Neural Correlates of Human Cognition in Real-World Environments

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Thesis outline

According to embodied accounts of human cognition, the mind is at the interface of the body and the environment. For practical reasons, however, neuroscientific research on human cognition has mostly been confined to the laboratory until now. The emergence of portable brain and body imaging research methods offers an unprecedented opportunity to capture the expression of cognitive processes during active behaviours performed in real-world contexts.

In the present thesis, electroencephalography (EEG) was used to investigate embodied aspects of human cognition in motion and in the real-world. This approach, however, presents new challenges in terms of signal processing because of the increased noise related to whole body movements. As the necessary signal processing tools were not well-established, the current work involved the development of new solutions to address the specific requirements of mobile EEG data before real-world brain recordings could be validly interpreted.

In a series of Event Related Potential (ERP) experiments, real-world conditions were compared to traditional lab-based conditions. The neural marker of attention (P300 ERP) was recorded when participants performed an attentional task while walking through the university's corridors versus standing in the lab. Differences in the classic P300 ERP effect show that attentional processes in the real-world are not the same as those recorded in the lab. Following up on this finding, the attenuation of the P300 effect under real-world conditions was shown to be driven by cognitive demands related to displacement through space rather than the act of walking itself. This is a demonstration, at a brain level, that when walking in the real-world, cognitive resources are reallocated to the processing of visual flow and vestibular information associated with displacement. The findings reflect

the dynamic interplay between mind, body, and environment, providing innovative evidence strengthening the embodied framework of human cognition.

The same dynamic interplay between body, environment and cognitive function is uniquely represented in real-world navigation. The literature on spatial navigation in humans, however, mainly involved navigating virtual reality environments often while lying on a scanner bed. Most of the evidence on the neural markers of spatial navigation comes from intracranially recorded brain oscillations in rodents. The innovation in this thesis was to investigate brain oscillations associated with cognitive function underlying real-world navigation in humans using surface electrodes. The present work demonstrates that human brain dynamics related to navigational cognitive processes can be recorded in active exploration of real-world environments. The key finding resulting from this novel approach is that real-world spatial navigation is associated with specific neural signatures underlying distinct cognitive functions. Frontal low-frequency oscillations were found to be associated with wayfinding, while parietal high-frequency oscillations were associated with spatial memory. Furthermore, these neural correlates were found to be dynamically modulated depending on the body's contextual positioning within the environment. Therefore, these findings again provide evidence in support of the embodiment theory of cognition.

The final study addressed the concern that findings might reflect walking speed variation. The existing animal literature has shown that low-frequency bands are modulated by walking speed. This study characterised the specific modulations in spectral power as a function of walking speed in humans. Critically the pattern showed no similarity to the spectral patterns found in relation to real-world spatial navigation, confirming the cognitive interpretation of this work.

Taken together, these findings provide innovative real-world evidence supporting the theoretical embodiment framework. The neural correlates of attention, memory, and spatial navigation were found to be modulated by the dynamic experience of one's environment. Beyond this work's theoretical implications for cognitive sciences, the present findings offer new perspectives for real-world application.

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Author’s Declaration

I hereby declare that the content of this dissertation is original and has not been submitted in whole or in part for consideration for any other degree or qualification in this, or any other University. The format of the present thesis adheres to the University of Stirling guidelines for thesis presentation.

The research conducted within the frame of this thesis was supported by a research studentship from the University of Stirling. The whole project was conducted and executed by myself, Simon Ladouce, at the University of Stirling. The experiments were designed based on the collaborative work with my supervisors Magdalena Ietswaart, David Donaldson and substantial feedback from Paul Dudchenko in his quality of research advisor. As such, I declare that the research presented here is issued from my own intellectual work and was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Auditory and visual stimuli employed in the studies presented in this thesis have been specifically created for the purpose of the experiment. These stimuli were created and presented through E-Prime and Psychopy software. Batch code used for stimulus presentation will be provided upon request.

Data was mainly handled through MATLAB. Raw data along with relative custom scripts used for data processing and analyses will be provided upon request. Moreover, a documented version of the mobile EEG processing pipeline script library has been made available through an open-source repository accessible online (github.com/sladouce).

