imagery: perception or action?. *Neuropsychologia, 33*(11), 1395-1417.

Arad, E., Bartsch, R. P., Kantelhardt, J. W., & Plotnik, M. (2018). Performance-based approach for movement artifact removal from electroencephalographic data recorded during locomotion. *PloS one, 13*(5), e0197153.

Armstrong, D. M., & Edgley, S. A. (1988). Discharges of interpositus and Purkinje cells of the cat cerebellum during locomotion under different conditions. *The Journal of physiology, 400*(1), 425-445.

Arnal, L. H., Wyart, V., & Giraud, A. L. (2011). Transitions in neural oscillations reflect prediction errors generated in audiovisual speech. *Nature neuroscience, 14*(6), 797-801.

Arnal, L. H., & Giraud, A. L. (2012). Cortical oscillations and sensory predictions. *Trends in cognitive sciences, 16*(7), 390-398.

Arns, M., Drinkenburg, W., & Kenemans, J. L. (2012). The effects of QEEG-informed neurofeedback in ADHD: an open-label pilot study. *Applied psychophysiology and biofeedback, 37*(3), 171-180.

Arnstein, D., Cui, F., Keysers, C., Maurits, N. M., & Gazzola, V. (2011). μ-suppression during action observation and execution correlates with BOLD in dorsal premotor, inferior parietal, and SI cortices. *Journal of Neuroscience, 31*(40), 14243-14249.

Artoni, F., Barsotti, A., Guanziroli, E., Micera, S., Landi, A., & Molteni, F. (2018). Effective synchronization of EEG and EMG for mobile brain/body imaging in clinical settings. *Frontiers in human neuroscience, 11*, 652.

Artoni, F., Barsotti, A., Guanziroli, E., Molteni, F., Landi, A., & Micera, S. (2017, July). EEG and EMG synchronization and jitter estimation for MOBI experiments. In *The First Biannual Neuroadaptive Technology Conference* (p. 103).

Aspinall, P., Mavros, P., Coyne, R., & Roe, J. (2015). The urban brain: analysing outdoor physical activity with mobile EEG. *British journal of sports medicine, 49*(4), 272-276.

Ataullah, A. H. M., & De Jesus, O. (2021). Gait Disturbances. *StatPearls [Internet]*.

Avanzini, P., Fabbri-Destro, M., Dalla Volta, R., Daprati, E., Rizzolatti, G., & Cantalupo, G. (2012). The dynamics of sensorimotor cortical oscillations during the observation of hand movements: an EEG study. *PLoS One, 7*(5), e37534.

Avanzino, L., Gueugneau, N., Bisio, A., Ruggeri, P., Papaxanthis, C., & Bove, M. (2015). Motor cortical plasticity induced by motor learning through mental practice. *Frontiers in behavioral neuroscience, 9*, 105.

Babiloni, C., Babiloni, F., Carducci, F., Cincotti, F., Cocozza, G., Del Percio, C., Moretti, D. V, & Rossini, P. M. (2002). Human cortical electroencephalography (EEG) rhythms during the observation of simple aimless movements: a high-resolution EEG study. *Neuroimage, 17*(2), 559-572.

Babiloni, C., Carducci, F., Cincotti, F., Rossini, P. M., Neuper, C., Pfurtscheller, G., & Babiloni, F. (1999). Human movement-related potentials vs desynchronization of EEG alpha rhythm: a high-resolution EEG study. *Neuroimage, 10*(6), 658-665.

Babiloni, C., Del Percio, C., Lopez, S., Di Gennaro, G., Quarato, P. P., Pavone, L., Morace, R., Soricelli, A., Noce, G., Esposito, V., Gallese, V., & Mirabella, G. (2017). Frontal functional connectivity of electrocorticographic delta and theta rhythms during action execution versus action observation in humans. *Frontiers in Behavioral Neuroscience, 11*, 20.

Babiloni, C., Vecchio, F., Bultrini, A., Luca Romani, G., & Rossini, P. M. (2006). Pre-and poststimulus alpha rhythms are related to conscious visual perception: a high-resolution EEG study. *Cerebral cortex, 16*(12), 1690-1700.

Baillet, S., Mosher, J. C., & Leahy, R. M. (2001). Electromagnetic brain mapping. *IEEE Signal processing magazine, 18*(6), 14-30.-1700.

Baker, S. N. (2007). Oscillatory interactions between sensorimotor cortex and the periphery. *Current opinion in neurobiology, 17*(6), 649-655.

Bakker, M., De Lange, F. P., Helmich, R. C., Scheeringa, R., Bloem, B. R., & Toni, I. (2008). Cerebral correlates of motor imagery of normal and precision gait. *Neuroimage, 41*(3), 998-1010.

Bakker, M., De Lange, F. P., Stevens, J. A., Toni, I., & Bloem, B. R. (2007). Motor imagery of gait: a quantitative approach. *Experimental Brain Research, 179*(3), 497-504.

Ballard, D. H., Hayhoe, M. M., & Pelz, J. B. (1995). Memory representations in natural tasks. *Journal of cognitive neuroscience, 7*(1), 66-80.

Bandura, A. (2008). Observational learning. *The international encyclopedia of communication*.

Bandura, A., Grusec, J. E., & Menlove, F. L. (1966). Observational learning as a function of symbolization and incentive set. *Child development*, 499-506.

Bang, D. H., Shin, W. S., Kim, S. Y., & Choi, J. D. (2013). The effects of action observational training on walking ability in chronic stroke patients: a double-blind randomized controlled trial. *Clinical rehabilitation, 27*(12), 1118-1125.

Banquet, J. P. (1973). Spectral analysis of the EEG in meditation. *Electroencephalography and clinical neurophysiology, 35*(2), 143-151.

Barclay, R. E., Stevenson, T. J., Poluha, W., Semenko, B., & Schubert, J. (2020). Mental practice for treating upper extremity deficits in individuals with hemiparesis after stroke. Cochrane Database of Systematic Reviews, (5).

Barsalou, L. W. (2008). Grounded cognition. *Annual Review of Psychology, 59*, 617-645.

Barton, J., & Pretty, J. (2010). What is the best dose of nature and green exercise for improving mental health? A multi-study analysis. *Environmental science & technology, 44*(10), 3947-3955.

Başar, E., Schürmann, M., Başar-Eroglu, C., & Karakaş, S. (1997). Alpha oscillations in brain functioning: an integrative theory. *International journal of psychophysiology, 26*(1-3), 5-29.

Bastiaansen, M. C., Oostenveld, R., Jensen, O., & Hagoort, P. (2008). I see what you mean: theta power increases are involved in the retrieval of lexical semantic information. *Brain and language, 106*(1), 15-28.

Baumeister, J., Reinecke, K., Liesen, H., & Weiss, M. (2008). Cortical activity of skilled performance in a complex sports related motor task. *European journal of applied physiology, 104*(4), 625-631.

Beauchet, O., Annweiler, C., Callisaya, M. L., De Cock, A. M., Helbostad, J. L., Kressig, R. W., srikanth, V., Steinmetz, J. P., Blumen, H., Verghese, J., & Allali, G. (2016).

Poor gait performance and prediction of dementia: results from a meta-analysis. *Journal of the American Medical Directors Association, 17*(6), 482-490.

Beisteiner, R., Höllinger, P., Lindinger, G., Lang, W., & Berthoz, A. (1995). Mental representations of movements. Brain potentials associated with imagination of hand movements. *Electroencephalography and Clinical Neurophysiology/Evoked Potentials Section, 96*(2), 183-193.

Bell, A. J., & Sejnowski, T. J. (1995). An information-maximization approach to blind separation and blind deconvolution. *Neural computation, 7*(6), 1129-1159.

Bellelli, G., Buccino, G., Bernardini, B., Padovani, A., & Trabucchi, M. (2010). Action observation treatment improves recovery of postsurgical orthopedic patients: evidence for a top-down effect?. *Archives of physical medicine and rehabilitation, 91*(10), 1489-1494.

Beloozerova, I. N., & Sirota, M. G. (1988). Role of motor cortex in control of locomotion. In *Stance and Motion* (pp. 163-176). Springer, Boston, MA.

Berends, H. I., Wolkorte, R., IJzerman, M. J., & van Putten, M. J. A. M. (2013). Differential cortical activation during observation and observation-and-imagination. *Experimental brain research, 229*(3), 337-345.

Berger, H. (1929). Über das elektroenkephalogramm des menschen. *Archiv für psychiatrie und nervenkrankheiten, 87*(1), 527-570.

Berger, H. (1933). Über das elektrenkephalogramm des menschen. *Archiv für Psychiatrie und Nervenkrankheiten, 98*(1), 231-254.

Bernstein, N. (1967) The co-ordination and regulation of movements. Pergamon, London

Bernstein, N. A., *Dexterity and its development*.1996 in Latash, M. L., & Turvey, M. T. (2014). *Dexterity and its development*. Psychology Press.

Bhatt, T., Patel, P., Dusane, S., DelDonno, S. R., & Langenecker, S. A. (2018). Neural mechanisms involved in mental imagery of slip-perturbation while walking: a preliminary fMRI study. *Frontiers in behavioral neuroscience, 12*, 203.

Bland, B. H. (1986). The physiology and pharmacology of hippocampal formation theta rhythms. *Progress in neurobiology, 26*(1), 1-54.

Bland, B. H., & Oddie, S. D. (2001). Theta band oscillation and synchrony in the hippocampal formation and associated structures: the case for its role in sensorimotor integration. *Behavioural brain research, 127*(1-2), 119-136.

Blasi, G., Goldberg, T. E., Weickert, T., Das, S., Kohn, P., Zoltick, B., Bertolino, A., Callicott, J. H., Weinberger, D. R., Venkata, S., & Mattay, V. S. (2006). Brain regions underlying response inhibition and interference monitoring and suppression. *European Journal of Neuroscience, 23*(6), 1658-1664.

Blum, S., Jacobsen, N. S., Bleichner, M. G., &Debener, S. (2019). A Riemannian modification of artifact subspace reconstruction for EEG artifact handling. *Frontiers in human neuroscience*, *13,* 141.

Bogdanova, O. V., Bogdanov, V. B., Dureux, A., Farne, A., & Hadj-Bouziane, F. (2021). The peripersonal space in a social world. *Cortex*.

Bonini, L., Maranesi, M., Livi, A., Fogassi, L., & Rizzolatti, G. (2014). Space-dependent representation of objects and other's action in monkey ventral premotor grasping neurons. *Journal of Neuroscience*, *34*(11), 4108-4119

Boring, E. G. (1950). The influence of evolutionary theory upon American psychological thought.

Boripuntakul, S., Lord, S. R., Brodie, M. A. D., Smith, S. T., Methapatara, P., Wongpakaran, N., & Sungkarat, S. (2014). Spatial variability during gait initiation while dual tasking is increased in individuals with mild cognitive impairment. *The journal of nutrition, health & aging, 18*(3), 307-312.

Bradford, J. C., Lukos, J. R., & Ferris, D. P. (2016). Electrocortical activity distinguishes between uphill and level walking in humans. *Journal of neurophysiology, 115*(2), 958-966.

Brasil-Neto, J. P., Valls-Sole, J., Pascual-Leone, A., Cammarota, A., Amassian, V. E., Cracco, R., Hallett, M., & Cohen, L. G. (1993). Rapid modulation of human cortical motor outputs following ischaemic nerve block. *Brain, 116*(3), 511-525.

Brass, M., Bekkering, H., Wohlschläger, A., & Prinz, W. (2000). Compatibility between observed and executed finger movements: comparing symbolic, spatial, and imitative cues. *Brain and cognition, 44*(2), 124-143.

Braver, T. S. (2012). The variable nature of cognitive control: a dual mechanisms framework. *Trends in cognitive sciences*, *16*(2), 106-113.

Brechet, R., & Lecasble, R. (1965, January). Reactivity of mu rhythm to flicker. In Electroencephalography and clinical Neurophysiology (Vol. 18, No. 7, p. 721).

Brinkman, L., Stolk, A., Dijkerman, H. C., de Lange, F. P., & Toni, I. (2014). Distinct roles for alpha-and beta-band oscillations during mental simulation of goal-directed actions. *Journal of Neuroscience, 34*(44), 14783-14792.

Bronfenbrenner, U. (1977). Toward an experimental ecology of human development. *American psychologist, 32*(7), 513.

Brunswik, E. (1943). Organismic achievement and environmental probability. *Psychological review, 50*(3), 255.

Buccino, G., Binkofski, F., & Riggio, L. (2004). The mirror neuron system and action recognition. *Brain and language, 89*(2), 370-376.

Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., Seitz, R. J., Zilles, K., Rizzolatti, G., & Freund, H. J. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *European journal of neuroscience, 13*(2), 400-404.

Buccino, G., Gatti, R., Giusti, M. C., Negrotti, A., Rossi, A., Calzetti, S., & Cappa, S. F. (2011). Action observation treatment improves autonomy in daily activities in Parkinson's disease patients: results from a pilot study. *Movement Disorders, 26*(10), 1963-1964.

Bulea, T. C., Kim, J., Damiano, D. L., Stanley, C. J., & Park, H. S. (2015). Prefrontal, posterior parietal and sensorimotor network activity underlying speed control during walking. *Frontiers in human neuroscience, 9*, 247.

Bulea, T. C., Prasad, S., Kilicarslan, A., & Contreras-Vidal, J. L. (2014). Sitting and standing intention can be decoded from scalp EEG recorded prior to movement execution. *Frontiers in neuroscience, 8*, 376.

Buneo, C. A., & Andersen, R. A. (2006) The posterior parietal cortex: sensorimotor interface for the planning and online control of visually guided movements. *Neuropsychologia, 44*(13), 2594-2606.

Busan, P., Monti, F., Semenic, M., Pizzolato, G., & Battaglini, P. P. (2009). Parieto-occipital cortex and planning of reaching movements: a transcranial magnetic stimulation study. *Behavioural brain research, 201*(1), 112-119.

Buxbaum, L. J. (2001). Ideomotor apraxia: a call to action. *Neurocase, 7*(6), 445-458.

Buxbaum, L. J., & Randerath, J. (2018). Limb apraxia and the left parietal lobe. *Handbook of clinical neurology, 151*, 349-363.

Buxbaum, L. J., Johnson-Frey, S. H., & Bartlett-Williams, M. (2005). Deficient internal models for planning hand–object interactions in apraxia. *Neuropsychologia, 43*(6), 917-929.

Buxbaum, L. J., Sirigu, A., Schwartz, M. F., & Klatzky, R. (2003). Cognitive representations of hand posture in ideomotor apraxia. *Neuropsychologia, 41*(8), 1091-1113.

Buzsaki, G. (2006). *Rhythms of the Brain*. Oxford university press.

Buzsáki, G. (2010). Neural syntax: cell assemblies, synapsembles, and readers. *Neuron, 68*(3), 362-385.

Buzsáki, G., & Draguhn, A. (2004) Neuronal oscillations in cortical networks. *Science, 304*(5679), 1926-1929.

Buzsáki, G., Logothetis, N., & Singer, W. (2013). Scaling brain size, keeping timing: evolutionary preservation of brain rhythms. *Neuron, 80*(3), 751-764.

Caggiano, V., Fogassi, L., Rizzolatti, G., Thier, P., & Casile, A. (2009). Mirror neurons differentially encode the peripersonal and extrapersonal space of monkeys. *Science, 324*(5925), 403-406.

Calmels, C., Holmes, P., Lopez, E., & Naman, V. (2006). Chronometric comparison of actual and imaged complex movement patterns. *Journal of motor behavior, 38*(5), 339-348.

Capaday, C., Lavoie, B. A., Barbeau, H., Schneider, C., & Bonnard, M. (1999). Studies on the corticospinal control of human walking. I. Responses to focal transcranial magnetic stimulation of the motor cortex. *Journal of neurophysiology, 81*(1), 129-139.

Caplan, J. B., Madsen, J. R., Raghavachari, S., & Kahana, M. J. (2001). Distinct patterns of brain oscillations underlie two basic parameters of human maze learning. *Journal of neurophysiology, 86*(1), 368-380.

Caplan, J. B., Madsen, J. R., Schulze-Bonhage, A., Aschenbrenner-Scheibe, R., Newman, E. L., & Kahana, M. J. (2003). Human θ oscillations related to sensorimotor integration and spatial learning. *Journal of Neuroscience, 23*(11), 4726-4736.

Carpenter, W. B. (1874). *Principles of mental physiology: With their applications to the training and discipline of the mind, and the study of its morbid conditions*. HS King & Company.

Carter, C. S., Braver, T. S., Barch, D. M., Botvinick, M. M., Noll, D., & Cohen, J. D. (1998). Anterior cingulate cortex, error detection, and the online monitoring of performance. *Science*, *280*(5364), 747-749.

Caspers, S., Zilles, K., Laird, A. R., & Eickhoff, S. B. (2010). ALE meta-analysis of action observation and imitation in the human brain. *Neuroimage, 50*(3), 1148-1167.

Cassim, F., Szurhaj, W., Sediri, H., Devos, D., Bourriez, J. L., Poirot, I., ... & Guieu, J. D. (2000). Brief and sustained movements: differences in event-related (de) synchronization (ERD/ERS) patterns. *Clinical neurophysiology, 111*(11), 2032-2039.

Castermans, T., Duvinage, M., Cheron, G., & Dutoit, T. (2014). About the cortical origin of the low-delta and high-gamma rhythms observed in EEG signals during treadmill walking. *Neuroscience letters, 561*, 166-170.

Castiello, U., Lusher, D., Mari, M., Edwards, M., & Humphreys, G. W. (2002). Observing a human or a robotic hand grasping an object: Differential motor priming effects.

Cattaneo, L., & Rizzolatti, G. (2009). The mirror neuron system. *Archives of neurology, 66*(5), 557-560.

Cavanagh, J. F., & Frank, M. J. (2014). Frontal theta as a mechanism for cognitive control. *Trends in cognitive sciences, 18*(8), 414-421.

Cavanagh, J. F., Cohen, M. X., & Allen, J. J. (2009). Prelude to and resolution of an error: EEG phase synchrony reveals cognitive control dynamics during action monitoring. *Journal of Neuroscience, 29*(1), 98-105.

Cavanagh, J. F., Frank, M. J., Klein, T. J., & Allen, J. J. (2010). Frontal theta links prediction errors to behavioral adaptation in reinforcement learning. *Neuroimage, 49*(4), 3198-3209.

Cerritelli, B., Maruff, P., Wilson, P., & Currie, J. (2000). The effect of an external load on the force and timing components of mentally represented actions. *Behavioural brain research, 108*(1), 91-96.

Cevallos, C., Zarka, D., Hoellinger, T., Leroy, A., Dan, B., & Chéron, G. (2015). Oscillations in the human brain during walking execution, imagination and observation. *Neuropsychologia, 79*, 223-232.

Chang, C. Y., Hsu, S. H., Pion-Tonachini, L., & Jung, T. P. (2018, July). Evaluation of artifact subspace reconstruction for automatic EEG artifact removal. In *2018 40th Annual International Conference of the IEEE Engineering in Medicine and Biology Society (EMBC)* (pp. 1242-1245). IEEE.