Scientific dissemination

Part of this work has been communicated as following:

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Chapter 1: General Introduction

In this introductory chapter, the rationale for investigating human cognition and behaviour in the real-world will be developed, with reference to empirical evidence supporting theoretical models of human cognition derived from the embodiment framework. A review of the state of the art of contemporary research using mobile technologies will then be presented, outlining the technical and conceptual challenges of a mobile cognition approach. Potential applications of these techniques within the frame of cognitive science are then discussed in terms of their contribution to studying embodied aspects of human cognitive experiences in natural settings. The vision of a real-world approach to the study of human cognition presented in this chapter reflects the work developed throughout this thesis.

1.1. Preface

There is a growing body of evidence that important aspects of human cognition have been marginalised, or overlooked, by traditional cognitive science. In particular, the use of laboratory-based experiments in which stimuli are artificial, and response options are fixed, inevitably results in findings that are less ecologically valid in relation to real-world behaviour. Novel mobile technologies allow traditionally lab-bound measurements to now be collected during natural interactions with the world, opening new avenues for cognitive science research. The theoretical support that mobile brain and body imaging methods receive from the embodiment framework will be outlined in the following introductory sections, along with examples from a widening range of evidence that illustrates the importance of examining cognitive processes in their context. Aspects of cognitive science research that would benefit from a mobile cognition approach will be developed, with a particular focus on research questions that have been the subject of empirical investigation as part of this thesis. Therefore, the relevance of mobile brain and body imaging for widening our understanding of the cognitive processes underlying navigation through space and the role of attention during natural behaviour will be discussed at the light of existing literature and preliminary work issued from the mobile brain imaging field. The point will be made that development of real-world mobile cognition offers both increased ecological validity, and the opportunity to examine the interactions between perception, cognition and action –

rather than examining each in isolation. This General Introduction will also present the technical and conceptual challenges brought by operating such a shift from carrying cognitive science research in tightly controlled laboratory environments towards real-world world environments, which require innovation in both paradigm design and analysis. Implications of a mobile cognition approach for human cognition research will be discussed along with potential applications of these technologies within the frame of real-world neurofeedback.

1.2. Rationale for a real-world approach

The human mind is a dynamic predictor that perceives, understands and acts within complex and ever-changing environments. To produce flexible and adaptive reactions that are relevant and appropriate to the individual's goals, the brain must integrate concurrent multi-modal sensory and motor signals, using continuous real-time feedback to guide the execution of on-going behaviour. Despite this dynamic reality, however, the traditional approach to understanding human cognition has been the collection of empirical findings from experiments taking place in relatively static, often simulated, laboratory settings. Typically, participants sit or lie down, are given explicit and highly constrained instructions, and are required to attend to artificial stimuli whilst performing deliberately stereotyped responses. The strength of such an approach is the experimental control it affords; the cost, however, is a loss of real-world dimensionality, and perhaps, relevance. In this General introduction, we present an alternative approach that capitalizes on recent technological developments to allow experimental work to be situated in the real world. This mobile cognition approach capitalises on the ability to record brain activity (e.g., EEG, fNIRS) and body dynamics (e.g., eye movements, kinematics, muscular activity) concurrent to natural behaviours. Mobile cognition, as an emerging field offers significant added value to traditional laboratory science, with particular implications for the translation of theoretical knowledge into impact. Before outlining this view, we first highlight the rationale for mobile cognition, which stems at least in part from dissatisfaction with assumptions underlying laboratory experiments: namely, that behavioural and neurobiological measures recorded under strictly controlled laboratory conditions accurately reflect the complexity of cognitive processing.

1.2.1. The issue of ecological validity

Psychology and cognitive sciences have made substantial progress through the use of laboratory based experimentation; such has been the success of this largely reductionist approach that concerns have been expressed about it crowding out other fields within Cognitive Science (Gentner, 2010). However, despite its acknowledged success, right from the very beginning of the psychological investigation of cognition, concerns were raised about how ecologically valid many of the findings were. For example, as early as 1943, Brunswik expressed concern that cognitive psychology was heading towards the study of narrow and artificially isolated conditions that were not representative of the actual functioning of cognition. Similarly, significant debate around ecological validity was raised in the 1970s. Perhaps the most well-known advocate of this concern is Ulric Neisser, who argued (e.g., see Neisser, 1976) that assessing cognitive processes in an artificial environment would only enhance our understanding of those specific circumstances – but not necessarily generalize to real-world cognition.