Chao, L. L., & Martin, A. (1999). Cortical regions associated with perceiving, naming, and knowing about colors. *Journal of cognitive neuroscience, 11*(1), 25-35.

Chatrian, G. E., Petersen, M. C., & Lazarte, J. A. (1959). The blocking of the rolandic wicket rhythm and some central changes related to movement. *Electroencephalography and clinical neurophysiology, 11*(3), 497-510.

Chaumon, M., Bishop, D. V., & Busch, N. A. (2015). A practical guide to the selection of independent components of the electroencephalogram for artifact correction. *Journal of neuroscience methods*, *250*, 47-63.

Chemin, B., Huang, G., Mulders, D., & Mouraux, A. (2018). EEG time-warping to study non-strictly-periodic EEG signals related to the production of rhythmic movements. *Journal of neuroscience methods*, *308*, 106-115.

Chen, H. C., Schultz, A. B., Ashton-Miller, J. A., Giordani, B., Alexander, N. B., & Guire, K. E. (1996). Stepping over obstacles: dividing attention impairs performance of old more than young adults. *The Journals of Gerontology Series A: Biological Sciences and Medical Sciences*, *51*(3), M116-M122.

Chen, R., Tam, A., Bütefisch, C., Corwell, B., Ziemann, U., Rothwell, J. C., & Cohen, L. G. (1998). Intracortical inhibition and facilitation in different representations of the human motor cortex. *Journal of neurophysiology*, *80*(6), 2870-2881.

Cho, H. Y., Kim, J. S., & Lee, G. C. (2013). Effects of motor imagery training on balance and gait abilities in post-stroke patients: a randomized controlled trial. *Clinical rehabilitation*, *27*(8), 675-680.

Choi, K., & Cichocki, A. (2008, November). Control of a wheelchair by motor imagery in real time. In *International conference on intelligent data engineering and automated learning* (pp. 330-337). Springer, Berlin, Heidelberg.

Choi, S., Kim, J., Kim, W., & Kim, C. (2019). Skeleton-based gait recognition via robust frame-level matching. *IEEE Transactions on Information Forensics and Security, 14*(10), 2577-2592.

Chong, B. W., & Stinear, C. M. (2017). Modulation of motor cortex inhibition during motor imagery. *Journal of neurophysiology*, *117*(4), 1776-1784.

Chung, J. W., Ofori, E., Misra, G., Hess, C. W., & Vaillancourt, D. E. (2017). Beta-band activity and connectivity in sensorimotor and parietal cortex are important for accurate motor performance. *Neuroimage*, *144*, 164-173.

Cisek, P., & Kalaska, J. F. (2010). Neural mechanisms for interacting with a world full of action choices. *Annual review of neuroscience*, *33*, 269-298.

Clark, A. (1999). An embodied cognitive science?. *Trends in cognitive sciences, 3*(9), 345-351.

Cochin, S., Barthelemy, C., Lejeune, B., Roux, S., & Martineau, J. (1998). Perception of motion and qEEG activity in human adults. *Electroencephalography and clinical neurophysiology, 107*(4), 287-295.

Cochin, S., Barthelemy, C., Roux, S., & Martineau, J. (1999). Observation and execution of movement: similarities demonstrated by quantified electroencephalography. *European journal of neuroscience, 11*(5), 1839-1842.

Cochin, S., Barthelemy, C., Roux, S., & Martineau, J. (2001). Electroencephalographic activity during perception of motion in childhood. *European Journal of Neuroscience, 13*(9), 1791-1796.

Cohen, J. D., Botvinick, M., & Carter, C. S. (2000). Anterior cingulate and prefrontal cortex: who's in control?. *Nature neuroscience, 3*(5), 421-423.

Cohen-Séat, G., Gastaut, H., Faure, J., & Heuyer, G. (1954). Etudes expérimentales de l’activité nerveuse pendant la projection cinématographique. *Revue Internationale. Filmologie, 5*, 7-64.

Colby, C. L., & Goldberg, M. E. (1999). Space and attention in parietal cortex. *Annual review of neuroscience, 22*(1), 319-349.

Coles, M. G., Gratton, G., Bashore, T. R., Eriksen, C. W., & Donchin, E. (1985). A psychophysiological investigation of the continuous flow model of human information processing. *Journal of Experimental Psychology: Human Perception and Performance, 11*(5), 529.

Comon, P. (1994). Independent component analysis, a new concept?. *Signal processing, 36*(3), 287-314.

Conson, M., Mazzarella, E., & Trojano, L. (2011). Self-touch affects motor imagery: a study on posture interference effect. *Experimental brain research, 215*(2), 115.

Cooper, P. S., Karayanidis, F., McKewen, M., McLellan-Hall, S., Wong, A. S., Skippen, P., & Cavanagh, J. F. (2019) Frontal theta predicts specific cognitive control-induced behavioural changes beyond general reaction time slowing. *Neuroimage, 189*, 130-140.

Cooper, P. S., Wong, A. S., Fulham, W. R., Thienel, R., Mansfield, E., Michie, P. T., & Karayanidis, F. (2015) Theta frontoparietal connectivity associated with proactive and reactive cognitive control processes. *Neuroimage, 108*, 354-363.

Cooper, P. S., Wong, A. S., McKewen, M., Michie, P. T., & Karayanidis, F. (2017). Frontoparietal theta oscillations during proactive control are associated with goal-updating and reduced behavioral variability. *Biological psychology, 129*, 253-264.

Cooper, R. P., Cook, R., Dickinson, A., & Heyes, C. M. (2013). Associative (not Hebbian) learning and the mirror neuron system. *Neuroscience Letters, 540*, 28-36.

Cremades, J. G. (2002). The effects of imagery perspective as a function of skill level on alpha activity. *International Journal of Psychophysiology, 43*(3), 261-271.

Cremades, J. G., & Pease, D. G. (2007). Concurrent validity and reliability of lower and upper alpha activities as measures of visual and kinesthetic imagery ability. *International Journal of Sport and Exercise Psychology, 5*(2), 187-202.

Crone, N. E., Miglioretti, D. L., Gordon, B., Sieracki, J. M., Wilson, M. T., Uematsu, S., & Lesser, R. P. (1998). Functional mapping of human sensorimotor cortex with electrocorticographic spectral analysis. I. Alpha and beta event-related desynchronization. *Brain: a journal of neurology, 121*(12), 2271-2299.

Cross, E. S., Kraemer, D. J., Hamilton, A. F. D. C., Kelley, W. M., & Grafton, S. T. (2009). Sensitivity of the action observation network to physical and observational learning. *Cerebral cortex, 19*(2), 315-326.

Cruikshank, L. C., Singhal, A., Hueppelsheuser, M., & Caplan, J. B. (2012). Theta oscillations reflect a putative neural mechanism for human sensorimotor integration. *Journal of Neurophysiology, 107*(1), 65-77.

Culham, J. C., Gallivan, J., Cavina-Pratesi, C., & Quinlan, D. J. (2008). fMRI investigations of reaching and ego space in human superior parieto-occipital cortex. *Embodiment, ego-space and action*, 247-274.

Cumming, J., & Eaves, D. L. (2018). The nature, measurement, and development of imagery ability. *Imagination, Cognition and Personality, 37*(4), 375-393.

Cumming, J., & Williams, S. E. (2012). The role of imagery in performance.

Daeglau, M., Wallhoff, F., Debener, S., Condro, I. S., Kranczioch, C., & Zich, C. (2020). Challenge accepted? Individual performance gains for motor imagery practice with humanoid robotic EEG neurofeedback. *Sensors, 20*(6), 1620.

Dahm, S. F. (2020). On the assessment of motor imagery ability: A research commentary. Imagination, Cognition and Personality, 39(4), 397-408.

Davidson, D. J., & Indefrey, P. (2007). An inverse relation between event-related and time–frequency violation responses in sentence processing. *Brain research, 1158,* 81-92.

De Araújo, D. B., Baffa, O., & Wakai, R. T. (2002). Theta oscillations and human navigation: a magnetoencephalography study. *Journal of Cognitive Neuroscience, 14*(1), 70-78.

de Lange, F. P., Helmich, R. C., & Toni, I. (2006). Posture influences motor imagery: an fMRI study. *Neuroimage, 33*(2), 609-617.

de Lange, F. P., Jensen, O., Bauer, M., & Toni, I. (2008). Interactions between posterior gamma and frontal alpha/beta oscillations during imagined actions. *Frontiers in human neuroscience, 2,* 7.

De Vos, M., Kroesen, M., Emkes, R., & Debener, S. (2014). P300 speller BCI with a mobile EEG system: comparison to a traditional amplifier. *Journal of neural engineering, 11*(3), 036008.

De Vries, S., & Mulder, T. (2007). Motor imagery and stroke rehabilitation: a critical discussion*. Journal of rehabilitation medicine, 39*(1), 5-13.

Decety, J. (1996a). The neurophysiological basis of motor imagery. *Behavioural brain research, 77*(1-2), 45-52.

Decety, J. (1996b). Do imagined and executed actions share the same neural substrate?. *Cognitive brain research, 3*(2), 87-93.

Decety, J., & Grèzes, J. (2006). The power of simulation: imagining one's own and other's behavior. *Brain research, 1079*(1), 4-14.

Decety, J., & Ingvar, D. H. (1990). Brain structures participating in mental simulation of motor behavior: A neuropsychological interpretation. *Acta psychologica, 73*(1), 13-34.

Decety, J., & Jeannerod, M. (1995). Mentally simulated movements in virtual reality: does Fitt's law hold in motor imagery?. *Behavioural brain research, 72*(1-2), 127-134.

Decety, J., & Michel, F. (1989). Comparative analysis of actual and mental movement times in two graphic tasks. *Brain and cognition, 11*(1), 87-97.

Decety, J., & Mick, G. (1988). Representation mentale du mouvement et performance motrice: Approche neuro-cognitive et inter& pratique. *MCdecine et Sport, 62*(25), 232-241.

Decety, J., Chaminade, T., Grèzes, J., & Meltzoff, A. N. (2002). A PET exploration of the neural mechanisms involved in reciprocal imitation. *Neuroimage, 15*(1), 265-272.

Decety, J., Jeannerod, M., & Prablanc, C. (1989). The timing of mentally represented actions. *Behavioural brain research*, 34(1-2), 35-42.

Decety, J., Jeannerod, M., Germain, M., & Pastene, J. (1991). Vegetative response during imagined movement is proportional to mental effort. *Behavioural brain research*, 42(1), 1-5.

Decety, J., Philippon, B., & Ingvar, D. H. (1988). rCBF landscapes during motor performance and motor ideation of a graphic gesture. *European archives of psychiatry and neurological sciences*, 238(1), 33-38.

Decety, J., Sjo, H., Ryding, E., Stenberg, G., & Ingvar, D. H. (1990). The cerebellum participates in mental activity: tomographic measurements of regional cerebral blood flow. *Brain research, 535(*2), 313-317.

Dehaene, S., Posner, M. I., & Tucker, D. M. (1994). Localization of a neural system for error detection and compensation. *Psychological science, 5*(5), 303-305.

Deiber, M. P., Missonnier, P., Bertrand, O., Gold, G., Fazio-Costa, L., Ibanez, V., & Giannakopoulos, P. (2007). Distinction between perceptual and attentional processing in working memory tasks: a study of phase-locked and induced oscillatory brain dynamics. *Journal of cognitive neuroscience, 19*(1), 158-172.

Delorme, A., & Makeig, S. (2004) EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods, 134*(1), 9-21.

Delorme, A., Palmer, J., Onton, J., Oostenveld, R., & Makeig, S. (2012). Independent EEG sources are dipolar. *PloS one,7*(2), e30135.

Delval, A., Bayot, M., Defebvre, L., & Dujardin, K. (2020). Cortical oscillations during gait: wouldn't walking be so automatic?. *Brain sciences, 10*(2), 90.

Den Otter, A. R., Geurts, A. C. H., Mulder, T., & Duysens, J. (2004). Speed related changes in muscle activity from normal to very slow walking speeds. *Gait & posture, 19*(3), 270-278.

Di Nota, P. M., Chartrand, J. M., Levkov, G. R., Montefusco-Siegmund, R., & DeSouza, J. F. (2017). Experience-dependent modulation of alpha and beta during action observation and motor imagery. *BMC neuroscience, 18*(1), 1-14

Di Pellegrino, G., & Làdavas, E. (2015). Peripersonal space in the brain. *Neuropsychologia, 66,* 126-133.

Di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: a neurophysiological study. *Experimental brain research, 91*(1), 176-180.

Dickstein, R., & Deutsch, J. E. (2007). Motor imagery in physical therapist practice. Physical therapy, 87(7), 942-953.

Dietz, V. (2003). Spinal cord pattern generators for locomotion. *Clinical Neurophysiology, 114*(8), 1379-1389.

Dietz, V., & Duysens, J. (2000). Significance of load receptor input during locomotion: a review. *Gait & posture, 11*(2), 102-110.

Dijkerman, H. C., Ietswaart, M., & Johnston, M. (2010). Motor imagery and the rehabilitation of movement disorders: an overview. *The neurophysiological foundations of mental and motor imagery*, 127-144.

Dimyan, M. A., & Cohen, L. G. (2011). Neuroplasticity in the context of motor rehabilitation after stroke. *Nature Reviews Neurology, 7*(2), 76-85.

Djebbara, Z., Fich, L. B., & Gramann, K. (2019). Understanding perceptual experience of art using Mobile Brain/Body imaging. In *Brain Art* (pp. 265-282). Springer, Cham.

Djebbara, Z., Fich, L. B., Petrini, L., & Gramann, K. (2019). Sensorimotor brain dynamics reflect architectural affordances. *Proceedings of the National Academy of Sciences, 116*(29), 14769-14778.

Dobkin, B. H., Firestine, A., West, M., Saremi, K., & Woods, R. (2004). Ankle dorsiflexion as an fMRI paradigm to assay motor control for walking during rehabilitation. *Neuroimage, 23*(1), 370-381.

Dominey, P., Decety, J., Broussolle, E., Chazot, G., & Jeannerod, M. (1995). Motor imagery of a lateralized sequential task is asymmetrically slowed in hemi-Parkinson's patients. *Neuropsychologia, 33*(6), 727-741.

Donchin, E., & Coles, M. G. (1988). Is the P300 component a manifestation of context updating?. *Behavioral and brain sciences*, *11*(3), 357-374.

Doppelmayr, M., Finkenzeller, T., & Sauseng, P. (2008). Frontal midline theta in the pre-shot phase of rifle shooting: differences between experts and novices. *Neuropsychologia, 46*(5), 1463-1467.

Doyle, L. M., Yarrow, K., & Brown, P. (2005). Lateralization of event-related beta desynchronization in the EEG during pre-cued reaction time tasks. *Clinical Neurophysiology, 116*(8), 1879-1888.

Drew, T., & Marigold, D. S. (2015). Taking the next step: cortical contributions to the control of locomotion. Current opinion in neurobiology, 33, 25-33.

Drew, T., Jiang, W., & Widajewicz, W. (2002). Contributions of the motor cortex to the control of the hindlimbs during locomotion in the cat. Brain research reviews, 40(1-3), 178-191.

Drew, T., Kalaska, J., & Krouchev, N. (2008) Muscle synergies during locomotion in the cat: a model for motor cortex control. J. Physiol., 586(5), 1239-1245.

Drew, T., Prentice, S., & Schepens, B. (2004). Cortical and brainstem control of locomotion. Progress in brain research, 143, 251-261.

Eaves, D. L., Riach, M., Holmes, P. S., & Wright, D. J. (2016a). Motor imagery during action observation: a brief review of evidence, theory and future research opportunities. *Frontiers in neuroscience, 10*, 514.

Eaves, D. L., Behmer Jr, L. P., & Vogt, S. (2016b). EEG and behavioural correlates of different forms of motor imagery during action observation in rhythmical actions. *Brain and cognition, 106*, 90-103.

Edeline, J. M., Pham, P., & Weinberger, N. M. (1993). Rapid development of learning-induced receptive field plasticity in the auditory cortex. *Behavioral neuroscience, 107*(4), 539.

Ehrsson, H. H., Geyer, S., & Naito, E. (2003). Imagery of voluntary movement of fingers, toes, and tongue activates corresponding body-part-specific motor representations. *Journal of neurophysiology*.

Ekstrom, A. D., Caplan, J. B., Ho, E., Shattuck, K., Fried, I., & Kahana, M. J. (2005). Human hippocampal theta activity during virtual navigation. *Hippocampus, 15*(7), 881-889.

Enders, H., Cortese, F., Maurer, C., Baltich, J., Protzner, A. B., & Nigg, B. M. (2016). Changes in cortical activity measured with EEG during a high-intensity cycling exercise. *Journal of neurophysiology, 115*(1), 379-388.

Engel, A. K., & Fries, P. (2010). Beta-band oscillations—signalling the status quo?. *Current opinion in neurobiology, 20*(2), 156-165.

Engel, A. K., Fries, P., & Singer, W. (2001). Dynamic predictions: oscillations and synchrony in top–down processing. *Nature Reviews Neuroscience, 2(*10), 704-716.

Eriksen, B. A., & Eriksen, C. W. (1974). Effects of noise letters upon the identification of a target letter in a nonsearch task. *Perception & psychophysics*, *16*(1), 143-149.

Ertelt, D., Small, S., Solodkin, A., Dettmers, C., McNamara, A., Binkofski, F., & Buccino, G. (2007). Action observation has a positive impact on rehabilitation of motor deficits after stroke. *Neuroimage, 36*, T164-T173.

Espenhahn, S., de Berker, A. O., van Wijk, B. C., Rossiter, H. E., & Ward, N. S. (2017). Movement-related beta oscillations show high intra-individual reliability. *Neuroimage, 147*, 175-185.

Evangeliou, M. N., Raos, V., Galletti, C., & Savaki, H. E. (2009). Functional imaging of the parietal cortex during action execution and observation. *Cerebral cortex*, *19*(3), 624-639.

Fadiga, L., & Craighero, L. (2003). New insights on sensorimotor integration: From hand action to speech perception. *Brain and cognition, 53*(3), 514-524.

Fadiga, L., Buccino, G., Craighero, L., Fogassi, L., Gallese, V., & Pavesi, G. (1998). Corticospinal excitability is specifically modulated by motor imagery: a magnetic stimulation study. *Neuropsychologia*, *37*(2), 147-158.

Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (2000). Visuomotor neurons: Ambiguity of the discharge or ‘motor’perception?. *International journal of psychophysiology*, *35*(2-3), 165-177.

Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor facilitation during action observation: a magnetic stimulation study. *Journal of neurophysiology*, *73*(6), 2608-2611.

Fairweather, M. M., & Sidaway, B. (1993). Ideokinetic imagery as a postural development technique. *Research quarterly for exercise and sport*, *64*(4), 385-392.

Falkenstein, M., Hohnsbein, J., Hoormann, J., & Blanke, L. (1991). Effects of crossmodal divided attention on late ERP components. II. Error processing in choice reaction tasks. *Electroencephalography and clinical neurophysiology*, *78*(6), 447-455.

Ferreira-Pinto, M. J., Ruder, L., Capelli, P., & Arber, S. (2018). Connecting circuits for supraspinal control of locomotion. *Neuron, 100*(2), 361-374.

Ferrero, L., Quiles, V., Ortiz, M., Iáñez, E., & Azorín, J. M. (2021, May). BCI based on lower-limb motor imagery and a state machine for walking on a treadmill. In *2021 10th International IEEE/EMBS Conference on Neural Engineering (NER)* (pp. 1-4). IEEE.

Fink, A., Graif, B., & Neubauer, A. C. (2009). Brain correlates underlying creative thinking: EEG alpha activity in professional vs. novice dancers. *NeuroImage, 46*(3), 854-862.

Finke, R. A. (1986). Mental imagery and the visual system. *Scientific American, 254*(3), 88-95.

Finke, R. A., & Kurtzman, H. S. (1981). Mapping the visual field in mental imagery. *Journal of Experimental Psychology: General, 110*(4), 501.

Fitts, P. M. (1954). The information capacity of the human motor system in controlling the amplitude of movement. *Journal of experimental psychology, 47*(6), 381.

Fodor, J. A. (1983). *The modularity of mind.* MIT press.

Fogassi, L., Ferrari, P. F., Gesierich, B., Rozzi, S., Chersi, F., & Rizzolatti, G. (2005). Parietal lobe: from action organization to intention understanding. *Science, 308*(5722), 662-667.

Foulsham, T., Walker, E., & Kingstone, A. (2011). The where, what and when of gaze allocation in the lab and the natural environment. *Vision research, 51*(17), 1920-1931.

Foxe, J. J., & Snyder, A. C. (2011). The role of alpha-band brain oscillations as a sensory suppression mechanism during selective attention. *Frontiers in psychology, 2*, 154.

Foxe, J. J., Simpson, G. V., & Ahlfors, S. P. (1998). Parieto-occipital~ 1 0Hz activity reflects anticipatory state of visual attention mechanisms. *Neuroreport, 9*(17), 3929-3933.

Frak, V., Paulignan, Y., & Jeannerod, M. (2001). Orientation of the opposition axis in mentally simulated grasping. *Experimental Brain Research, 136*(1), 120-127.

Franceschini, M., Agosti, M., Cantagallo, A., Sale, P., Mancuso, M., & Buccino, G. (2010). Mirror neurons: action observation treatment as a tool in stroke rehabilitation. *European Journal of Physical Rehabilitation Medicine, 46*(4), 517-523.

Franchak, J. M., & Adolph, K. E. (2010). Visually guided navigation: Head-mounted eye-tracking of natural locomotion in children and adults. *Vision research, 50*(24), 2766-2774.

Frenkel-Toledo, S., Liebermann, D. G., Bentin, S., & Soroker, N. (2016). Dysfunction of the human mirror neuron system in ideomotor apraxia: evidence from mu suppression. *Journal of cognitive neuroscience, 28*(6), 775-791.

Frese, M., & Sabini, J. (Eds.). (2021). Goal directed behavior: The concept of action in psychology.

Fries, P., Nikolić, D., & Singer, W. (2007). The gamma cycle. *Trends in neurosciences, 30*(7), 309-316.

Fry, A., Mullinger, K. J., O'Neill, G. C., Barratt, E. L., Morris, P. G., Bauer, M., Folland, J.P., & Brookes, M. J. (2016) Modulation of post-movement beta rebound by contraction force and rate of force development. *Hum. Brain Mapp, 37*(7), 2493-2511.

Gabbard, C. P., & Lee, J. (2014). A comparison of movement imagery ability self-report and imagery use in a motor task: A preliminary investigation. *Journal of Imagery Research in Sport and Physical Activity, 9*(1), 61-66.

Galambos, R. (1992). A comparison of certain gamma band (40-Hz) brain rhythms in cat and man. In *Induced rhythms in the brain* (pp. 201-216). Birkhäuser, Boston, MA.

Gallese, V. (2000). The inner sense of action. Agency and motor representations. *Journal of consciousness studies, 7*(10), 23-40.

Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain, 119*(2), 593-609.

Gallese, V., Keysers, C., & Rizzolatti, G. (2004). A unifying view of the basis of social cognition. *Trends in cognitive sciences, 8*(9), 396-403.

Galna, B., Murphy, A. T., & Morris, M. E. (2010). Obstacle crossing in people with Parkinson’s disease: foot clearance and spatiotemporal deficits. *Human movement science, 29*(5), 843-852.

Gandolfo, F., Mussa-Ivaldi, F. A., & Bizzi, E. (1996). Motor learning by field approximation. *Proceedings of the National Academy of Sciences, 93*(9), 3843-3846.

Garbarini, F., & Adenzato, M. (2004). At the root of embodied cognition: Cognitive science meets neurophysiology. *Brain and cognition, 56*(1), 100-106.

Gastaut, H. (1952). Etude électrocorticographique de la réactivité des rythmes rolandiques. *Revue Neurologique* (Paris), 87, 176-182.

Gastaut, H. J., & Bert, J. (1954). EEG changes during cinematographic presentation (Moving picture activation of the EEG). *Electroencephalography and clinical neurophysiology, 6,* 433-444.

Gatev, P., Darbin, O., & Wichmann, T. (2006). Oscillations in the basal ganglia under normal conditions and in movement disorders. *Movement disorders, 21*(10), 1566-1577.

Gehring, W. J., Coles, M. G., Meyer, D. E., & Donchin, E. (1995). A brain potential manifestation of error-related processing. *Electroencephalography and Clinical Neurophysiology-Supplements only, 44*, 261-272.

Gehring, W. J., Goss, B., Coles, M. G., Meyer, D. E., & Donchin, E. (1993). A neural system for error detection and compensation. *Psychological science, 4*(6), 385-390.

Georgopoulos, A. P., Lurito, J. T., Petrides, M., Schwartz, A. B., & Massey, J. T. (1989). Mental rotation of the neuronal population vector. *Science, 243*(4888), 234-236.

Gerardin, E., Sirigu, A., Lehéricy, S., Poline, J. B., Gaymard, B., Marsault, C., Agid, Y., & Le Bihan, D. (2000). Partially overlapping neural networks for real and imagined hand movements. *Cerebral cortex, 10*(11), 1093-1104.

Gerloff, C., Richard, J., Hadley, J., Schulman, A. E., Honda, M., & Hallett, M. (1998). Functional coupling and regional activation of human cortical motor areas during simple, internally paced and externally paced finger movements. *Brain: a journal of neurology, 121*(8), 1513-1531.

Geschwind, N., & Damasio, A. R. (1985). Apraxia. *Handbook of clinical neurology, 1*(49), 423-432.

Gevins, A., Smith, M. E., McEvoy, L., & Yu, D. (1997). High-resolution EEG mapping of cortical activation related to working memory: effects of task difficulty, type of processing, and practice. *Cerebral cortex (New York, NY: 1991), 7*(4), 374-385.

Gibson, E. J. (1988). Exploratory behavior in the development of perceiving, acting, and the acquiring of knowledge. *Annual review of psychology, 39*(1), 1-42.

Gibson, J. J. (1954). The visual perception of objective motion and subjective movement. *Psychological review, 61*(5), 304.

Gibson, J. J. (1979). The ecological approach to visual perception Houghton Mifflin. *New York.*

Gilbertson, T., Lalo, E., Doyle, L., Di Lazzaro, V., Cioni, B., & Brown, P. (2005). Existing motor state is favored at the expense of new movement during 13-35 Hz oscillatory synchrony in the human corticospinal system. *Journal of Neuroscience, 25*(34), 7771-7779.

Giszter, S. F. (2015). Motor primitives—new data and future questions. *Current opinion in neurobiology, 33*, 156-165.

Glover, S., & Baran, M. (2017). The motor-cognitive model of motor imagery: Evidence from timing errors in simulated reaching and grasping. *Journal of Experimental Psychology:Human Perception and Performance, 43*(7), 1359.

Glover, S., Bibby, E., & Tuomi, E. (2020). Executive functions in motor imagery: support for the motor-cognitive model over the functional equivalence model. *Experimental Brain Research, 238*(4), 931.

Gola, M., Magnuski, M., Szumska, I., & Wróbel, A. (2013). EEG beta band activity is related to attention and attentional deficits in the visual performance of elderly subjects. *International Journal of Psychophysiology, 89*(3), 334-341.

Goldenberg, G. (1992). Loss of visual imagery and loss of visual knowledge—a case study. *Neuropsychologia, 30*(12), 1081-1099.

Goldenberg, G. (2003). Apraxia and beyond: life and work of Hugo Liepmann. *Cortex, 39*(3), 509-524.

Goldenberg, G. (2009). Apraxia and the parietal lobes. *Neuropsychologia, 47*(6), 1449-1459.

Gomez-Rodriguez, M., Peters, J., Hill, J., Schölkopf, B., Gharabaghi, A., & Grosse-Wentrup, M. (2011). Closing the sensorimotor loop: haptic feedback facilitates decoding of motor imagery. *Journal of neural engineering, 8*(3), 036005.

Grafton, S. T., & Hamilton, A. F. D. C. (2007). Evidence for a distributed hierarchy of action representation in the brain. *Human movement science, 26*(4), 590-616.

Grafton, S. T., Arbib, M. A., Fadiga, L., & Rizzolatti, G. (1996). Localization of grasp representations in humans by positron emission tomography. *Experimental brain research, 112*(1), 103-111.

Gramann, K., Gwin, J. T., Bigdely-Shamlo, N., Ferris, D. P., & Makeig, S. (2010). Visual evoked responses during standing and walking. *Frontiers in human neuroscience, 4*, 202.

Gramann, K., Gwin, J. T., Ferris, D. P., Oie, K., Jung, T. P., Lin, C. T., Liao, L. D., & Makeig, S. (2011). Cognition in action: imaging brain/body dynamics in mobile humans.

Gramann, K., Jung, T. P., Ferris, D. P., Lin, C. T., & Makeig, S. (2014). Toward a new cognitive neuroscience: modeling natural brain dynamics. *Frontiers in human neuroscience, 8*, 444.

Grant, E. R., & Spivey, M. J. (2003). Eye movements and problem solving: Guiding attention guides thought. *Psychological Science, 14*(5), 462-466.

Grasso, R., Prévost, P., Ivanenko, Y. P., & Berthoz, A. (1998). Eye-head coordination for the steering of locomotion in humans: an anticipatory synergy. *Neuroscience Letters, 253*(2), 115-118.

Green, J. D., & Arduini, A. A. (1954). Hippocampal electrical activity in arousal. *Journal of neurophysiology, 17*(6), 533-557.

Gregg, M., Hall, C., & Butler, A. (2010). The MIQ-RS: a suitable option for examining movement imagery ability. *Evidence-Based Complementary and Alternative Medicine, 7*(2), 249-257.

Grèzes, J. (1998). Top down effect of strategy on the perception of human biological motion: A PET investigation. *Cognitive Neuropsychology, 15*(6-8), 553-582.

Grezes, J., & Decety, J. (2001). Functional anatomy of execution, mental simulation, observation, and verb generation of actions: A meta-analysis. *Human brain mapping, 12*(1), 1-19.

Grillner, S. (2006). Biological pattern generation: the cellular and computational logic of networks in motion. *Neuron, 52*(5), 751-766.

Grillner, S., Wallén, P., Saitoh, K., Kozlov, A., & Robertson, B. (2008). Neural bases of goal-directed locomotion in vertebrates—an overview. *Brain research reviews, 57*(1), 2-12.

Gruber, T., Tsivilis, D., Giabbiconi, C. M., & Müller, M. M. (2008). Induced electroencephalogram oscillations during source memory: familiarity is reflected in the gamma band, recollection in the theta band. *Journal of cognitive neuroscience, 20*(6), 1043-1053.

Grush, R. (2004). The emulation theory of representation: Motor control, imagery, and perception. *Behavioral and brain sciences, 27*(3), 377-396.

Grush, R. (2007). *Time and experience*. na.

Guerra, Z. F., Lucchetti, A. L., & Lucchetti, G. (2017). Motor imagery training after stroke: a systematic review and meta-analysis of randomized controlled trials. *Journal of Neurologic Physical Therapy, 41*(4), 205-214.

Guillot, A., & Collet, C. (2008). Construction of the motor imagery integrative model in sport: a review and theoretical investigation of motor imagery use. International Review of Sport and Exercise Psychology, 1(1), 31-44.

Guillot, A., Collet, C., & Dittmar, A. (2004). Relationship between visual and kinesthetic imagery, field dependence-independence, and complex motor skills. *Journal of Psychophysiology, 18*(4), 190-198.

Guillot, A., Collet, C., Nguyen, V. A., Malouin, F., Richards, C., & Doyon, J. (2009). Brain activity during visual versus kinesthetic imagery: an fMRI study. *Human brain mapping, 30*(7), 2157-2172.

Guillot, A., Di Rienzo, F., & Collet, C. (2014). The neurofunctional architecture of motor imagery. *Advanced Brain Neuroimaging Topics in Health and Disease-Methods and Applications*, 433-456.

Gulyaeva, N. V. (2017). Molecular mechanisms of neuroplasticity: an expanding universe. *Biochemistry (Moscow), 82*(3), 237-242.

Güntekin, B., & Basar, E. (2007). Emotional face expressions are differentiated with brain oscillations. *International Journal of Psychophysiology, 64*(1), 91-100.

Gwin, J. T., Gramann, K., Makeig, S., & Ferris, D. P. (2010). Removal of movement artifact from high-density EEG recorded during walking and running. *Journal of neurophysiology*, *103*(6), 3526-3534.

Gwin, J. T., Gramann, K., Makeig, S., & Ferris, D. P. (2011) Electrocortical activity is coupled to gait cycle phase during treadmill walking. *Neuroimage*, *54*(2), 1289-1296.

Haefeli, J., Vögeli, S., Michel, J., & Dietz, V. (2011). Preparation and performance of obstacle steps: interaction between brain and spinal neuronal activity. *European Journal of Neuroscience*, *33*(2), 338-348..

Hald, L. A., Bastiaansen, M. C., & Hagoort, P. (2006). EEG theta and gamma responses to semantic violations in online sentence processing. *Brain and language*, *96*(1), 90-105.

Hall, C. R., & Martin, K. A. (1997). Measuring movement imagery abilities: a revision of the movement imagery questionnaire. *Journal of mental imagery*.

Hallett, M. (2005). Neuroplasticity and rehabilitation. *Journal of rehabilitation research and development, 42*(4), R17.

Hallett, M., Fieldman, J., Cohen, L. G., Sadato, N., & Pascual-Leone, A. (1994). Involvement of primary motor cortex in motor imagery and mental practice. *Behavioral and Brain Sciences, 17*(2), 210-210.

Hamacher, D., Herold, F., Wiegel, P., Hamacher, D., & Schega, L. (2015). Brain activity during walking: a systematic review. *Neuroscience & Biobehavioral Reviews, 57*, 310-327.

Hamilton, A. F. (2013). The mirror neuron system contributes to social responding. *Cortex, 49*(10), 2957-2959.

Hammond, D. C. (2007). What is neurofeedback?. *Journal of neurotherapy, 10*(4), 25-36.

Hanslmayr, S., Sauseng, P., Doppelmayr, M., Schabus, M., & Klimesch, W. (2005). Increasing individual upper alpha power by neurofeedback improves cognitive performance in human subjects. *Applied psychophysiology and biofeedback, 30*(1), 1-10.

Harada, T., Miyai, I., Suzuki, M., & Kubota, K. (2009). Gait capacity affects cortical activation patterns related to speed control in the elderly. *Experimental brain research, 193*(3), 445-454.

Hardwick, R. M., Caspers, S., Eickhoff, S. B., & Swinnen, S. P. (2018). Neural correlates of action: Comparing meta-analyses of imagery, observation, and execution. *Neuroscience & Biobehavioral Reviews, 94*, 31-44.

Hardwick, R. M., Rajan, V. A., Bastian, A. J., Krakauer, J. W., & Celnik, P. A. (2017). Motor learning in stroke: trained patients are not equal to untrained patients with less impairment. *Neurorehabilitation and neural repair, 31*(2), 178-189.

Hari, R., & Kujala, M. V. (2009). Brain basis of human social interaction: from concepts to brain imaging. *Physiological reviews, 89*(2), 453-479.

Hari, R., & Salmelin, R. (1997). Human cortical oscillations: a neuromagnetic view through the skull. *Trends in neurosciences, 20*(1), 44-49.

Hari, R., Forss, N., Avikainen, S., Kirveskari, E., Salenius, S., & Rizzolatti, G. (1998). Activation of human primary motor cortex during action observation: a neuromagnetic study. *Proceedings of the National Academy of Sciences*, *95*(25), 15061-15065.

Hari, R., Levänen, S., & Raij, T. (2000). Timing of human cortical functions during cognition: role of MEG. *Trends in cognitive sciences, 4*(12), 455-462.

Hasan, S. S., Siddiquee, M. R., Atri, R., Ramon, R., Marquez, J. S., & Bai, O. (2020). Prediction of gait intention from pre-movement EEG signals: a feasibility study. *Journal of neuroengineering and rehabilitation, 17*(1), 1-16.

Hashimoto, Y., & Ushiba, J. (2013). EEG-based classification of imaginary left and right foot movements using beta rebound. *Clinical neurophysiology, 124*(11), 2153-2160.

Hatsopoulos, N. G., & Donoghue, J. P. (2009). The science of neural interface systems. *Annual review of neuroscience, 32*, 249-266.

Haufler, A. J., Spalding, T. W., Santa Maria, D. L., & Hatfield, B. D. (2000). Neuro-cognitive activity during a self-paced visuospatial task: comparative EEG profiles in marksmen and novice shooters. *Biological psychology*, *53*(2-3), 131-160.

Hayhoe, M. (2000). Vision using routines: A functional account of vision. *Visual Cognition*, *7*(1-3), 43-64.

Hayhoe, M. M., Shrivastava, A., Mruczek, R., & Pelz, J. B. (2003). Visual memory and motor planning in a natural task. *Journal of vision, 3*(1), 6-6.

Heida, T., Poppe, N. R., de Vos, C. C., van Putten, M. J. A. M., & van Vugt, J. P. P. (2014). Event-related mu-rhythm desynchronization during movement observation is impaired in Parkinson's disease. *Clinical neurophysiology, 125*(9), 1819-1825.

Heilman, K. M., & Valenstein, E. E. (2003). *Clinical neuropsychology.* Oxford University Press.

Heilman, K. M., Rothi, L. J., & Valenstein, E. (1982). Two forms of ideomotor apraxia. *Neurology*, *32*(4), 342-342.

Heimann, M. (1989). Neonatal imitation, gaze aversion, and mother-infant interaction. *Infant Behavior and Development, 12*(4), 495-505.

Heinrichs-Graham, E., Kurz, M. J., Becker, K. M., Santamaria, P. M., Gendelman, H. E., & Wilson, T. W. (2014). Hypersynchrony despite pathologically reduced beta oscillations in patients with Parkinson's disease: a pharmaco-magnetoencephalography study. *Journal of Neurophysiology, 112*(7), 1739-1747.