More pointedly, Brofenbrenner (1977) added that measuring restricted responses in artificial setups would generate behaviours that are in fact different from the behaviours displayed in a natural context. By this view, having participants sit at a computer looking at pixelated images or scenes may not allow researchers to fully characterise cognition – because the processes being engaged, or representations being accessed, occur in far more complex forms in real life. For example, researchers interested in recognition (as per witness identification scenarios in real life) typically present photographic images of people on computer screens – which are inevitably less rich than interacting with a real person. A striking example of the implications of this restriction can be found in the clinical case of agnosic patients (e.g. Goodale, Milner, Jakobson, & Carey, 1991), who despite being unable to recognize or even describe the features (size, colour, shape) of objects presented visually, are nonetheless able to appropriately adjust their movement towards these objects when interacting with them. This finding provided evidence that the internal representations associated with objects are accessed differently depending on the purpose of the output (vision for recognition versus vision for action). A significant advantage of the mobile cognition approach is that it encourages researchers to investigate cognition in context, in relation to our natural interactions within the environment, rather than abstracted away from it.

Paradoxically, one significant contribution to the problem of ecological validity has been the over enthusiastic pursuit of internal validity. Attempts to ensure that cognitive phenomena under investigation are being measured accurately and precisely (i.e., with high internal validity) have resulted in an ever-increasing drive towards greater resolution of data acquisition (e.g., greater number of electrodes during EEG recording, or finer-grained assessment of where a participant looks during eye-tracking). Furthermore, the concern for internal validity has contributed to the desire for ever improved signal to noise ratios during measurement and the removal of potential confounding variables via more and more artificial experimental set ups (Schmuckler, 2001). Equally, individual cognitive functions have gradually been studied at a greater and greater level of detail (i.e., specificity), with distinct processes being further and further subdivided in to sub processes of sub processes (e.g., declarative memory dividing into episodic and semantic memory, episodic memory dividing into recollection and familiarity, recollection into rate and precision, etc). Whilst the push for greater internal validity is warranted, the increasing abstraction, isolation and focussing of measurements have, inevitably perhaps, contributed to an unintended reduction in ecological validity.

In summary, the issue of ecological validity, or how research conducted in the lab applies to everyday life situations, has been a longstanding concern in the fields of research related to human cognition. The emergence of portable brain and body imaging methods offers an unprecedented opportunity to address this critical issue by departing from traditional laboratory-based setups to investigate cognitive processes directly in the real-world.

Of course, such a real-world approach is not to replace laboratory work and the two must work in parallel and actively inform each other. While mobile techniques offer the unprecedented opportunity to investigate cognition in real-world context, they however do not currently compete with lab-based counterparts in terms of qualitative and quantitative features. The spatial resolution offered by a fMRI scanner will never be matched by a mobile fNIRS or EEG system. Furthermore, some research questions are better served by the experimental control afforded in laboratory research. Our view is that the mobile cognition approach will add considerable value to existing laboratory based cognitive neuroscience: indeed, there are many research questions that can only really be sensibly addressed in real-world contexts.

1.2.2. Cognition is embodied

The lack of ecological validity in cognitive science has become even more of an issue with the emergence of evidence that cognition is embodied (for reviews, see Barsalou, 2008; Gallagher, 2005). Over the past 20 years it has become apparent that cognition is inherently reliant on its situated position in the environment. Chiel and Beer (1997) were one of the first to argue that understanding the interactions between brain, body and environment is crucial. The significance of this view has become more apparent through recent research that shows that bodily experience in fact shapes the way we process the environment. To be clear, the broad idea of interdependence between perception/action and the environment had already been emphasised by Gibson in his theory of affordances (Gibson, 1979), which states that the external information available to us is processed in relation to the opportunities for action that they provide. Although it was developed largely independently, embodiment theory also argues that cognition is for action, and furthermore that cognition is actually dependent on the bodily experience (e.g. Clark, 1999). Understanding cognition through abstract experimental paradigms that lack interaction with the environment, due to their artificial nature, therefore makes little sense from an embodied perspective.