Heinrichs-Graham, E., Kurz, M. J., Gehringer, J. E., & Wilson, T. W. (2017) The functional role of post-movement beta oscillations in motor termination. *Brain Struct. Funct., 222*(7), 3075-3086.

Helfrich, R. F., Breska, A., & Knight, R. T. (2019). Neural entrainment and network resonance in support of top-down guided attention. *Current opinion in psychology*, *29*, 82-89.

Herranz-Gómez, A., Gaudiosi, C., Angulo-Díaz-Parreño, S., Suso-Martí, L., La Touche, R., & Cuenca-Martínez, F. (2020). Effectiveness of motor imagery and action observation on functional variables: An umbrella and mapping review with meta-meta-analysis. *Neuroscience & Biobehavioral Reviews.*

Hétu, S., Grégoire, M., Saimpont, A., Coll, M. P., Eugène, F., Michon, P. E., & Jackson, P. L. (2013). The neural network of motor imagery: an ALE meta-analysis. Neuroscience & Biobehavioral Reviews, 37(5), 930-949.

Heuer, H., & Sanders, A. (Eds.). (2016). *Perspectives on perception and action.* Routledge.

Holgado, A. J. N., Terry, J. R., & Bogacz, R. (2010). Conditions for the generation of beta oscillations in the subthalamic nucleus–globus pallidus network. *Journal of Neuroscience, 30*(37), 12340-12352.

Holmes, N. P., & Spence, C. (2004). The body schema and multisensory representation (s) of peripersonal space. *Cognitive processing, 5*(2), 94-105.

Holtzer, R., Epstein, N., Mahoney, J. R., Izzetoglu, M., & Blumen, H. M. (2014). Neuroimaging of mobility in aging: a targeted review. *Journals of Gerontology Series A: Biomedical Sciences and Medical Sciences*, *69*(11), 1375-1388.

Horak, F. B. (2006) Postural orientation and equilibrium: what do we need to know about neural control of balance to prevent falls?. *Age and ageing, 35*, ii7-ii11.

Horak, F. B., Shupert, C. L., Dietz, V., & Horstmann, G. (1994). Vestibular and somatosensory contributions to responses to head and body displacements in stance. *Experimental Brain Research, 100*(1), 93-106.

Hötting, K., & Röder, B. (2013). Beneficial effects of physical exercise on neuroplasticity and cognition. *Neuroscience & Biobehavioral Reviews, 37*(9), 2243-2257.

Hsu, W. C., Lin, L. F., Chou, C. W., Hsiao, Y. T., & Liu, Y. H. (2017). EEG classification of imaginary lower limb stepping movements based on fuzzy support vector machine with kernel-induced membership function. *International Journal of Fuzzy Systems*, *19*(2), 566-579.

Hughlings Jackson, J. (1874). On the nature of the duality of the brain. *Medical Press and Circular, 1*, 80-86.

Hummel, F., Kirsammer, R., & Gerloff, C. (2003). Ipsilateral cortical activation during finger sequences of increasing complexity: representation of movement difficulty or memory load?. *Clinical Neurophysiology, 114*(4), 605-613.

Husain, M., & Nachev, P. (2007). Space and the parietal cortex. *Trends in cognitive sciences, 11*(1), 30-36.

Hutcheon, B., & Yarom, Y. (2000). Resonance, oscillation and the intrinsic frequency preferences of neurons. *Trends in neurosciences, 23*(5), 216-222.

Hyvarinen, A. (1999). Fast and robust fixed-point algorithms for independent component analysis. *IEEE transactions on Neural Networks, 10*(3), 626-634.

Iacoboni, M., Lieberman, M. D., Knowlton, B. J., Molnar-Szakacs, I., Moritz, M., Throop, C. J., & Fiske, A. P. (2004). Watching social interactions produces dorsomedial prefrontal and medial parietal BOLD fMRI signal increases compared to a resting baseline. *Neuroimage, 21*(3), 1167-1173.

Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *science, 286*(5449), 2526-2528.

Ietswaart, M., Johnston, M., Dijkerman, H. C., Joice, S., Scott, C. L., MacWalter, R. S., & Hamilton, S. J. (2011). Mental practice with motor imagery in stroke recovery: randomized controlled trial of efficacy. *Brain, 134*(5), 1373-1386.

Jackson, P. L., Lafleur, M. F., Malouin, F., Richards, C. L., & Doyon, J. (2003). Functional cerebral reorganization following motor sequence learning through mental practice with motor imagery. *Neuroimage, 20*(2), 1171-1180.

Jackson, P. L., Meltzoff, A. N., & Decety, J. (2006). Neural circuits involved in imitation and perspective-taking. *Neuroimage, 31*(1), 429-439.

Jacobsen, N. S. J., Blum, S., Witt, K., & Debener, S. (2020). A walk in the park? Characterizing gait-related artifacts in mobile EEG recordings. *European Journal of Neuroscience*.

Jahn, K., Deutschländer, A., Stephan, T., Kalla, R., Wiesmann, M., Strupp, M., & Brandt, T. (2008). Imaging human supraspinal locomotor centers in brainstem and cerebellum. *Neuroimage, 39*(2), 786-792.

Jahn, K., Zwergal, A., & Schniepp, R. (2010). Gait disturbances in old age: classification, diagnosis, and treatment from a neurological perspective. *Deutsches Ärzteblatt International, 107*(17), 306.

Jain, S., Gourab, K., Schindler-Ivens, S., & Schmit, B. D. (2013). EEG during pedaling: evidence for cortical control of locomotor tasks. *Clinical Neurophysiology*, *124*(2), 379-390.

James, W. (1890). The perception of reality. *Principles of psychology, 2*, 283-324.

Järveläinen, J., Schürmann, M., & Hari, R. (2004). Activation of the human primary motor cortex during observation of tool use. *Neuroimage*, *23*(1), 187-192.

Jeannerod, M. (1994). The representing brain: Neural correlates of motor intention and imagery. *Behavioral and Brain sciences, 17*(2), 187-201.

Jeannerod, M. (2001). Neural simulation of action: a unifying mechanism for motor cognition. *Neuroimage, 14*(1), S103-S109.

Jeannerod, M. (2006*). Motor cognition: What actions tell the self* (No. 42). Oxford University Press.

Jeannerod, M., & Decety, J. (1995). Mental motor imagery: a window into the representational stages of action. *Current opinion in neurobiology, 5*(6), 727-732.

Jenkinson, N., & Brown, P. (2011). New insights into the relationship between dopamine, beta oscillations and motor function. *Trends in neurosciences, 34*(12), 611-618.

Jensen, O., & Tesche, C. D. (2002). Frontal theta activity in humans increases with memory load in a working memory task. *European journal of Neuroscience, 15*(8), 1395-1399.

Jensen, O., Goel, P., Kopell, N., Pohja, M., Hari, R., & Ermentrout, B. (2005). On the human sensorimotor-cortex beta rhythm: sources and modeling. *Neuroimage, 26*(2), 347-355.

Johansson, R. S., Westling, G., Bäckström, A., & Flanagan, J. R. (2001). Eye–hand coordination in object manipulation. *Journal of neuroscience, 21*(17), 6917-6932.

Johnson, R.A.Y. (1988). Scalp-recorded P300 activity in patients following unilateral temporal lobectomy. *Brain, 111*(6), 1517-1529.

Johnson-Frey, S. H. (2004). The neural bases of complex tool use in humans. *Trends in cognitive sciences, 8*(2), 71-78.

Johnson-Frey, S. H., Maloof, F. R., Newman-Norlund, R., Farrer, C., Inati, S., & Grafton, S. T. (2003). Actions or hand-object interactions? Human inferior frontal cortex and action observation. *Neuron, 39*(6), 1053-1058.

Jones, S. R., Kerr, C. E., Wan, Q., Pritchett, D. L., Hämäläinen, M., & Moore, C. I. (2010). Cued spatial attention drives functionally relevant modulation of the mu rhythm in primary somatosensory cortex. *Journal of Neuroscience, 30*(41), 13760-13765.

Joundi, R. A., Jenkinson, N., Brittain, J. S., Aziz, T. Z., & Brown, P. (2012). Driving oscillatory activity in the human cortex enhances motor performance. *Current Biology, 22*(5), 403-407.

Jung, T. P., Makeig, S., Westerfield, M., Townsend, J., Courchesne, E., & Sejnowski, T. J. (2000). Removal of eye activity artifacts from visual event-related potentials in normal and clinical subjects. *Clinical Neurophysiology, 111*(10), 1745-1758.

Jurkiewicz, M. T., Gaetz, W. C., Bostan, A. C., & Cheyne, D. (2006) Post-movement beta rebound is generated in motor cortex: evidence from neuromagnetic recordings. *Neuroimage, 32*(3), 1281-1289.

Kahana, M. J., Seelig, D., & Madsen, J. R. (2001). Theta returns. *Current opinion in neurobiology, 11*(6), 739-744.

Kahana, M. J., Sekuler, R., Caplan, J. B., Kirschen, M., & Madsen, J. R. (1999). Human theta oscillations exhibit task dependence during virtual maze navigation. *Nature, 399*(6738), 781-784.

Kaiser, J., Birbaumer, N., & Lutzenberger, W. (2001). Event-related beta desynchronization indicates timing of response selection in a delayed-response paradigm in humans. *Neuroscience letters, 312*(3), 149-152.

Kaiser, J., Ulrich, R., & Lutzenberger, W. (2003). Dynamics of sensorimotor cortex activation to spatial sounds precueing ipsi-versus contralateral manual responses. *Cognitive brain research, 17*(3), 573-583.

Kamiya, J. (1968). Conscious control of brain waves. *Psychology Today, 1.*

Kaneko, N., Yokoyama, H., Masugi, Y., Watanabe, K., & Nakazawa, K. (2021). Phase dependent modulation of cortical activity during action observation and motor imagery of walking: An EEG study. *NeuroImage, 225*, 117486.

Kaufman, L., Schwartz, B., Salustri, C., & Williamson, S. J. (1990). Modulation of spontaneous brain activity during mental imagery. *Journal of Cognitive Neuroscience, 2*(2), 124-132.

Kawato, M., & Wolpert, D. (1998). Internal models for motor control. *Sensory guidance of movement, 218*, 291-307.

Kelso, J. A., & Holt, K. G. (1980). Exploring a vibratory systems analysis of human movement production. *Journal of Neurophysiology, 43*(5), 1183-1196.

Keysers, C., & Gazzola, V. (2014). Hebbian learning and predictive mirror neurons for actions, sensations and emotions. Philosophical Transactions of the Royal Society B: Biological Sciences, 369(1644), 20130175.

Khan, H., Naseer, N., Yazidi, A., Eide, P. K., Hassan, H. W., & Mirtaheri, P. (2021). Analysis of Human Gait Using Hybrid EEG-fNIRS-Based BCI System: A Review. *Frontiers in Human Neuroscience*, 605.

Kiehn, O. (2016). Decoding the organization of spinal circuits that control locomotion. *Nature Reviews Neuroscience, 17*(4), 224-238.

Kilavik, B. E., Zaepffel, M., Brovelli, A., MacKay, W. A., & Riehle, A. (2013). The ups and downs of beta oscillations in sensorimotor cortex. *Experimental neurology, 245*, 15-26.

Kilner, J. M., Marchant, J. L., & Frith, C. D. (2006). Modulation of the mirror system by social relevance. *Social cognitive and affective neuroscience, 1*(2), 143-148.

Kilner, J. M., Marchant, J. L., & Frith, C. D. (2009). Relationship between activity in human primary motor cortex during action observation and the mirror neuron system. *PLoS One, 4*(3), e4925.

Kim, D. W., Hwang, H. J., Lim, J. H., Lee, Y. H., Jung, K. Y., & Im, C. H. (2011). Classification of selective attention to auditory stimuli: toward vision-free brain–computer interfacing. *Journal of neuroscience methods, 197*(1), 180-185.

Kimberley, T. J., Khandekar, G., Skraba, L. L., Spencer, J. A., Van Gorp, E. A., & Walker, S. R. (2006). Neural substrates for motor imagery in severe hemiparesis. *Neurorehabilitation and Neural Repair, 20*(2), 268-277.

King, C. E., Dave, K. R., Wang, P. T., Mizuta, M., Reinkensmeyer, D. J., Do, A. H., Moromugi, S., & Nenadic, Z. (2014). Performance assessment of a brain–computer interface driven hand orthosis. *Annals of biomedical engineering, 42*(10), 2095-2105.

Klass, D. W., & Bickford, R. G. (1957, January). Observations on the rolandic arceau rhythm. In Electroencephalography and Clinical Neurophysiology (Vol. 9, No. 3, pp. 570-570).

Klimesch, W. (2012). Alpha-band oscillations, attention, and controlled access to stored information. *Trends in cognitive sciences, 16*(12), 606-617.

Klimesch, W. (2018). The frequency architecture of brain and brain body oscillations: an analysis. *European Journal of Neuroscience, 48*(7), 2431-2453.

Klimesch, W., Doppelmayr, M., & Hanslmayr, S. (2006). Upper alpha ERD and absolute power: their meaning for memory performance. *Progress in brain research,* 159, 151-165.

Klimesch, W., Doppelmayr, M., Pachinger, T., & Russegger, H. (1997). Event-related desynchronization in the alpha band and the processing of semantic information. *Cognitive Brain Research*, 6(2), 83-94.

Klimesch, W., Doppelmayr, M., Schwaiger, J., Auinger, P., & Winkler, T. H. (1999). Paradoxical'alpha synchronization in a memory task. *Cognitive Brain Research, 7*(4), 493-501.

Klimesch, W., Doppelmayr, M., Wimmer, H., Schwaiger, J., Röhm, D., Gruber, W., & Hutzler, F. (2001). Theta band power changes in normal and dyslexic children. *Clinical Neurophysiology, 112*(7), 1174-1185.

Klimesch, W., Freunberger, R., & Sauseng, P. (2010). Oscillatory mechanisms of process binding in memory. *Neuroscience & Biobehavioral Reviews, 34*(7), 1002-1014.

Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: the inhibition–timing hypothesis. *Brain research reviews, 53*(1), 63-88.

Kline, J. E., Huang, H. J., Snyder, K. L., & Ferris, D. P. (2015). Isolating gait-related movement artifacts in electroencephalography during human walking. *Journal of neural engineering, 12(*4), 046022.

Klug, M., & Gramann, K. (2021). Identifying key factors for improving ICA-based decomposition of EEG data in mobile and stationary experiments. *European Journal of Neuroscience*, *54*(12), 8406-8420.

Koenraadt, K. L., Roelofsen, E. G., Duysens, J., & Keijsers, N. L. (2014). Cortical control of normal gait and precision stepping: an fNIRS study. *Neuroimage, 85*, 415-422.

Kohler, E., Keysers, C., Umilta, M. A., Fogassi, L., Gallese, V., & Rizzolatti, G. (2002). Hearing sounds, understanding actions: action representation in mirror neurons. *Science, 297*(5582), 846-848.

Konczak, J. (1994). Effects of optic flow on the kinematics of human gait: a comparison of young and older adults. *Journal of motor behavior, 26*(3), 225-236.

Konorski, J. (1967). Integrative activity of the brain; an interdisciplinary approach.

Koski, L., Iacoboni, M., Dubeau, M. C., Woods, R. P., & Mazziotta, J. C. (2003). Modulation of cortical activity during different imitative behaviors. *Journal of neurophysiology.*

Kosslyn, S. M. (1978). Measuring the visual angle of the mind's eye. *Cognitive psychology, 10*(3), 356-389.

Kosslyn, S. M. (1980). Image and mind. *Harvard University Press*.

Kosslyn, S. M., & Hatfield, G. (1984). Representation without symbol systems. *Social Research,* 1019-1045.

Kosslyn, S. M., Thompson, W. L., & Ganis, G. (2006). The case for mental imagery. *Oxford University Press*.

Kothe, C. (2014). Lab streaming layer (LSL).

Kovacs, C. R. (2005) Age-related changes in gait and obstacle avoidance capabilities in older adults: a review. *Journal of applied gerontology, 24*(1), 21-34.

Kraeutner, S. N., Eppler, S. N., Stratas, A., & Boe, S. G. (2020). Generate, maintain, manipulate? Exploring the multidimensional nature of motor imagery. *Psychology of Sport and Exercise, 48,* 101673.

Kramis, R., Vanderwolf, C. H., & Bland, B. H. (1975). Two types of hippocampal rhythmical slow activity in both the rabbit and the rat: relations to behavior and effects of atropine, diethyl ether, urethane, and pentobarbital. *Experimental neurology, 49*(1), 58-85.

Kranczioch, C., Zich, C., Schierholz, I., & Sterr, A. (2014). Mobile EEG and its potential to promote the theory and application of imagery-based motor rehabilitation. *International Journal of Psychophysiology, 91*(1), 10-15.

Krause, C. M., Sillanmäki, L., Koivisto, M., Saarela, C., Häggqvist, A., Laine, M., & Hämäläinen, H. (2000). The effects of memory load on event-related EEG desynchronization and synchronization. *Clinical neurophysiology, 111*(11), 2071-2078.

Krüger, B., Zabicki, A., Grosse, L., Naumann, T., & Munzert, J. (2020). Sensory features of mental images in the framework of human actions. *Consciousness and Cognition, 83*, 102970.

Kubota, Y., Sato, W., Toichi, M., Murai, T., Okada, T., Hayashi, A., & Sengoku, A. (2001). Frontal midline theta rhythm is correlated with cardiac autonomic activities during the performance of an attention demanding meditation procedure. *Cognitive brain research, 11*(2), 281-287.

Kuhl, P. K., & Meltzoff, A. N. (1996). Infant vocalizations in response to speech: Vocal imitation and developmental change. *The journal of the Acoustical Society of America, 100*(4), 2425-2438.

Kuhlman, W. N. (1978). Functional topography of the human mu rhythm. *Electroencephalography and clinical neurophysiology, 44*(1), 83-93.

La Fougere, C., Zwergal, A., Rominger, A., Förster, S., Fesl, G., Dieterich, M., Brandt, T., Strupp, M., & Jahn, K. (2010). Real versus imagined locomotion: a [18F]-FDG PET-fMRI comparison. *Neuroimage, 50*(4), 1589-1598.

Lacourse, M. G., Orr, E. L., Cramer, S. C., & Cohen, M. J. (2005). Brain activation during execution and motor imagery of novel and skilled sequential hand movements. *Neuroimage, 27*(3), 505-519.

Ladouce, S., Donaldson, D. I., Dudchenko, P. A., & Ietswaart, M. (2017). Understanding minds in real-world environments: toward a mobile cognition approach. *Frontiers in human neuroscience, 10*, 694.

Ladouce, S., Donaldson, D. I., Dudchenko, P. A., & Ietswaart, M. (2019). Mobile EEG identifies the re-allocation of attention during real-world activity. *Scientific reports, 9*(1), 1-10.

LaFleur, K., Cassady, K., Doud, A., Shades, K., Rogin, E., & He, B. (2013). Quadcopter control in three-dimensional space using a noninvasive motor imagery-based brain–computer interface. *Journal of neural engineering, 10*(4), 046003.

Land, M. F. (2006). Eye movements and the control of actions in everyday life. *Progress in retinal and eye research, 25*(3), 296-324.

Land, M. F., & Lee, D. N. (1994). Where we look when we steer. *Nature*, *369*(6483), 742-744.

Land, M. F., & McLeod, P. (2000). From eye movements to actions: how batsmen hit the ball. *Nature neuroscience, 3*(12), 1340-1345.

Land, M., Mennie, N., & Rusted, J. (1999). The roles of vision and eye movements in the control of activities of daily living. *Perception, 28*(11), 1311-1328.

Landers, D. M., Petruzzello, S. J., Salazar, W., Crews, D. J., Kubitz, K. A., Gannon, T. L., & Han, M. (1991). The influence of electrocortical biofeedback on performance in pre-elite archers. *Medicine & Science in Sports & Exercise.*

Lawrence, G., Callow, N., & Roberts, R. (2013). Watch me if you can: imagery ability moderates observational learning effectiveness. *Frontiers in human neuroscience, 7*, 522.

Leeb, R., Friedman, D., Müller-Putz, G. R., Scherer, R., Slater, M., & Pfurtscheller, G. (2007). Self-paced (asynchronous) BCI control of a wheelchair in virtual environments: a case study with a tetraplegic. *Computational intelligence and neuroscience, 2007.*

Leocani, L., Toro, C., Zhuang, P., Gerloff, C., & Hallett, M. (2001). Event-related desynchronization in reaction time paradigms: a comparison with event-related potentials and corticospinal excitability. *Clinical Neurophysiology, 112*(5), 923-930.

Leuthardt, E. C., Schalk, G., Roland, J., Rouse, A., & Moran, D. W. (2009). Evolution of brain-computer interfaces: going beyond classic motor physiology. *Neurosurgical focus, 27*(1), E4.

Liebe, S., Hoerzer, G. M., Logothetis, N. K., & Rainer, G. (2012). Theta coupling between V4 and prefrontal cortex predicts visual short-term memory performance. *Nature neuroscience*, *15*(3), 456-462.

Liebrand, M., Pein, I., Tzvi, E., & Krämer, U. M. (2017). Temporal dynamics of proactive and reactive motor inhibition. *Frontiers in human neuroscience, 11*, 204.

Liepmann, H. (1900). The syndrome of apraxia (motor asymboly) based on a case of unilateral apraxia. (Translated by WHO Bohne, K. Liepmann, & DA Rottenberg from Monatschrift für Psychiatrie und Neurologie 1900, 8, 15–44). *Neurological classics in modern translation. New York: Hafner*.

Liepmann, H. (1920). Apraxia. *Ergebnisse der Gesamten Medizin, 1*, 516-523.

Little, S., & Brown, P. (2014). The functional role of beta oscillations in Parkinson's disease. *Parkinsonism & related disorders*, *20*, S44-S48.

Liu, Y. H., Lin, L. F., Chou, C. W., Chang, Y., Hsiao, Y. T., & Hsu, W. C. (2019). Analysis of electroencephalography event-related desynchronisation and synchronisation induced by lower-limb stepping motor imagery. *Journal of Medical and Biological Engineering*, *39*(1), 54-69.

Logan, D., Kiemel, T., Dominici, N., Cappellini, G., Ivanenko, Y., Lacquaniti, F., & Jeka, J. J. (2010). The many roles of vision during walking. *Experimental brain research, 206*(3), 337-350.

Lopez-Gordo, M. A., Sanchez-Morillo, D., & Valle, F. P. (2014) Dry EEG electrodes. *Sensors, 14*(7), 12847-12870.

Lorey, B., Bischoff, M., Pilgramm, S., Stark, R., Munzert, J., & Zentgraf, K. (2009). The embodied nature of motor imagery: the influence of posture and perspective. *Experimental brain research, 194*(2), 233-243.

Lotze, M., Montoya, P., Erb, M., Hülsmann, E., Flor, H., Klose, U., Birbaumer, N., & Grodd, W. (1999). Activation of cortical and cerebellar motor areas during executed and imagined hand movements: an fMRI study. *Journal of cognitive neuroscience, 11*(5), 491-501.

Lotze, R. H. (1852). *Medicinische Psychologie oder Physiologie der Seele. Von Dr. Rudolph Hermann Lotze Professor in Göttingen.* Weidmann'sche Buchhandlung.

Louis, M., Collet, C., & Guillot, A. (2011). Differences in motor imagery times during aroused and relaxed conditions. *Journal of Cognitive Psychology, 23*(3), 374-382.

Luchsinger, H., Sandbakk, Ø., Schubert, M., Ettema, G., & Baumeister, J. (2016). A comparison of frontal theta activity during shooting among biathletes and cross-country skiers before and after vigorous exercise. *PLoS One, 11*(3), e0150461.

Luft, A. R., Smith, G. V., Forrester, L., Whitall, J., Macko, R. F., Hauser, T. K., Hauser, A. P., & Hanley, D. F. (2002). Comparing brain activation associated with isolated upper and lower limb movement across corresponding joints. *Human brain mapping, 17*(2), 131-140.

Lütkenhöner, B., Menninghaus, E., Steinsträter, O., Wienbruch, C., Gißler, H. M., & Elbert, T. (1995). Neuromagnetic source analysis using magnetic resonance images for the construction of source and volume conductor model. *Brain Topography, 7*(4), 291-299.

Luu, P., & Tucker, D. M. (2001). Regulating action: alternating activation of midline frontal and motor cortical networks. *Clinical neurophysiology, 112*(7), 1295-1306.

Luu, P., Tucker, D. M., & Makeig, S. (2004). Frontal midline theta and the error-related negativity: neurophysiological mechanisms of action regulation. *Clinical neurophysiology, 115*(8), 1821-1835.

Luu, P., Tucker, D. M., Derryberry, D., Reed, M., & Poulsen, C. (2003). Electrophysiological responses to errors and feedback in the process of action regulation. *Psychological Science, 14*(1), 47-53.

Luu, T. P., Brantley, J. A., Nakagome, S., Zhu, F., & Contreras-Vidal, J. L. (2017). Electrocortical correlates of human level-ground, slope, and stair walking. *PloS one, 12*(11), e0188500.

MacIntyre, T. E., Madan, C. R., Moran, A. P., Collet, C., & Guillot, A. (2018). Motor imagery, performance and motor rehabilitation. *Progress in brain research, 240,* 141-159.

MacLean, P. D., & Delgado, J. R. (1953). Electrical and chemical stimulation of frontotemporal portion of limbic system in the waking animal. *Electroencephalography and clinical neurophysiology, 5*(1), 91-100.

Macuga, K. L., & Frey, S. H. (2012). Neural representations involved in observed, imagined, and imitated actions are dissociable and hierarchically organized. *Neuroimage, 59*(3), 2798-2807.

Macuga, K. L., Papailiou, A. P., & Frey, S. H. (2012). Motor imagery of tool use: relationship to actual use and adherence to Fitts' law across tasks. *Experimental brain research, 218*(2), 169-179.

Maeda, F., Kleiner-Fisman, G., & Pascual-Leone, A. (2002). Motor facilitation while observing hand actions: specificity of the effect and role of observer's orientation. *Journal of neurophysiology, 87*(3), 1329-1335.

Maidan, I., Shustak, S., Sharon, T., Bernad-Elazari, H., Geffen, N., Giladi, N., Hausdorf, J. M., & Mirelman, A. (2018). Prefrontal cortex activation during obstacle negotiation: what's the effect size and timing?. *Brain and cognition, 122,* 45-51.

Makeig, S., & Jung, T. P. (1995). Changes in alertness are a principal component of variance in the EEG spectrum. *NeuroReport-International Journal for Rapid Communications of Research in Neuroscience, 7*(1), 213-216.

Makeig, S., Bell, A. J., Jung, T. P., & Sejnowski, T. J. (1996) Independent component analysis of electroencephalographic data. In Advances in neural information processing systems (pp. 145-151).

Makeig, S., Debener, S., Onton, J., & Delorme, A. (2004). Mining event-related brain dynamics. *Trends in cognitive sciences, 8*(5), 204-210.

Makeig, S., Gramann, K., Jung, T. P., Sejnowski, T. J., & Poizner, H. (2009). Linking brain, mind and behavior. *International Journal of psychophysiology, 73*(2), 95-100.

Makeig, S., Westerfield, M., Jung, T. P., Enghoff, S., Townsend, J., Courchesne, E., & Sejnowski, T. J. (2002). Dynamic brain sources of visual evoked responses. *Science, 295*(5555), 690-694.

Malouin, F., & Richards, C. L. (2010). Mental practice for relearning locomotor skills. Physical therapy, 90(2), 240-251.

Malouin, F., Richards, C. L., Jackson, P. L., Dumas, F., & Doyon, J. (2003). Brain activations during motor imagery of locomotor-related tasks: A PET study. *Human brain mapping, 19*(1), 47-62.

Menicucci, D., Di Gruttola, F., Cesari, V., Gemignani, A., Manzoni, D., & Sebastiani, L. (2020). Task-independent electrophysiological correlates of motor imagery ability from kinaesthetic and visual perspectives. *Neuroscience, 443*, 176-187.

Marder, E., & Bucher, D. (2001). Central pattern generators and the control of rhythmic movements. *Current biology, 11*(23), R986-R996.

Marigold, D. S., & Drew, T. (2017). Posterior parietal cortex estimates the relationship between object and body location during locomotion. *Elife, 6*, e28143.

Mars, R. B., Piekema, C., Coles, M. G., Hulstijn, W., & Toni, I. (2007) On the programming and reprogramming of actions. *Cerebral Cortex, 17*(12), 2972-2979.

Marshall, B., Wright, D. J., Holmes, P. S., & Wood, G. (2019). Combining action observation and motor imagery improves eye–hand Coordination during novel Visuomotor task performance. *Journal of motor behavior*.

Marshall, P. J., & Meltzoff, A. N. (2015). Body maps in the infant brain. *Trends in CognitiveSciences, 19*(9), 499-505.

Martin, A., & Chao, L. L. (2001). Semantic memory and the brain: structure and processes. *Current opinion in neurobiology, 11*(2), 194-201.

Martineau, J., Cochin, S., Magne, R., & Barthelemy, C. (2008). Impaired cortical activation in autistic children: is the mirror neuron system involved?. *International Journal of Psychophysiology, 68*(1), 35-40.

Massar, S. A., Kenemans, J. L., & Schutter, D. J. (2014). Resting-state EEG theta activity and risk learning: sensitivity to reward or punishment?. *International Journal of Psychophysiology, 91*(3), 172-177.

Mattar, A. A., & Gribble, P. L. (2005). Motor learning by observing. *Neuron, 46*(1), 153-160.

Mavros, P., Austwick, M. Z., & Smith, A. H. (2016). Geo-EEG: towards the use of EEG in the study of urban behaviour. *Applied Spatial Analysis and Policy, 9*(2), 191-212.

McCarthy, M. M., Moore-Kochlacs, C., Gu, X., Boyden, E. S., Han, X., & Kopell, N. (2011). Striatal origin of the pathologic beta oscillations in Parkinson's disease. *Proceedings of the National Academy of Sciences, 108*(28), 11620-11625.

McFadyen, B. J., Bouyer, L., Bent, L. R., & Inglis, J. T. (2007). Visual-vestibular influences on locomotor adjustments for stepping over an obstacle. *Experimental brain research, 179*(2), 235-243.

McFadyen, B. J., Gagné, M. È., Cossette, I., & Ouellet, M. C. (2017). Using dual task walking as an aid to assess executive dysfunction ecologically in neurological populations: a narrative review. *Neuropsychological rehabilitation, 27*(5), 722-743.

McFarland, D. J., Miner, L. A., Vaughan, T. M., & Wolpaw, J. R. (2000). Mu and beta rhythm topographies during motor imagery and actual movements. *Brain topography, 12*(3), 177-186.

McFarland, D., & Wolpaw, J. R. (2017). EEG-based brain–computer interfaces. *Current opinion in Biomedical Engineering, 4*, 194-200.

McInnes, K., Friesen, C., & Boe, S. (2016). Specific brain lesions impair explicit motor imagery ability: a systematic review of the evidence. *Archives of physical medicine and rehabilitation, 97*(3), 478-489.

Mehta, J. P., Verber, M. D., Wieser, J. A., Schmit, B. D., & Schindler-Ivens, S. M. (2009). A novel technique for examining human brain activity associated with pedaling using fMRI. *Journal of neuroscience methods, 179*(2), 230-239.

Meijer, D., Te Woerd, E., & Praamstra, P. (2016). Timing of beta oscillatory synchronization and temporal prediction of upcoming stimuli. *NeuroImage, 138*, 233-241.

Meijer, O. G., & Roth, K. (Eds.). (1988). *Complex movement behaviour:'The'motor-action controversy*. Elsevier.

Mele, M. L., & Federici, S. (2012). Gaze and eye-tracking solutions for psychological research. *Cognitive processing, 13*(1), 261-265.

Meltzoff, A. N. (1988). Imitation, objects, tools, and the rudiments of language in human ontogeny. *Human evolution, 3*(1-2), 45-64.

Meltzoff, A. N. (1996). The human infant as imitative generalist: A 20-year progress report on infant imitation with implications for comparative psychology. Social learning in animals: *The roots of culture*, 347-370.

Meltzoff, A. N. (2017). Elements of a comprehensive theory of infant imitation. *Behavioral and Brain Sciences, 40*.

Meltzoff, A. N., & Moore, M. K. (1983). The origins of imitation in infancy: Paradigm, phenomena, and theories. *Advances in infancy research*.

Meltzoff, A. N., & Prinz, W. (Eds.). (2002). *The imitative mind:Development, evolution and brain bases* (Vol. 6). Cambridge University Press.

Menicucci, D., Di Gruttola, F., Cesari, V., Gemignani, A., Manzoni, D., & Sebastiani, L. (2020). Task-independent electrophysiological correlates of motor imagery ability from kinaesthetic and visual perspectives. *Neuroscience, 443*, 176-187.

Mennie, N., Hayhoe, M., & Sullivan, B. (2007). Look-ahead fixations: anticipatory eye movements in natural tasks. *Experimental brain research, 179*(3), 427-442.

Miall, R. C., & Wolpert, D. M. (1996). Forward models for physiological motor control. *Neural networks, 9*(8), 1265-1279.

Michel, C. M., Kaufman, L., & Williamson, S. J. (1994). Duration of EEG and MEG α suppression increases with angle in a mental rotation task. *Journal of cognitive neuroscience, 6*(2), 139-150.

Mihara, M., Hattori, N., Hatakenaka, M., Yagura, H., Kawano, T., Hino, T., & Miyai, I. (2013). Near-infrared spectroscopy–mediated neurofeedback enhances efficacy of motor imagery–based training in poststroke victims: a pilot study. *Stroke, 44*(4), 1091-1098.

Millan, J., Ferrez, P. W., Galán, F., Lew, E., & Chavarriaga, R. (2008). Non-invasive brain-machine interaction. *International Journal of Pattern Recognition and Artificial Intelligence, 22*(05), 959-972.

Miller, E. K., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual review of neuroscience, 24*(1), 167-202.

Miller, G. A. (1956). The magical number seven, plus or minus two: Some limits on our capacity for processing information. *Psychological review, 63*(2), 81.

Miller, G. A., Galanter, E., & Pribram, K. H. (1960a). The unit of analysis.

Miller, G. A., Galanter, E., & Pribram, K. H. (1960b). The integration of plans.

Miller, K. J., Schalk, G., Fetz, E. E., den Nijs, M., Ojemann, J. G., & Rao, R. P. (2010). Cortical activity during motor execution, motor imagery, and imagery-based online feedback. *Proceedings of the National Academy of Sciences, 107*(9), 4430-4435.

Miyai, I., Tanabe, H. C., Sase, I., Eda, H., Oda, I., Konishi, I., Tsunazawa, Y., Suzuki, T., Yanagida, T., & Kubota, K. (2001). Cortical mapping of gait in humans: a near-infrared spectroscopic topography study. *Neuroimage*, *14*(5), 1186-1192.

Mizuguchi, N., Nakamura, M., & Kanosue, K. (2017). Task-dependent engagements of the primary visual cortex during kinesthetic and visual motor imagery. *Neuroscience letters, 636,* 108-112.

Mizuguchi, N., Yamagishi, T., Nakata, H., & Kanosue, K. (2015). The effect of somatosensory input on motor imagery depends upon motor imagery capability. *Frontiers in psychology, 6*, 104.

Mizuki, Y., Takii, O., Tanaka, T., Tanaka, M., & Inanaga, K. (1982). Periodic appearance of frontal midline theta activity during performance of a sensory-motor task. *Psychiatry and Clinical Neurosciences, 36*(4), 375-382.

Mognon, A., Jovicich, J., Bruzzone, L., & Buiatti, M. (2011). ADJUST: An automatic EEG artifact detector based on the joint use of spatial and temporal features. *Psychophysiology, 48*(2), 229-240.

Mohler, B. J., Thompson, W. B., Creem-Regehr, S. H., Pick, H. L., & Warren, W. H. (2007). Visual flow influences gait transition speed and preferred walking speed. *Experimental brain research, 181*(2), 221-228.

Montero-Odasso, M., Oteng-Amoako, A., Speechley, M., Gopaul, K., Beauchet, O., Annweiler, C., & Muir-Hunter, S. W. (2014). The motor signature of mild cognitive impairment: results from the gait and brain study. Journals of Gerontology Series A: *Biomedical Sciences and Medical Sciences, 69*(11), 1415-1421.

Moosmann, M., Ritter, P., Krastel, I., Brink, A., Thees, S., Blankenburg, F., Taskin, B., Obrig, H., & Villringer, A. (2003). Correlates of alpha rhythm in functional magnetic resonance imaging and near infrared spectroscopy. *Neuroimage, 20*(1), 145-158.

Mowbray, R., & Cowie, D. (2020). Mind your step: learning to walk in complex environments. *Experimental brain research, 238*, 1455-1465.

Mulder, T. (2007). Motor imagery and action observation: cognitive tools for rehabilitation. *Journal of neural transmission, 114*(10), 1265-1278.

Müller-Putz, G. R., Kaiser, V., Solis-Escalante, T., & Pfurtscheller, G. (2010). Fast set-up asynchronous brain-switch based on detection of foot motor imagery in 1-channel EEG. *Medical & biological engineering & computing, 48*(3), 229-233.

Mundy-Castle, A. C. (1957). The electroencephalogram and mental activity. *Electroencephalography and clinical neurophysiology, 9*(4), 643-655.

Munzert, J., Lorey, B., & Zentgraf, K. (2009). Cognitive motor processes: the role of motor imagery in the study of motor representations. *Brain research reviews, 60*(2), 306-326.

Muthukumaraswamy, S. D., & Johnson, B. W. (2004a). Primary motor cortex activation during action observation revealed by wavelet analysis of the EEG. *Clinical Neurophysiology*, *115*(8), 1760-1766.