Support for the embodiment of cognition can also be found in findings from modern day neuroscience. For example, evidence regarding neural plasticity collected over the last twenty years has made clear that brain and behaviour are constantly shaped by our experience in interacting with the world (for a review, see Poldrack, 2000). Even at the level of the functional organisation of vision, it is clear that representations reflect top-down action potentialities rather than bottom-up sensory inputs (Bracci, Cavina-Pratesi, Ietswaart, Caramazza, & Peelen, 2012). One compelling example is provided by Thaler, Arnott, & Goodale, (2011), who have shown that blind people can use echolocation to navigate in space (listening to the echo of clicks-sound to locate the reflection point), giving rise to functional restructuring of brain regions typically involved in vision. Perhaps the most famous example of how our behaviour shapes our brain is the work on taxi drivers presenting with increased hippocampal size, which is thought to be due to their experience of navigating the maze of London streets (Maguire et al., 2000). Taken together, these finding highlight the fact that interaction with the surrounding world shapes brain structure and function. From this perspective, recent acceptance of cognition as being embodied emphasises a problem inherent to traditional cognitive experiments – highly controlled and artificial experimental testing tends to separate cognition from natural bodily experiences. Furthermore, by separating cognition from the bodily experience, it is argued that the intrinsic interaction that defines the human mind as an active agent is overlooked.

The embodiment account of human cognition has been theorized in many different ways. From a general cognitive science perspective, embodied cognition refers to the encoding and retrieval of knowledge regarding one's physical competencies and ability to interact with the environment (Grafton, 2009). According to an embodied view of human cognition, cognitive experiences are necessarily affected by one's perception of which kind of interactions are possible at any given time and location within an environment, underlining the body, mind and environment interdependent interactions.

The concept of situated cognition, stemming from the embodiment framework, postulates that our cognitive experience is dependent on the body's position in the environment. This interdependence implies that when embodied agents actualise their intentions they have to ensure their behaviour accommodates the contingencies of the environment. In contrast, by looking at cognition through an ever-narrower lens, cognitive science has focused on the study of specific cognitive processes in isolation. Consequently, the complex interplay of perception, cognition and action has not generally been investigated.

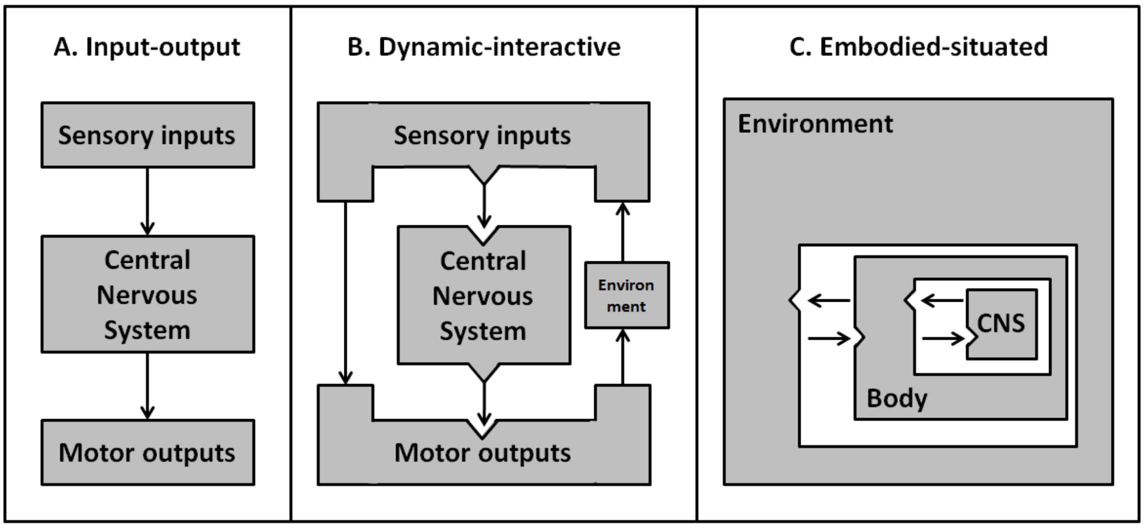

Figure 1.1. Development of psychological models about the interactions between environment, body and central nervous system. Early simple input-output models [A] ignore the environment and represent sensory inputs as being processed discretely to produce motor outputs. More sophisticated dynamic-interactive models [B] include environmental factors. By this account, direct feedback from motor output can interact with, and act on, the environment – resulting in a change to future sensory inputs. In embodied-situated models [C] the nervous system is embedded within the environment through the body. From this perspective input and output systems are integrated rather than discrete separable elements, and the nervous system is inherently linked with the environment – as parts of a dynamic system. Adapted from Chiel & Beer (1997).