Muthukumaraswamy, S. D., & Johnson, B. W. (2004b). Changes in rolandic mu rhythm during observation of a precision grip. *Psychophysiology*, *41*(1), 152-156.

Muthukumaraswamy, S. D., Johnson, B. W., & McNair, N. A. (2004). Mu rhythm modulation during observation of an object-directed grasp. *Cognitive brain research*, *19*(2), 195-201.

Nadel, J., & Butterworth, G. (Eds.). (1999). *Imitation in infancy* (Vol. 16). Cambridge: Cambridge University Press.

Naish, K. R., Houston-Price, C., Bremner, A. J., & Holmes, N. P. (2014). Effects of action observation on corticospinal excitability: Muscle specificity, direction, and timing of the mirror response. *Neuropsychologia*, *64*, 331-348.

Naito, E., Kochiyama, T., Kitada, R., Nakamura, S., Matsumura, M., Yonekura, Y., & Sadato, N. (2002). Internally simulated movement sensations during motor imagery activate cortical motor areas and the cerebellum. *Journal of Neuroscience*, *22*(9), 3683-3691.

Nakagawa, K., Aokage, Y., Fukuri, T., Kawahara, Y., Hashizume, A., Kurisu, K., & Yuge, L. (2011). Neuromagnetic beta oscillation changes during motor imagery and motor execution of skilled movements. *Neuroreport*, *22*(5), 217-222.

Nakashima, K., & Sato, H. (1993). Relationship between frontal midline theta activity in EEG and concentration. *Journal of human ergology*, *22*(1), 63-67.

Nam, C. S., Jeon, Y., Kim, Y. J., Lee, I., & Park, K. (2011). Movement imagery-related lateralization of event-related (de) synchronization (ERD/ERS): motor-imagery duration effects. *Clinical Neurophysiology*, *122*(3), 567-577.

Negri, G. A., Rumiati, R. I., Zadini, A., Ukmar, M., Mahon, B. Z., & Caramazza, A. (2007). What is the role of motor simulation in action and object recognition? Evidence from apraxia. *Cognitive neuropsychology, 24*(8), 795-816.

Neisser, U. (1979). The concept of intelligence. *Intelligence, 3*(3), 217-227.

Nelson, A. B., Moisello, C., Lin, J., Panday, P., Ricci, S., Canessa, A., Di Rocco, A., Quartarone, A., Frazzitta, G., Isaias, I. U., Tononi, G., Cirelli, C., & Ghilardi, M. F. (2017). Beta oscillatory changes and retention of motor skills during practice in healthy subjects and in patients with Parkinson's disease. *Frontiers in human neuroscience, 11*, 104.

Neuper, C., & Pfurtscheller, G. (1998). 134 ERD/ERS based brain computer interface (BCI): effects of motor imagery on sensorimotor rhythms. *International Journal of Psychophysiology, 1*(30), 53-54.

Neuper, C., & Pfurtscheller, G. (2001). Event-related dynamics of cortical rhythms: frequency-specific features and functional correlates. *International journal of psychophysiology, 43*(1), 41-58.

Neuper, C., Scherer, R., Reiner, M., & Pfurtscheller, G. (2005). Imagery of motor actions: Differential effects of kinesthetic and visual–motor mode of imagery in single-trial EEG. *Cognitive brain research, 25*(3), 668-677.

Neuper, C., Schlögl, A., & Pfurtscheller, G. (1999). Enhancement of left-right sensorimotor EEG differences during feedback-regulated motor imagery. *Journal of Clinical Neurophysiology, 16*(4), 373-382.

Neuper, C., Wörtz, M., & Pfurtscheller, G. (2006). ERD/ERS patterns reflecting sensorimotor activation and deactivation. *Progress in brain research, 159*, 211-222.

Niedermeyer, E. (1997). Alpha rhythms as physiological and abnormal phenomena. *International Journal of Psychophysiology, 26*(1-3), 31-49.

Nielsen, J. B. (2003). How we walk: central control of muscle activity during human walking. *The Neuroscientist, 9*(3), 195-204.

Nishimura, K., Ohta, M., Saito, M., Morita-Isogai, Y., Sato, H., Kuramoto, E., Yin, D. X., Maeda, Y., Kaneko, T., Yamashiro, T., Takada, K., Bae Oh, S., Toyoda, H., & Kang, Y. (2018). Electrophysiological and morphological properties of α and γ motoneurons in the rat trigeminal motor nucleus. *Frontiers in cellular neuroscience, 12*, 9.

Nordin, A. D., Hairston, W. D., & Ferris, D. P. (2019). Human electrocortical dynamics while stepping over obstacles. *Scientific reports*, *9*(1), 1-12.

Nozaradan, S., Zerouali, Y., Peretz, I., & Mouraux, A. (2015). Capturing with EEG the neural entrainment and coupling underlying sensorimotor synchronization to the beat. *Cerebral Cortex*, *25*(3), 736-747.

Nunez, P. L., & Srinivasan, R. (2006). A theoretical basis for standing and traveling brain waves measured with human EEG with implications for an integrated consciousness. *Clinical neurophysiology*, *117*(11), 2424-2435.

O'Shea, H., & Moran, A. (2017). Does motor simulation theory explain the cognitive mechanisms underlying motor imagery? A critical review. *Frontiers in Human Neuroscience, 11*, 72.

Oberman, L. M., McCleery, J. P., Hubbard, E. M., Bernier, R., Wiersema, J. R., Raymaekers, R., & Pineda, J. A. (2013). Developmental changes in mu suppression to observed and executed actions in autism spectrum disorders. *Social cognitive and affective neuroscience*, *8*(3), 300-304.

Obleser, J., & Kayser, C. (2019). Neural entrainment and attentional selection in the listening brain. *Trends in cognitive sciences*, *23*(11), 913-926.

Ochipa, C., Rothi, L. G., & Heilman, K. M. (1989). Ideational apraxia: A deficit in tool selection and use. *Annals of Neurology: Official Journal of the American Neurological Association and the Child Neurology Society*, *25*(2), 190-193.

Olsson, C. J., & Nyberg, L. (2010). Motor imagery: if you can't do it, you won't think it. *Scandinavian journal of medicine & science in sports, 20*(5), 711-715.

Onton, J., Delorme, A., & Makeig, S. (2005). Frontal midline EEG dynamics during working memory. *Neuroimage, 27*(2), 341-356.

Orlandi, A., Arno, E., & Proverbio, A. M. (2020). The effect of expertise on kinesthetic motor imagery of complex actions. *Brain topography, 33*(2), 238-254.

Osipova, D., Takashima, A., Oostenveld, R., Fernández, G., Maris, E., & Jensen, O. (2006). Theta and gamma oscillations predict encoding and retrieval of declarative memory. *Journal of neuroscience, 26*(28), 7523-7531.

Page, S. J. (2000). Imagery improves upper extremity motor function in chronic stroke patients: a pilot study. *The Occupational Therapy Journal of Research, 20*(3), 200-215.

Page, S. J., Levine, P., & Leonard, A. (2007). Mental practice in chronic stroke: results of a randomized, placebo-controlled trial. *Stroke, 38*(4), 1293-1297.

Page, S. J., Levine, P., Sisto, S., & Johnston, M. V. (2001). A randomized efficacy and feasibility study of imagery in acute stroke. *Clinical rehabilitation, 15*(3), 233-240.

Parasuraman, R., & Rizzo, M. (Eds.). (2008). *Neuroergonomics: The brain at work*. Oxford University Press.

Park, J. L., & Donaldson, D. I. (2019) Detecting the neural correlates of episodic memory with mobile EEG: Recollecting objects in the real world. *NeuroImage, 193*, 1-9.

Park, J. L., Dudchenko, P. A., & Donaldson, D. I. (2018). Navigation in real-world environments: New opportunities afforded by advances in mobile brain imaging. *Frontiers in Human Neuroscience, 12*, 361.

Park, J. L., Fairweather, M. M., & Donaldson, D. I. (2015). Making the case for mobile cognition: EEG and sports performance. *Neuroscience & Biobehavioral Reviews, 52*, 117-130.

Parsons, L. M. (1987). Imagined spatial transformations of one's hands and feet. *Cognitive psychology, 19*(2), 178-241.

Parsons, L. M. (1994). Temporal and kinematic properties of motor behavior reflected in mentally simulated action. *Journal of Experimental Psychology: Human Perception and Performance, 20*(4), 709.

Pascual-Leone, A., Amedi, A., Fregni, F., & Merabet, L. B. (2005). The plastic human brain cortex. *Annual Review of Neuroscience, 28,* 377-401.

Patel, P., Lamar, M., & Bhatt, T. (2014). Effect of type of cognitive task and walking speed on cognitive-motor interference during dual-task walking. *Neuroscience, 260,* 140-148.

Patla, A. E., & Vickers, J. N. (1997). Where and when do we look as we approach and step over an obstacle in the travel path?. *Neuroreport, 8*(17), 3661-3665.

Pazzaglia, M., Smania, N., Corato, E., & Aglioti, S. M. (2008). Neural underpinnings of gesture discrimination in patients with limb apraxia. *Journal of Neuroscience, 28*(12), 3030-3041.

Pelosin, E., Avanzino, L., Bove, M., Stramesi, P., Nieuwboer, A., & Abbruzzese, G. (2010). Action observation improves freezing of gait in patients with Parkinson’s disease. *Neurorehabilitation and neural repair, 24*(8), 746-752.

Penfield, W., & Jasper, H. (1954). Epilepsy and the functional anatomy of the human brain.

Peniston, E. G., & Kulkosky, P. J. (1991). Alpha-theta brainwave neurofeedback for Vietnam veterans with combat-related post-traumatic stress disorder. *Medical Psychotherapy, 4*(1), 47-60.

Perfetti, B., Moisello, C., Landsness, E. C., Kvint, S., Lanzafame, S., Onofrj, M., Di Rocco, A., Tononi, G., & Ghilardi, M. F. (2011). Modulation of gamma and theta spectral amplitude and phase synchronization is associated with the development of visuo-motor learning. *Journal of Neuroscience, 31*(41), 14810-14819.

Perry, J., & Davids, J. R. (1992). Gait analysis: normal and pathological function. *Journal of Pediatric Orthopaedics, 12*(6), 815.

Petersen, N., Christensen, L. O. D., Morita, H., Sinkjær, T., & Nielsen, J. (1998). Evidence that a transcortical pathway contributes to stretch reflexes in the tibialis anterior muscle in man. *The Journal of physiology, 512*(1), 267-276.

Petersen, T. H., Willerslev-Olsen, M., Conway, B. A., & Nielsen, J. B. (2012). The motor cortex drives the muscles during walking in human subjects. *The Journal of physiology*, *590*(10), 2443-2452.

Peterson, D. S., & Horak, F. B. (2016) Neural control of walking in people with parkinsonism. *Physiology, 31*(2), 95-107.

Peterson, D. S., King, L. A., Cohen, R. G., & Horak, F. B. (2016). Cognitive contributions to freezing of gait in Parkinson disease: implications for physical rehabilitation. *Physical therapy*, *96*(5), 659-670.

Peterson, S. M., & Ferris, D. P. (2018). Differentiation in theta and beta electrocortical activity between visual and physical perturbations to walking and standing balance. *eneuro, 5*(4).

Pezzulo, G., & Ognibene, D. (2012) Proactive action preparation: Seeing action preparation as a continuous and proactive process. *Motor control, 16*(3), 386-424.

Pezzulo, G., Donnarumma, F., & Dindo, H. (2013). Human sensorimotor communication: A theory of signaling in online social interactions. *PloS one*, *8*(11), e79876.

Pezzulo, G., Donnarumma, F., Dindo, H., D'Ausilio, A., Konvalinka, I., & Castelfranchi, C. (2019). The body talks: Sensorimotor communication and its brain and kinematic signatures. *Physics of life reviews*, *28*, 1-21.

Pfurtscheller, G. (1989). Functional topography during sensorimotor activation studied with event-related desynchronization mapping. *Journal of clinical neurophysiology: official publication of the American Electroencephalographic Society*, *6*(1), 75-84.

Pfurtscheller, G. (1992). Event-related synchronization (ERS): an electrophysiological correlate of cortical areas at rest. *Electroencephalography and clinical neurophysiology*, *83*(1), 62-69.

Pfurtscheller, G. (1999). Event-related desynchronization and related oscillatory phenomena of the brain. *Handbook of electroencephalography and clinical neurophysiology*.

Pfurtscheller, G. (2001). Functional brain imaging based on ERD/ERS. *Vision research, 41*(10-11), 1257-1260.

Pfurtscheller, G., & Aranibar, A. (1977). Event-related cortical desynchronization detected by power measurements of scalp EEG. *Electroencephalography and clinical neurophysiology, 42*(6), 817-826.

Pfurtscheller, G., & Aranibar, A. (1979). Evaluation of event-related desynchronization (ERD) preceding and following voluntary self-paced movement. *Electroencephalography and clinical neurophysiology, 46*(2), 138-146.

Pfurtscheller, G., & Berghold, A. (1989). Patterns of cortical activation during planning of voluntary movement. *Electroencephalography and clinical neurophysiology, 72*(3), 250-258.

Pfurtscheller, G., & Da Silva, F. L. (1999). Event-related EEG/MEG synchronization and desynchronization: basic principles. *Clinical neurophysiology, 110*(11), 1842-1857.

Pfurtscheller, G., & Klimesch, W. (1992). Event-related synchronization and desynchronization of alpha and beta waves in a cognitive task. In *Induced rhythms in the brain* (pp. 117-128). Birkhäuser, Boston, MA.

Pfurtscheller, G., & Lopes da Silva, F. H. (1999). Functional meaning of event-related desynchronization (ERD) end synchronization (ERS).

Pfurtscheller, G., & Neuper, C. (1994). Event-related synchronization of mu rhythm in the EEG over the cortical hand area in man. *Neuroscience letters, 174*(1), 93-96.

Pfurtscheller, G., & Neuper, C. (1997). Motor imagery activates primary sensorimotor area in humans. *Neuroscience letters, 239*(2-3), 65-68.

Pfurtscheller, G., & Solis-Escalante, T. (2009) Could the beta rebound in the EEG be suitable to realize a “brain switch”?. *Clinical Neurophysiology, 120*(1), 24-29.

Pfurtscheller, G., Brunner, C., Schlögl, A., & Da Silva, F. L. (2006a). Mu rhythm (de) synchronization and EEG single-trial classification of different motor imagery tasks. *NeuroImage, 31*(1), 153-159.

Pfurtscheller, G., Leeb, R., Keinrath, C., Friedman, D., Neuper, C., Guger, C., & Slater, M. (2006b). Walking from thought. *Brain research*, *1071*(1), 145-152

Pfurtscheller, G., Graimann, B., Huggins, J. E., Levine, S. P., & Schuh, L. A. (2003). Spatiotemporal patterns of beta desynchronization and gamma synchronization in corticographic data during self-paced movement. *Clinical neurophysiology, 114*(7), 1226-1236.

Pfurtscheller, G., Neuper, C., & Krausz, G. (2000). Functional dissociation of lower and upper frequency mu rhythms in relation to voluntary limb movement. *Clinical neurophysiology, 111*(10), 1873-1879.

Pfurtscheller, G., Neuper, C., Andrew, C., & Edlinger, G. (1997). Foot and hand area mu rhythms. *International Journal of Psychophysiology, 26*(1-3), 121-135.

Pfurtscheller, G., Neuper, C., Brunner, C., & Da Silva, F. L. (2005). Beta rebound after different types of motor imagery in man. *Neuroscience letters, 378*(3), 156-159.

Pfurtscheller, G., Stancák Jr, A., & Neuper, C. (1996a) Post-movement beta synchronization. A correlate of an idling motor area?. *Electroencephalogr Clin Neurophysiol, 98*(4), 281-293.

Pfurtscheller, G., Stancák Jr, A., & Neuper, C. (1996b). Event-related synchronization (ERS) in the alpha band—an electrophysiological correlate of cortical idling: a review. *International journal of psychophysiology, 24*(1-2), 39-46.

Pfurtscheller, G., Woertz, M., Müller, G., Wriessnegger, S., & Pfurtscheller, K. (2002). Contrasting behavior of beta event-related synchronization and somatosensory evoked potential after median nerve stimulation during finger manipulation in man. *Neuroscience letters, 323*(2), 113-116.

Pineda, J. A. (2005). The functional significance of mu rhythms: translating “seeing” and “hearing” into “doing”. *Brain research reviews, 50*(1), 57-68.

Pion-Tonachini, L., Kreutz-Delgado, K., & Makeig, S. (2019). ICLabel: An automated electroencephalographic independent component classifier, dataset, and website. *NeuroImage, 198*, 181-197.

Pirker, W., & Katzenschlager, R. (2017). Gait disorders in adults and the elderly. *Wiener Klinische Wochenschrift, 129*(3), 81-95.

Plechawska-Wójcik, M., Tokovarov, M., Kaczorowska, M., & Zapała, D. (2019). A three-class classification of cognitive workload based on EEG spectral data. *Applied Sciences*, *9*(24), 5340.

Pobric, G., & Hamilton, A. F. D. C. (2006). Action understanding requires the left inferior frontal cortex. *Current Biology, 16*(5), 524-529.

Polich, J. (2007). Updating P300: an integrative theory of P3a and P3b. *Clinical neurophysiology, 118*(10), 2128-2148.

Porro, C. A., Facchin, P., Fusi, S., Dri, G., & Fadiga, L. (2007). Enhancement of force after action observation: behavioural and neurophysiological studies. *Neuropsychologia, 45*(13), 3114-3121.

Porro, C. A., Francescato, M. P., Cettolo, V., Diamond, M. E., Baraldi, P., Zuiani, C., Bazzocchi, M., & Di Prampero, P. E. (1996). Primary motor and sensory cortex activation during motor performance and motor imagery: a functional magnetic resonance imaging study. *Journal of Neuroscience, 16*(23), 7688-7698.

Presacco, A., Forrester, L. W., & Contreras-Vidal, J. L. (2012). Decoding intra-limb and inter-limb kinematics during treadmill walking from scalp electroencephalographic (EEG) signals. *IEEE Transactions on neural systems and rehabilitation engineering, 20*(2), 212-219.

Presacco, A., Goodman, R., Forrester, L., & Contreras-Vidal, J. L. (2011). Neural decoding of treadmill walking from noninvasive electroencephalographic signals. *Journal of neurophysiology*, *106*(4), 1875-1887.

Prinz, W., Heuer, H., & Sanders, A. (1987). Perspectives on perception and action.

Prokop, T., Schubert, M., & Berger, W. (1997). Visual influence on human locomotion modulation to changes in optic flow. *Experimental brain research, 114*(1), 63-70.

Proverbio, A. M. (2012). Tool perception suppresses 10–12 Hz μ rhythm of EEG over the somatosensory area. *Biological psychology, 91*(1), 1-7.

Ptak, R., Schnider, A., & Fellrath, J. (2017). The dorsal frontoparietal network: a core system for emulated action. *Trends in cognitive sciences*, *21*(8), 589-599.

Rao, S. M., Binder, J. R., Bandettini, P. A., Hammeke, T. A., Yetkin, F. Z., Jesmanowicz, A., ... & Hyde, J. S. (1993). Functional magnetic resonance imaging of complex human movements. *Neurology, 43*(11), 2311-2311.

Raymond, J., Varney, C., Parkinson, L. A., & Gruzelier, J. H. (2005). The effects of alpha/theta neurofeedback on personality and mood. *Cognitive brain research, 23*(2-3), 287-292.

Reed, E. S. (1982). An outline of a theory of action systems. *Journal of motor behavior, 14*(2), 98-134.

Reiser, J. E., Wascher, E., & Arnau, S. (2019). Recording mobile EEG in an outdoor environment reveals cognitive-motor interference dependent on movement complexity. *Scientific reports, 9*(1), 1-14.

Rhodes, E., Gaetz, W. C., Marsden, J., & Hall, S. D. (2018). Transient alpha and beta synchrony underlies preparatory recruitment of directional motor networks. *Journal of cognitive neuroscience, 30*(6), 867-875.

Rothi G., L. J., Ochipa, C., & Heilman, K. M. (1991). A cognitive neuropsychological model of limb praxis. *Cognitive Neuropsychology, 8*(6), 443-458.

Richards, C. L., Malouin, F., Wood-Dauphinee, S., Williams, J. I., Bouchard, J. P., & Brunet, D. (1993). Task-specific physical therapy for optimization of gait recovery in acute stroke patients. *Archives of physical medicine and rehabilitation, 74*(6), 612-620.

Richardson, D. C., Spivey, M. J., & Cheung, J. (2001). Motor Representations in Memory and Mental Models: Embodiement in Cognition. In *Proceedings of the Annual Meeting of the Cognitive Science Society* (Vol. 23, No. 23).

Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review Neuroscience, 27*, 169-192.

Rizzolatti, G., & Fadiga, L. (1998). Grasping objects and grasping action meanings: the dual role of monkey rostroventral premotor cortex (area F5). *Sensory guidance of movement, 218*, 81-103.

Rizzolatti, G., & Fogassi, L. (2014). The mirror mechanism: recent findings and perspectives. Philosophical Transactions of the Royal Society B: *Biological Sciences, 369*(1644), 20130420.

Rizzolatti, G., & Sinigaglia, C. (2010). The functional role of the parieto-frontal mirror circuit: interpretations and misinterpretations. *Nature reviews neuroscience, 11*(4), 264-274.

Rizzolatti, G., & Wolpert, D. M. (2005). Motor systems. *Current opinion in neurobiology, 6*(15), 623-625.

Rizzolatti, G., Camarda, R., Fogassi, L., Gentilucci, M., Luppino, G., & Matelli, M. (1988). Functional organization of inferior area 6 in the macaque monkey. *Experimental brain research, 71*(3), 491-507.

Rizzolatti, G., Craighero, L., & Fadiga, L. (2002). The mirror system in humans. *Advances in consciousness research, 42,* 37-62.

Rizzolatti, G., Fadiga, L., Fogassi, L., & Gallese, V. (1997). The space around us. *Science, 277*(5323), 190-191.

Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive brain research, 3*(2), 131-141.

Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature reviews neuroscience, 2*(9), 661-670.

Rizzolatti, G., Gentilucci, M., Fogassi, L., Luppino, G., Matelli, M., & Ponzoni-Maggi, S. (1987). Neurons related to goal-directed motor acts in inferior area 6 of the macaque monkey. *Experimental Brain Research, 67*(1), 220-224.

Roberts, R., Callow, N., Hardy, L., Markland, D., & Bringer, J. (2008). Movement imagery ability: development and assessment of a revised version of the vividness of movement imagery questionnaire. *Journal of Sport and Exercise Psychology, 30*(2), 200-221.

Rochat, M. J., Caruana, F., Jezzini, A., Intskirveli, I., Grammont, F., Gallese, V., Rizzolatti, G., & Umiltà, M. A. (2010). Responses of mirror neurons in area F5 to hand and tool grasping observation. *Experimental brain research, 204*(4), 605-616.

Roland, P. E., Larsen, B., Lassen, N. A., & Skinhoj, E. (1980). Supplementary motor area and other cortical areas in organization of voluntary movements in man. *Journal of neurophysiology, 43*(1), 118-136.

Romano Smith, S., Wood, G., Coyles, G., Roberts, J. W., & Wakefield, C. J. (2019). The effect of action observation and motor imagery combinations on upper limb kinematics and EMG during dart-throwing. *Scandinavian journal of medicine & science in sports, 29*(12), 1917-1929.

Ronnqvist, K. C., McAllister, C. J., Woodhall, G. L., Stanford, I. M., & Hall, S. D. (2013). A multimodal perspective on the composition of cortical oscillations. *Frontiers in human neuroscience, 7,* 132.

Roopun, A. K., Middleton, S. J., Cunningham, M. O., LeBeau, F. E., Bibbig, A., Whittington, M. A., & Traub, R. D. (2006). A beta2-frequency (20–30 Hz) oscillation in nonsynaptic networks of somatosensory cortex. *Proceedings of the National Academy of Sciences, 103*(42), 15646-15650.

Rosano, C., Aizenstein, H., Brach, J., Longenberger, A., Studenski, S., & Newman, A. B. (2008). Gait measures indicate underlying focal gray matter atrophy in the brain of older adults. *The Journals of Gerontology Series A*: *Biological Sciences and Medical Sciences, 63*(12), 1380-1388.

Rosenbaum, D. A. (2009). Human motor control. Academic press.

Rottschy, C., Langner, R., Dogan, I., Reetz, K., Laird, A. R., Schulz, J. B., Fox, P. T., & Eickhoff, S. B. (2012). Modelling neural correlates of working memory: a coordinate-based meta-analysis. *Neuroimage, 60*(1), 830-846.

Roy, E. A., Brown, L., Winchester, T., Square, P., Hall, C., & Black, S. (1993). Memory processes and gestural performance in apraxia. *Adapted Physical Activity Quarterly, 10*(4), 293-311.

Ruffino, C., Papaxanthis, C., & Lebon, F. (2017). Neural plasticity during motor learning with motor imagery practice: Review and perspectives. *Neuroscience, 341*, 61-78.

Ruggirello, S., Campioni, L., Piermanni, S., Sebastiani, L., & Santarcangelo, E. L. (2019). Does hypnotic assessment predict the functional equivalence between motor imagery and action?. *Brain and cognition, 136*, 103598.

Rumiati, R., & Tessari, A. (2002). Imitation of novel and well-known actions. *Experimental Brain Research, 142*(3), 425-433.

Sackett, R. S. (1934). The influence of symbolic rehearsal upon the retention of a maze habit. *The Journal of General Psychology, 10*(2), 376-398.

Sackett, R. S. (1935). The relationship between amount of symbolic rehearsal and retention of a maze habit. *The Journal of general psychology, 13*(1), 113-130.

Saimpont, A., Malouin, F., Tousignant, B., & Jackson, P. L. (2012). The influence of body configuration on motor imagery of walking in younger and older adults. *Neuroscience, 222*, 49-57.

Sakamoto, M., Muraoka, T., Mizuguchi, N., & Kanosue, K. (2009). Combining observation and imagery of an action enhances human corticospinal excitability. *Neuroscience research, 65*(1), 23-27.

Sakoe, H., & Chiba, S. (1978). Dynamic programming algorithm optimization for spoken word recognition. *IEEE transactions on acoustics, speech, and signal processing*, *26*(1), 43-49.

Salazar-Varas, R., Costa, Á., Iáñez, E., Úbeda, A., Hortal, E., & Azorín, J. M. (2015). Analyzing EEG signals to detect unexpected obstacles during walking. *Journal of neuroengineering and rehabilitation, 12*(1), 1-15.

Salenius, S., Kajola, M., Thompson, W. L., Kosslyn, S., & Hari, R. (1995). Reactivity of magnetic parieto-occipital alpha rhythm during visual imagery. *Electroencephalography and clinical neurophysiology, 95*(6), 453-462.

Salenius, S., Portin, K., Kajola, M., Salmelin, R., & Hari, R. (1997). Cortical control of human motoneuron firing during isometric contraction. *Journal of neurophysiology, 77*(6), 3401-3405.

Salmelin, R., Hámáaláinen, M., Kajola, M., & Hari, R. (1995). Functional segregation of movement-related rhythmic activity in the human brain. *Neuroimage, 2*(4), 237-243.

Saltzman, E., & Kelso, J. A. (1987). Skilled actions: a task-dynamic approach. *Psychological review, 94*(1), 84.

Sauseng, P., & Klimesch, W. (2008). What does phase information of oscillatory brain activity tell us about cognitive processes?. *Neuroscience & Biobehavioral Reviews, 32*(5), 1001-1013.

Sauseng, P., Klimesch, W., Freunberger, R., Pecherstorfer, T., Hanslmayr, S., & Doppelmayr, M. (2006). Relevance of EEG alpha and theta oscillations during task switching. *Experimental brain research, 170*(3), 295-301.

Sauseng, P., Klimesch, W., Schabus, M., & Doppelmayr, M. (2005). Fronto-parietal EEG coherence in theta and upper alpha reflect central executive functions of working memory. *International Journal of Psychophysiology, 57*(2), 97-103.

Savić, A., Lontis, R., Jiang, N., Popović, M., Farina, D., Dremstrup, K., & Mrachacz-Kersting, N. (2014). Movement related cortical potentials and sensory motor rhythms during self initiated and cued movements. In *Replace, Repair, Restore, Relieve–Bridging Clinical and Engineering Solutions in Neurorehabilitation* (pp. 701-707). Springer, Cham.

Sburlea, A. I., Montesano, L., & Minguez, J. (2015). Continuous detection of the self-initiated walking pre-movement state from EEG correlates without session-to-session recalibration. *Journal of neural engineering*, *12*(3), 036007.

Schack, B., Klimesch, W., & Sauseng, P. (2005). Phase synchronization between theta and upper alpha oscillations in a working memory task. *International Journal of Psychophysiology, 57*(2), 105-114.

Scheffers, M. K., Coles, M. G., Bernstein, P., Gehring, W. J., & Donchin, E. (1996). Event-related brain potentials and error-related processing: An analysis of incorrect responses to go and no-go stimuli. *Psychophysiology, 33*(1), 42-53.

Scherberger, H. (2009). Neural control of motor prostheses. *Current opinion in neurobiology, 19*(6), 629-633.

Schippers, M. B., & Keysers, C. (2011). Mapping the flow of information within the putative mirror neuron system during gesture observation. *Neuroimage, 57*(1), 37-44.

Schneider, W., & Shiffrin, R. M. (1977). Controlled and automatic human information processing: I. Detection, search, and attention. *Psychological review, 84*(1), 1.

Schnitzler, A., Salenius, S., Salmelin, R., Jousmäki, V., & Hari, R. (1997). Involvement of primary motor cortex in motor imagery: a neuromagnetic study. *Neuroimage, 6*(3), 201-208.

Schroeder, C. E., & Lakatos, P. (2009). Low-frequency neuronal oscillations as instruments of sensory selection. *Trends in neurosciences, 32*(1), 9-18.

Schubert, M., Bohner, C., Berger, W., Sprundel, M. V., & Duysens, J. E. J. (2003). The role of vision in maintaining heading direction: effects of changing gaze and optic flow on human gait. *Experimental brain research, 150*(2), 163-173.

Schubert, M., Curt, A., Jensen, L., & Dietz, V. (1997). Corticospinal input in human gait: modulation of magnetically evoked motor responses. *Experimental brain research, 115*(2), 234-246.

Schubert, R., Haufe, S., Blankenburg, F., Villringer, A., & Curio, G. (2009). Now you'll feel it, now you won't: EEG rhythms predict the effectiveness of perceptual masking. *Journal of cognitive neuroscience, 21*(12), 2407-2419.

Schwartz, M. F., Reed, E. S., Montgomery, M., Palmer, C., & Mayer, N. H. (1991). The quantitative description of action disorganisation after brain damage: A case study. *Cognitive Neuropsychology, 8*(5), 381-414.

Sederberg, P. B., Gauthier, L. V., Terushkin, V., Miller, J. F., Barnathan, J. A., & Kahana, M. J. (2006). Oscillatory correlates of the primacy effect in episodic memory. *NeuroImage, 32*(3), 1422-1431.

Sederberg, P. B., Kahana, M. J., Howard, M. W., Donner, E. J., & Madsen, J. R. (2003). Theta and gamma oscillations during encoding predict subsequent recall. *Journal of Neuroscience, 23*(34), 10809-10814.

Seeber, M., Scherer, R., Wagner, J., Solis-Escalante, T., & Müller-Putz, G. R. (2014). EEG beta suppression and low gamma modulation are different elements of human upright walking. *Frontiers in human neuroscience, 8*, 485.

Seeber, M., Scherer, R., Wagner, J., Solis-Escalante, T., & Müller-Putz, G. R. (2015) High and low gamma EEG oscillations in central sensorimotor areas are conversely modulated during the human gait cycle. *Neuroimage*, *112*, 318-326.

Sekiyama, K. (1983). Mental and physical movements of hands Kinesthetic information preserved in representational systems. *Japanese Psychological Research, 25*(2), 95-102.

Senzai, Y., Fernandez-Ruiz, A., & Buzsáki, G. (2019). Layer-specific physiological features and interlaminar interactions in the primary visual cortex of the mouse. *Neuron*, *101*(3), 500-513.

Severens, M., Nienhuis, B., Desain, P., & Duysens, J. (2012, August) Feasibility of measuring event related desynchronization with electroencephalography during walking. In *2012 Annual International Conference of the IEEE Engineering in Medicine and Biology Society* (pp. 2764-2767). IEEE.

Severens, M., Perusquia-Hernandez, M., Nienhuis, B., Farquhar, J., & Duysens, J. (2014). Using actual and imagined walking related desynchronization features in a BCI. *IEEE transactions on neural systems and rehabilitation engineering*, *23*(5), 877-886.

Shahin, A. J., Picton, T. W., & Miller, L. M. (2009). Brain oscillations during semantic evaluation of speech. *Brain and cognition, 70*(3), 259-266.

Sharma, N., & Baron, J. C. (2013). Does motor imagery share neural networks with executed movement: a multivariate fMRI analysis. *Frontiers in human neuroscience, 7,* 564.

Sheridan, P. L., & Hausdorff, J. M. (2007). The role of higher-level cognitive function in gait: executive dysfunction contributes to fall risk in Alzheimer's disease. *Dementia and geriatric cognitive disorders, 24*(2), 125-137.

Sherman, M. A., Lee, S., Law, R., Haegens, S., Thorn, C. A., Hämäläinen, M. S., Moore, C. I., & Jones, S. R. (2016). Neural mechanisms of transient neocortical beta rhythms: Converging evidence from humans, computational modeling, monkeys, and mice. *Proceedings of the National Academy of Sciences, 113*(33), E4885-E4894.

Sherrington, C. S. (1906). Observations on the scratch-reflex in the spinal dog. *The Journal of physiology*, *34*(1-2), 1-50.

Shibasaki, H., & Hallett, M. (2006). What is the Bereitschaftspotential?. *Clinical neurophysiology, 117*(11), 2341-2356.

Shiffrin, R. M., & Schneider, W. (1977). Controlled and automatic human information processing: II. Perceptual learning, automatic attending and a general theory. *Psychological review, 84*(2), 127.

Shumway-Cook, A., & Woollacott, M. H. (2007) *Motor control: translating research into clinical practice*. Lippincott Williams & Wilkins.

Singer, W. (2018). Neuronal oscillations: unavoidable and useful?. *European Journal of Neuroscience, 48*(7), 2389-2398.

Sinigaglia, C. (2013). What type of action understanding is subserved by mirror neurons?. *Neuroscience letters, 540*, 59-61.

Sipp, A. R., Gwin, J. T., Makeig, S., & Ferris, D. P. (2013). Loss of balance during balance beam walking elicits a multifocal theta band electrocortical response. *Journal of neurophysiology, 110*(9), 2050-2060.

Sirigu, A., Cohen, L., Duhamel, J. R., Pillon, B., Dubois, B., Agid, Y., & Pierrot-Deseilligny, C. (1995). Congruent unilateral impairments for real and imagined hand movements. *Neuroreport, 6*(7), 997-1001.

Slobounov, S., Cao, C., Jaiswal, N., & Newell, K. M. (2009). Neural basis of postural instability identified by VTC and EEG. *Experimental brain research, 199*(1), 1-16.

Solis-Escalante, T., Müller-Putz, G. R., Pfurtscheller, G., & Neuper, C. (2012). Cue-induced beta rebound during withholding of overt and covert foot movement. *Clinical Neurophysiology, 123*(6), 1182-1190.

Solis-Escalante, T., Müller-Putz, G., & Pfurtscheller, G. (2008). Overt foot movement detection in one single Laplacian EEG derivation. *Journal of neuroscience methods, 175*(1), 148-153.

Solodkin, A., Hlustik, P., Chen, E. E., & Small, S. L. (2004). Fine modulation in network activation during motor execution and motor imagery. *Cerebral cortex, 14*(11), 1246-1255.

Sperber, D. (1994). The modularity of thought and the epidemiology of representations. *Mapping the mind: Domain specificity in cognition and culture, 39-67.*

Spitzer, B., & Haegens, S. (2017). Beyond the status quo: a role for beta oscillations in endogenous content (re) activation. *eneuro, 4*(4).

Spivey, M. J., & Geng, J. J. (2001). Oculomotor mechanisms activated by imagery and memory: Eye movements to absent objects. *Psychological research, 65*(4), 235-241.

Stancák Jr, A., & Pfurtscheller, G. (1996). Event-related desynchronisation of central beta-rhythms during brisk and slow self-paced finger movements of dominant and nondominant hand. *Cognitive brain research, 4*(3), 171-183.

Stančák Jr, A., Riml, A., & Pfurtscheller, G. (1997). The effects of external load on movement-related changes of the sensorimotor EEG rhythms. *Electroencephalography and Clinical Neurophysiology, 102*(6), 495-504.

Stecklow, M. V., Infantosi, A. F. C., & Cagy, M. (2010). EEG changes during sequences of visual and kinesthetic motor imagery. *Arquivos de neuro-psiquiatria, 68*(4), 556-561.

Stegemöller, E. L., Allen, D. P., Simuni, T., & MacKinnon, C. D. (2016). Motor cortical oscillations are abnormally suppressed during repetitive movement in patients with Parkinson's disease. *Clinical Neurophysiology*, *127*(1), 664-674.

Stegemöller, E. L., Allen, D. P., Simuni, T., & MacKinnon, C. D. (2017). Altered premotor cortical oscillations during repetitive movement in persons with Parkinson's disease. *Behavioural brain research, 317*, 141-146.

Stephan, K. M., Fink, G. R., Passingham, R. E., Silbersweig, D., Ceballos-Baumann, A. O., Frith, C. D., & Frackowiak, R. S. (1995). Functional anatomy of the mental representation of upper extremity movements in healthy subjects. *Journal of neurophysiology, 73*(1), 373-386.

Stevens, J. A., & Stoykov, M. E. P. (2003). Using motor imagery in the rehabilitation of hemiparesis. *Archives of physical medicine and rehabilitation, 84*(7), 1090-1092.