The isolated cognitive account of classic input-output models is clearly represented by the idea of minds as machines, decoding sensory inputs (perception) to then deliver output commands (behaviour) to the body (see Figure 1.1.A). Whilst the unilateral direction from input to output implies a major bottom-up influence (and questions the very existence of self-motivated behaviour), there is now abundant evidence of top-down and dynamic influences on the selection and processing of features relevant to the ongoing task (Henderson, 2007). For example, the execution of naturalistic goal-oriented tasks induces anticipatory eye movements towards relevant affordances (e.g. Hayhoe, McKinney, Chajka, & Pelz, 2012; Mennie, Hayhoe, & Sullivan, 2007; Pelz & Canosa, 2001). Another example of this dynamic interplay between input and output is the integration of visuomotor feedback, allowing for online correction of movements to sudden changes of the environment (e.g. adaptive reaching movements to avoid obstacles; Chapman & Goodale, 2010). This body of evidence emphasizes that perception and action are interdependent and that bodily experience influences the way we process (input) and act on (output) the environment (see Figure 1.1.B). By assessing only one aspect in isolation, as previously done in cognitive research, the dynamic interplay between cognitive functions cannot be captured. Ultimately, therefore, it will be necessary to integrate concurrent measurement of input and output if in order to account for the dynamic interplay of cognitive functions in the face of a rich and dynamic real-world environment (see Figure 1.1.C).

1.2.3. Brain states differ during movement

A growing animal literature demonstrates the fundamental importance of interactions between brain, body and environment. For example, in the mouse hippocampus, 75% of place cells (neurons which encode specific locations in the animal’s environment) show a significant decrease in firing when the mouse is prevented from moving (Chen et al., 2013). Further, in rats, changes in theta power associated with ambulation (McFarland, Teitelbaum, & Hedges, 1975; Long, Hinman, Chen, Escabi, & Chrobak, 2014) are also modulated by the anticipation and initiation of goal-directed instrumental behaviour (Sinnamon, 2006; Wyble, Hyman, Rossi, & Hasselmo, 2004). In monkeys, the hippocampus is essential for a task where the animal must walk to a to-be-remembered location (Hampton et al., 2004), but it is not needed when the same type of memory task is performed while the animal is seated (Malkova & Mishkin, 2003). Importantly, the inter-dependence between locomotion and cognition is bi-directional: brain dynamics in Drosophila suggest that the processing of visual information is different in flight compared to resting state (Maimon, Straw, & Dickinson, 2010). To be clear, existing data reveals an inter-dependence between cognition and the exploration of the environment that emphasises the importance of understanding cognition in real-world contexts (suggesting that even studies in virtual reality will be insufficient to characterise cognitive processes as they support everyday behaviour). Strikingly, emerging findings support the claims made by Brofenbrenner (1977) that cognitive responses measured in artificial experimental conditions are different from those in natural exploration, and furthermore that ecological validity is not just desirable but essential if we are to fully understanding cognition.

Whilst existing evidence clearly demonstrates that the neural correlates of visual perception or locomotion can be altered by context, one reading of these data is that they only argue for sensitivity in sensory or motor systems, rather than in association cortex linked to higher order cognitive processing. However, the dual-task literature demonstrates that introduction of gait and balance control has a significant interfering effect on higher-order cognitive processes such as executive functions (i.e. inhibition, divided attention), verbal fluency, decision-making and working memory (for a review, see Al-Yahya et al., 2011). As well as linking bodily changes to cognitive performance, these data also question the validity of static single-task experiments in particular, because everyday life necessarily involves considerable cognitive-motor multitasking. Based on such premises, it can be hypothesized that the nature of sensory inputs related to natural movements are different (i.e., visual, vestibular, interoceptive…) partly due to the physical effects of movement, but also and importantly because of the richness and variety of the ever-changing environment. In turn, the dynamic environmental changes will potentially lead to changes in the firing patterns of neuronal populations, which in turn may facilitate the activation of processing structures in the brain that are not normally recruited while stationary (through the specific promotion of context-dependent neural populations, e.g., Meyer wave-type oscillation changes). In short, embodied cognition theory argues that sensory, motor and cognitive processing are interdependent, and evidence supports this claim, providing a strong rationale for studying cognition in motion or while engaged in natural motor tasks (Schaefer, 2014).