Stippich, C., Ochmann, H., & Sartor, K. (2002). Somatotopic mapping of the human primary sensorimotor cortex during motor imagery and motor execution by functional magnetic resonance imaging. *Neuroscience letters, 331*(1), 50-54.

Stolk, A., Brinkman, L., Vansteensel, M. J., Aarnoutse, E., Leijten, F. S., Dijkerman, C. H., Knight, R. T., de Lange, F. P., & Toni, I. (2019). Electrocorticographic dissociation of alpha and beta rhythmic activity in the human sensorimotor system. *Elife*, *8*, e48065.

Storzer, L., Butz, M., Hirschmann, J., Abbasi, O., Gratkowski, M., Saupe, D., Schnitzler, A., & Dalal, S. S. (2016). Bicycling and walking are associated with different cortical oscillatory dynamics. *Frontiers in human neuroscience, 10*, 61.

Strafella, A. P., & Paus, T. (2000). Modulation of cortical excitability during action observation: a transcranial magnetic stimulation study. *Neuroreport, 11*(10), 2289-2292.

Suffczynski, P. (1999). Event-related dynamics of alpha band rhythms: a neuronal network model of focal ERD/surround ERS. *Event-related desynchronization: handbook of electroencephalography and clinical neurophysiology, 6*, 67-85.

Suzuki, M., Miyai, I., Ono, T., & Kubota, K. (2008). Activities in the frontal cortex and gait performance are modulated by preparation. An fNIRS study. *Neuroimage, 39*(2), 600-607.

Suzuki, M., Miyai, I., Ono, T., Oda, I., Konishi, I., Kochiyama, T., & Kubota, K. (2004). Prefrontal and premotor cortices are involved in adapting walking and running speed on the treadmill: an optical imaging study. *Neuroimage, 23*(3), 1020-1026.

Tallon-Baudry, C., Bertrand, O., Peronnet, F., & Pernier, J. (1998). Induced γ-band activity during the delay of a visual short-term memory task in humans. *Journal of Neuroscience, 18*(11), 4244-4254.

Tamir, R., Dickstein, R., & Huberman, M. (2007). Integration of motor imagery and physical practice in group treatment applied to subjects with Parkinson's disease. *Neurorehabilitation and Neural Repair, 21*(1), 68-75.

Tang, J., Liu, Y., Hu, D., & Zhou, Z. (2018). Towards BCI-actuated smart wheelchair system. *Biomedical engineering online, 17*(1), 1-22.

Taube, W., Mouthon, M., Leukel, C., Hoogewoud, H. M., Annoni, J. M., & Keller, M. (2015). Brain activity during observation and motor imagery of different balance tasks: an fMRI study. *cortex*, *64*, 102-114.

Tempel, T., Frings, C., & Pastötter, B. (2020). EEG beta power increase indicates inhibition in motor memory. *International Journal of Psychophysiology, 150*, 92-99.

Teneggi, C., Canzoneri, E., di Pellegrino, G., & Serino, A. (2013). Social modulation of peripersonal space boundaries. *Current biology, 23*(5), 406-411.

Thelen, E., & Smith, L. B. (1996). *A dynamic systems approach to the development of cognition and action*. MIT press.

Thorndike, E. L. (1913). Ideo-motor action. *Psychological Review, 20*(2), 91.

Tinetti, M. E., Speechley, M., & Ginter, S. F. (1988). Risk factors for falls among elderly persons living in the community. *New England journal of medicine*, *319*(26), 1701-1707.

Tognoli, E., Lagarde, J., DeGuzman, G. C., & Kelso, J. S. (2007). The phi complex as a neuromarker of human social coordination. *Proceedings of the National Academy of Sciences, 104*(19), 8190-8195.

Tombini, M., Zappasodi, F., Zollo, L., Pellegrino, G., Cavallo, G., Tecchio, F., Guglielmelli, E., & Rossini, P. M. (2009). Brain activity preceding a 2D manual catching task. *Neuroimage, 47*(4), 1735-1746.

Tönnies, J. F. (1934). Die unipolare Ableitung elektrischer Spannungen vom menschlichen Gehirn. *Naturwissenschaften, 22*(22), 411-414.

Tononi, G., Edelman, G. M., & Sporns, O. (1998). Complexity and coherency: integrating information in the brain. *Trends in cognitive sciences, 2*(12), 474-484.

Trambaiolli, L. R., Dean, P. J., Cravo, A. M., Sterr, A., & Sato, J. R. (2019, October). On-task theta power is correlated to motor imagery performance. In *2019 IEEE International Conference on Systems, Man and Cybernetics (SMC)* (pp. 3937-3942). IEEE.

Trujillo, L. T., & Allen, J. J. (2007). Theta EEG dynamics of the error-related negativity. *Clinical Neurophysiology, 118*(3), 645-668.

Tunik, E., Rice, N. J., Hamilton, A., & Grafton, S. T. (2007). Beyond grasping: representation of action in human anterior intraparietal sulcus. *Neuroimage, 36,* T77-T86.

Tzagarakis, C., Ince, N. F., Leuthold, A. C., & Pellizzer, G. (2010). Beta-band activity during motor planning reflects response uncertainty. *Journal of Neuroscience, 30*(34), 11270-11277.

Ulloa, E. R., & Pineda, J. A. (2007). Recognition of point-light biological motion: mu rhythms and mirror neuron activity. *Behavioural brain research, 183*(2), 188-194.

Umiltà, M. A., Intskirveli, I., Grammont, F., Rochat, M., Caruana, F., Jezzini, A., Gallese, V., & Rizzolatti, G. (2008). When pliers become fingers in the monkey motor system. *Proceedings of the National Academy of Sciences, 105*(6), 2209-2213.

Umilta, M. A., Kohler, E., Gallese, V., Fogassi, L., Fadiga, L., Keysers, C., & Rizzolatti, G. (2001). I know what you are doing: A neurophysiological study. *Neuron, 31*(1), 155-165.

Urgen, B. A., Plank, M., Ishiguro, H., Poizner, H., & Saygin, A. P. (2013). EEG theta and Mu oscillations during perception of human and robot actions. *Frontiers in neurorobotics, 7*, 19.

Urgesi, C., Candidi, M., Fabbro, F., Romani, M., & Aglioti, S. M. (2006). Motor facilitation during action observation: topographic mapping of the target muscle and influence of the onlooker's posture. *European Journal of Neuroscience, 23*(9), 2522-2530.

Uzgiris, I. C. (1981). Two functions of imitation during infancy. *International Journal of Behavioral Development, 4*(1), 1-12.

Van der Lubbe, R. H., Sobierajewicz, J., Jongsma, M. L., Verwey, W. B., & Przekoracka-Krawczyk, A. (2021). Frontal brain areas are more involved during motor imagery than during motor execution/preparation of a response sequence. *International Journal of Psychophysiology, 164*, 71-86.

Van Ede, F., De Lange, F., Jensen, O., & Maris, E. (2011). Orienting attention to an upcoming tactile event involves a spatially and temporally specific modulation of sensorimotor alpha-and beta-band oscillations. *Journal of Neuroscience, 31*(6), 2016-2024.

Van Wijk, B. C. M., Beek, P. J., & Daffertshofer, A. (2012). Differential modulations of ipsilateral and contralateral beta (de) synchronization during unimanual force production. *European Journal of Neuroscience, 36*(1), 2088-2097.

Vanderwolf, C. H. (1967). Behavioral correlates of “theta” waves. *Proceedings of the Canadian Federation of Biological Sciences, 10*, 41-42.

Vanderwolf, C. H. (1969). Hippocampal electrical activity and voluntary movement in the rat. *Electroencephalography and clinical neurophysiology, 26*(4), 407-418.

Vanthornhout, J., Decruy, L., Wouters, J., Simon, J. Z., & Francart, T. (2018). Speech intelligibility predicted from neural entrainment of the speech envelope. *Journal of the Association for Research in Otolaryngology, 19*(2), 181-191.

Varela, F. J., Rosch, E., & Thompson, E. (1992). The embodied mind: *Cognitive science and human experience*. MIT press.

Varela, F., Lachaux, J. P., Rodriguez, E., & Martinerie, J. (2001). The brainweb: phase synchronization and large-scale integration. *Nature reviews neuroscience, 2*(4), 229-239.

Verghese, J., Ambrose, A. F., Lipton, R. B., & Wang, C. (2010). Neurological gait abnormalities and risk of falls in older adults. *Journal of neurology, 257*(3), 392-398.

Verghese, J., Lipton, R. B., Hall, C. B., Kuslansky, G., Katz, M. J., & Buschke, H. (2002). Abnormality of gait as a predictor of non-Alzheimer's dementia. *New England Journal of Medicine, 347*(22), 1761-1768.

Verghese, J., Wang, C., Lipton, R. B., & Holtzer, R. (2013). Motoric cognitive risk syndrome and the risk of dementia. *Journals of Gerontology Series A:Biomedical Sciences and Medical Sciences, 68*(4), 412-418.

Verleger, R., Siller, B., Ouyang, G., &Śmigasiewicz, K. (2017). Effects on P3 of spreading targets and response prompts apart. *Biological Psychology*, *126*, 1-11.

Verleger, R. (2020). Effects of relevance and response frequency on P3b amplitudes: Review of findings and comparison of hypotheses about the process reflected by P3b. *Psychophysiology*, *57*(7), e13542.

Vidal, F., Burle, B., Bonnet, M., Grapperon, J., & Hasbroucq, T. (2003). Error negativity on correct trials: a reexamination of available data. *Biological psychology, 64*(3), 265-282.

Vidal, F., Hasbroucq, T., Grapperon, J., & Bonnet, M. (2000). Is the ‘error negativity’specific to errors?. *Biological psychology, 51*(2-3), 109-128.

Vigário, R., Sarela, J., Jousmiki, V., Hamalainen, M., & Oja, E. (2000). Independent component approach to the analysis of EEG and MEG recordings. *IEEE transactions on biomedical engineering, 47*(5), 589-593.

Vitório, R., Pieruccini-Faria, F., Stella, F., Gobbi, S., & Gobbi, L. T. B. (2010) Effects of obstacle height on obstacle crossing in mild Parkinson's disease. *Gait Posture, 31*(1), 143-146.

Vitorio, R., Stuart, S., Rochester, L., Alcock, L., & Pantall, A. (2017). fNIRS response during walking—Artefact or cortical activity? A systematic review. *Neuroscience & Biobehavioral Reviews, 83*, 160-172.

Vogt, S., Taylor, P., & Hopkins, B. (2003). Visuomotor priming by pictures of hand postures: perspective matters. *Neuropsychologia, 41*(8), 941-951.

Wagner, J., Makeig, S., Gola, M., Neuper, C., & Müller-Putz, G. (2016). Distinct β band oscillatory networks subserving motor and cognitive control during gait adaptation. *Journal of Neuroscience, 36*(7), 2212-2226.

Wagner, J., Martínez-Cancino, R., & Makeig, S. (2019) Trial-by-trial source-resolved EEG responses to gait task challenges predict subsequent step adaptation. *Neuroimage, 199*, 691-703.

Wagner, J., Solis-Escalante, T., Grieshofer, P., Neuper, C., Müller-Putz, G., & Scherer, R. (2012) Level of participation in robotic-assisted treadmill walking modulates midline sensorimotor EEG rhythms in able-bodied subjects. *Neuroimage, 63*(3), 1203-1211.

Wagner, J., Solis-Escalante, T., Scherer, R., Neuper, C., & Müller-Putz, G. (2014). It's how you get there: walking down a virtual alley activates premotor and parietal areas. *Frontiers in human neuroscience, 8*, 93.

Wagner, J., Stephan, T., Kalla, R., Brückmann, H., Strupp, M., Brandt, T., & Jahn, K. (2008). Mind the bend: cerebral activations associated with mental imagery of walking along a curved path. *Experimental brain research, 191*(2), 247.

Walter, W. G. (1950). The twenty-fourth Maudsley lecture: the functions of electrical rhythms in the brain. *Journal of Mental Science, 96*(402), 1-31.

Wamain, Y., Gabrielli, F., & Coello, Y. (2016). EEG μ rhythm in virtual reality reveals that motor coding of visual objects in peripersonal space is task dependent. *Cortex, 74*, 20-30.

Wang, Y., Yang, W., Winter, P., & Walker, L. (2008). Walk-through weighing of pigs using machine vision and an artificial neural network. *Biosystems Engineering, 100*(1), 117-125.

Ward, L. M. (2003). Synchronous neural oscillations and cognitive processes. *Trends in cognitive sciences, 7*(12), 553-559.

Warren, W. H., Kay, B. A., Zosh, W. D., Duchon, A. P., & Sahuc, S. (2001). Optic flow is used to control human walking. *Nature neuroscience, 4*(2), 213-216.

Wascher, E., Reiser, J., Rinkenauer, G., Larrá, M., Dreger, F. A., Schneider, D., Karthaus, M., Getzmann, S., Gutberlet, S., & Arnau, S. (2021). Neuroergonomics on the Go: An Evaluation of the Potential of Mobile EEG for Workplace Assessment and Design. *Human Factors*, 00187208211007707.

Weber, E., & Doppelmayr, M. (2016). Kinesthetic motor imagery training modulates frontal midline theta during imagination of a dart throw. *International journal of Psychophysiology, 110*, 137-145.

Weerdesteyn, V., Rijken, H., Geurts, A. C., Smits-Engelsman, B. C., Mulder, T., & Duysens, J. (2006) A five-week exercise program can reduce falls and improve obstacle avoidance in the elderly. *Gerontology, 52*(3), 131-141.

Wheaton, K. J., Thompson, J. C., Syngeniotis, A., Abbott, D. F., & Puce, A. (2004). Viewing the motion of human body parts activates different regions of premotor, temporal, and parietal cortex. *Neuroimage, 22*(1), 277-288.

Whitman, G. T., Tang, T., Lin, A., & Baloh, R. W. (2001). A prospective study of cerebral white matter abnormalities in older people with gait dysfunction. *Neurology, 57*(6), 990-994.

Wiener, N. (1955). Time and organization. In: P.Masani (Ed.), Norbert Wiener: Collected Works, Vol IV, MIT Press, 1985

Wiener, N. (1956). Brain waves and interferometer. *Journal of the Physical Society of Japan, 18*, 499-507.

Wieser, M., Haefeli, J., Bütler, L., Jäncke, L., Riener, R., & Koeneke, S. (2010). Temporal and spatial patterns of cortical activation during assisted lower limb movement. *Experimental brain research*, *203*(1), 181-191.

Williams, J., Pearce, A. J., Loporto, M., Morris, T., & Holmes, P. S. (2012). The relationship between corticospinal excitability during motor imagery and motor imagery ability. *Behavioural brain research, 226*(2), 369-375.

Williams, S. E., & Cumming, J. (2011). Measuring athlete imagery ability: The sport imagery ability questionnaire. *Journal of Sport and Exercise Psychology*, *33*(3), 416-440.

Williams, S. E., Guillot, A., Di Rienzo, F., & Cumming, J. (2015). Comparing self-report and mental chronometry measures of motor imagery ability. *European Journal of Sport Science*, *15*(8), 703-711..

Wimmer, K., Ramon, M., Pasternak, T., & Compte, A. (2016). Transitions between multiband oscillatory patterns characterize memory-guided perceptual decisions in prefrontal circuits. *Journal of Neuroscience, 36*(2), 489-505.

Winkler, I., Haufe, S., &Tangermann, M. (2011). Automatic classification of artifactual ICA-components for artifact removal in EEG signals. *Behavioral and Brain Functions*, *7*(1), 1-15.

Wolpaw, J. R. (2013). Brain–computer interfaces. In *Handbook of Clinical Neurology* (Vol. 110, pp. 67-74). Elsevier.

Wolpaw, J. R., & Wolpaw, E. W. (2012). Brain-computer interfaces: something new under the sun. *Brain-computer interfaces: principles and practice, 14*.

Wolpaw, J. R., Birbaumer, N., McFarland, D. J., Pfurtscheller, G., & Vaughan, T. M. (2002). Brain–computer interfaces for communication and control. *Clinical neurophysiology, 113*(6), 767-791.

Wolpert, D. M. (1997). Computational approaches to motor control. *Trends in cognitive sciences, 1*(6), 209-216.

Wolpert, D. M., & Flanagan, J. R. (2001). Motor prediction. *Current biology, 11*(18), R729-R732.

Wolpert, D. M., & Kawato, M. (1998). Multiple paired forward and inverse models for motor control. *Neural networks, 11*(7-8), 1317-1329.

World Health Organization. (2021). *Physical activity fact sheet*. World Health Organization.

Xie, S., Kaiser, D., & Cichy, R. M. (2020). Visual imagery and perception share neural representations in the alpha frequency band. *Current Biology, 30*(13), 2621-2627.

Y Tseng, B., Munro Cullum, C., & Zhang, R. (2014). Older adults with amnestic mild cognitive impairment exhibit exacerbated gait slowing under dual-task challenges. *Current Alzheimer Research, 11*(5), 494-500.

Yahagi, S., Shimura, K., & Kasai, T. (1996). An increase in cortical excitability with no change in spinal excitability during motor imagery. *Perceptual and motor skills, 83*(1), 288-290.

Yokoyama, H., Kaneko, N., Masugi, Y., Ogawa, T., Watanabe, K., & Nakazawa, K. (2020). Gait-phase-dependent and gait-phase-independent cortical activity across multiple regions involved in voluntary gait modifications in humans. *European Journal of Neuroscience*.

Zabielska-Mendyk, E., Francuz, P., Jaśkiewicz, M., & Augustynowicz, P. (2018). The effects of motor expertise on sensorimotor rhythm desynchronization during execution and imagery of sequential movements. *Neuroscience, 384,* 101-110.

Zarka, D., Cevallos, C., Petieau, M., Hoellinger, T., Dan, B., & Cheron, G. (2014). Neural rhythmic symphony of human walking observation: Upside-down and Uncoordinated condition on cortical theta, alpha, beta and gamma oscillations. *Frontiers in systems neuroscience, 8,* 169.

Zhang, Y., Chen, Y., Bressler, S. L., & Ding, M. (2008). Response preparation and inhibition: the role of the cortical sensorimotor beta rhythm. *Neuroscience, 156*(1), 238-246.

Zich, C., Schweinitz, C., Debener, S., & Kranczioch, C. (2015). Multimodal evaluation of home-based motor imagery training supported by mobile EEG: A case report. In *Zich, C., Schweinitz, C., Debener, S., and &Kranczioch, CTS, editors, Systems, Man, and Cybernetics (SMC), 2015 IEEE International Conference on. IEEE.*

Zink, R., Hunyadi, B., Van Huffel, S., & De Vos, M. (2016). Mobile EEG on the bike: disentangling attentional and physical contributions to auditory attention tasks. *Journal of neural engineering, 13*(4), 046017.

Zion-Golumbic, E., Kutas, M., & Bentin, S. (2010). Neural dynamics associated with semantic and episodic memory for faces: evidence from multiple frequency bands. *Journal of cognitive neuroscience, 22*(2), 263-277.