1.3. The emergence of mobile methods

Despite long standing awareness of the issue of ecological validity, and the recent accumulation of evidence highlighting the need for a real-world approach in cognitive research (e.g., Clark, 1997; Smilek, Birmingham, Cameron, Bischof, & Kingstone, 2006; Williams & Long, 2015), the issue has not been widely addressed in practice. Indeed, on the whole, these concerns are only incidentally acknowledged in the literature (Burgess, Alderman, Evans, Emslie, & Wilson, 1998; Chaytor & Schmitter-Edgecombe, 2003; Sbordone, 1996; Spooner & Pachana, 2006; Williams & Long, 2015). At least in part, this inertia can be explained by a lack of satisfactory solutions to conduct ecologically valid studies while maintaining scientific rigour and high levels of data quality. Studying cognition in the real-world demands a combination of technical and methodological requirements (Makeig, Gramann, Jung, Sejnowski, & Poizner, 2009; Reis, Hebenstreit, Gabsteiger, von Tscharner, & Lochmann, 2014), including portable devices that can operate with minimal noise, whilst also developing paradigms that retain an adequate degree of experimental control (see Figure 1.2).

Recent technological developments have led to the advancement of portability of traditional brain imaging and behavioural measurement techniques. Research techniques that were previously restricted to laboratory settings due to hardware limitations (e.g., weight, size, battery life) have become fully portable. Whilst it is beyond the scope of the current thesis to exhaustively review available equipment (for a comprehensive review see Gramann et al., 2011), here we highlight a number of key developments that illustrate the changing landscape of tools with which cognition can be measured.

Figure 1.2. An example of the differences between a laboratory-based (left) and a mobile real-world (right) experimental setup using EEG. [1] EEG sensors, [2] Amplifier and data storage unit, [3] Stimulus presentation. Using the example of a classic face recognition paradigm, this figure illustrates the typical laboratory setup (left) in contrast to recording of real-world face recognition (right). In the latter, faces are presented in-context, while the participants are behaving naturally experiencing a real-world environment. Note that event triggers are also implemented differently, i.e., based on computer-controlled timing of stimulus presentation or on behavioural response in the laboratory, in contrast to event registration based on natural behaviour in relation to stimuli in the scene (e.g., as assessed by fixation points recorded with a head mounted eye tracking device).

The last decade has seen the emergence of compact, lightweight, non-invasive and wireless brain imaging hardware that do not hinder everyday movements, and yet still provides accurate recordings of brain cortical dynamics. Indeed, mobile iterations of electroencephalography (EEG) and functional near-infrared spectroscopy (fNIRS) systems have evolved rapidly to closely match the standards of high-density laboratory versions in both spatial and temporal resolution (Gramann, Jung, Ferris, Lin, Makeig, et al., 2014). More than just recording of brain activity in motion, mobile techniques allow brain processes to be captured ‘on the go’, in relation to natural behaviours in real-world environments (such as navigating the streets of London either on foot or as a taxi driver, choosing products in a shop, putting a golf ball, or an elderly person getting up and moving about). Importantly, early proof-of-concept studies have reported successful recording of classic EEG components during motion (Debener, Minow, Emkes, Gandras, & de Vos, 2012; Gramann, Gwin, Bigdely-Shamlo, Ferris, & Makeig, 2010; Severens, Nienhuis, Desain, & Duysens, 2012) and the detection of task-related changes in haemoglobin concentration using wearable fNIRS (Koenraadt, Roelofsen, Duysens, & Keijsers, 2014; Piper et al., 2014).

While a range of mobile imaging techniques exists, it is important to recognise that they each offer particular strengths. Multi-channel fNIRS offers a good spatial resolution over a delimited cortical surface, describing neuro-vascular changes at a cortical level, but this technique lacks the temporal resolution required to investigate fast cognitive processes. In contrast, the high temporal resolution of EEG can reveal rapid changes in electro-cortical activity related to the ever-changing demands of real-world cognition. An additional advantage of mobile EEG as a neuroimaging tool is that EEG has been used extensively in laboratory-based settings, providing a background of information against which mobile cognition data can be benchmarked. Nevertheless, as discussed below under ‘current challenges’, there are considerable methodological issues associated with the application of mobile brain imaging - and an important element of current research is to overcome these remaining issues and demonstrate the viability of mobile neuroimaging.

Methodologies used to capture behavioural responses have evolved from simple movement measures (button presses, singular body part acceleration) to the measurement of natural whole body kinematics (Aminian & Najafi, 2004). In particular, motion capture systems have become increasingly portable, allowing the positioning of multiple independent wireless sensors on a single participant, such that movement can be recorded unconstrained (Lim, Luo, Chen, & Yeo, 2011; Marin-Perianu et al., 2013). While most current motion capture solutions still require external cameras to track the position of sensors (thereby restricting the recording area), camera-less motion-capture alternatives using networks of inertial and magnetic sensors methods (exoskeleton suits composed of accelerometers, gyroscopes and magnetic sensors) may be used to detect changes in position, orientation and acceleration of body parts, allowing kinematics to be tracked in complete autonomy of external stationary devices (Luinge & Veltink, 2005; Roetenberg, Slycke, & Veltink, 2007; Zhu & Zhou, 2004). Similar to mobile EEG, wireless electromyography (EMG) systems have also been developed to record muscular activity in complete freedom of movement (Roy et al., 2013). From a mobile cognition perspective, the integration of high resolution behavioural measurements with real-world mobile brain imaging make it possible to study the cognitive markers related to natural behaviour in relevant environments. Indeed, in this context, one important role of body kinematics and EMG data may be to define the onset of behavioural responses and motor outputs (see Figure 1.3).

Recent studies have applied this multi-modal brain and body imaging approach to characterize brain dynamics related to upright walking through the integration of simultaneously recorded multi-modal data streams (Bulea, Kilicarslan, Ozdemir, Paloski, & Contreras-Vidal, 2013). By using gait dynamics such as heel strikes to time-lock continuous EEG recordings, Gwin, Gramann, Makeig, & Ferris (2011) have reported increased power spectral activity in the left and right sensorimotor cortex during contralateral foot suspension in subjects walking at a steady pace on a treadmill, suggesting increased cortical involvement related to visuo-motor integration and error monitoring. More recently, Wagner, Makeig, Gola, Neuper, & Muller-Putz (2016) reported different patterns of power spectral activity reflecting movement initiation and execution (Alpha 8-13Hz and Beta 12-30Hz desynchronization in sensorimotor and parietal cortex) and motor control and inhibition (increased frontal Beta power) during a gait adaptation task. These important early findings demonstrate the feasibility of characterizing modulations of EEG activity in relation to body dynamics through the integration of brain and body measurements. Nonetheless, whilst treadmill studies are undeniably important for establishing the feasibility of recording brain activity in motion, they inherently remain lab-based demonstrations rather than real-world applications.

Mobile technological development has also occurred for eye-trackers, which have developed into wearable devices that can track gaze dynamics during head rotations and full body motion (Babcock & Pelz, 2004; Pelz et al., 2000). As a result, mobile eye-trackers are now able to provide insight on the deployment of attention in real environments. Additionally, eye-tracking glasses are now typically equipped with a high-resolution camera enabling synchronous audio-visual recording. An increasing number of studies are using head-mounted eye-tracking devices to record natural visual exploration during natural behaviour (e.g., see Hayhoe & Ballard, 2005). Mobile eye tracking has been applied to the investigation of visual memory and motor planning of everyday-life behaviours (e.g., Mennie, Hayhoe, & Sullivan, 2007b; Pelz & Canosa, 2001), predictive eye movements in sports (e.g., in squash, Hayhoe et al., 2012), in developmental research (e.g., see Franchak, Kretch, Soska, & Adolph, 2010), and has been adopted in the context of marketing research (e.g., see Gidlöf, Wallin, Dewhurst, & Holmqvist, 2013). Here we highlight one important consequence of the development of mobile EEG and eye-tracking: in future the combination of gaze dynamics and first-person scene capture will enable the timestamping of visual events either based on fixations (Baccino & Manunta, 2005) or saccades (Jagla, Jergelová, & Riecanský, 2007) in event-related real-world brain imaging (see Figure 1.3). Taken together, the combinations of these techniques make possible the extraction of brain and gaze dynamics related to real-time, every-day, real-world cognitive processing.

1.4. Current Challenges

For the first time these mobile devices are enabling researchers to record behavioural, neural and physiological markers that reflect cognitive processing as it occurs in natural contexts, while subjects are freely exploring and interacting with their environment (Makeig et al., 2009). These new technologies allow researchers to investigate cognition in an ecologically valid and integrated manner that is more representative of the intrinsic interdependence of perception, cognition and action. But although mobile equipment is typically smaller and lighter in weight (and often wireless) than the static equivalent, they nonetheless remain subject to similar constraints in terms of data acquisition and analysis and associated methodological challenges. Furthermore, there are a number of additional methodological challenges associated with mobile cognition that require innovation.

One critical concern is the optimization of the signal-to-noise ratio, and the fact that mobile participation inevitably produces more noise (Gwin, Gramann, Makeig, & Ferris, 2010). Considering the complexity of disentangling neural signal from noise, traditionally researchers have opted to act pre-emptively by minimising the potential for “artifacts” (data unrelated to the cognitive process under investigation). For example, during EEG data acquisition, eye movements, along with facial and neck muscle activity, are prevalent sources of noise. Attempts to minimize the impact of artifacts has typically translated into avoidance techniques, instructing participants to remain still and suppress any movement not directly related to the performance of the experimental task, and requiring participants to inhibit natural reflexes such as blinks and swallowing (Picton et al., 2000). Within the mobile cognition approach, however, the aspiration is to allow natural unconstrained behaviour – precluding the use of avoidance techniques.

The introduction of motion in itself requires the wholesale re-evaluation of established practices in laboratory-based cognitive research. Success may therefore require innovation in experimental design, data processing methods, and analysis techniques to reveal the patterns hidden within real world brain dynamics. Advanced processing methods to deal with the inevitable motion-related artifacts are in development. Independent Components Analysis (ICA) (Makeig, Bell., Jung, & Sejnowski, 1996), which involves the statistical linear decomposition of EEG data into maximally independent components, can be applied to the identification and dissociation of non-brain signals (e.g. line noise, mechanical artifacts) from cognitive brain activity, eye movements and muscular activity (Delorme, Sejnowski, & Makeig, 2007).

As noted above, mobile EEG studies have successfully addressed motion-related artifacts present in data recorded during high physical activities such as running on a treadmill (Gwin et al., 2010). Equally impressively, recent study successfully demonstrated the feasibility of parsing non-brain from brain signals in subjects cycling in a natural environment (Zink, Hunyadi, Huffel, & Vos, 2016). Moreover, advanced EEG data analyses can be applied towards signal source localization based on the reconstruction of equivalent dipoles of independent components (Gramann et al., 2010; Wagner et al., 2016). However, EEG source modelling methods are essentially based on computational derivations and therefore require a feed of high-dimensional EEG data (i.e., 120+ channels) in order to reach sufficient approximations of signals' origins. While offering an interesting option for brain signal source estimation, high density EEG is still impractical for the use in real-world environments. The high-density set-up required for this approach are not truly mobile at present: for example the studies by (Gramann et al., 2010; Gwin et al., 2010) took place on a treadmill with EEG cables suspended from the ceiling. Therefore, although such solutions allow recording of brain activity in motion, they are not yet useable in truly real-world settings.

Even if high-density EEG recording was developed to allow free movement through natural spaces, advanced signal processing methods would still require sufficient amount of data points. The same is true for the most popular approach of isolating brain signals and their dynamics from the ambient noise in the raw data: time-locked averaging of many trials linked to hypothetical cognitive processes. This approach yields Event-Related Potentials

(ERP), time-locked deflections in the EEG trace reflecting sensory, cognitive and motor processes in the time domain at a milliseconds scale (Luck, 2005). Brain signals of interest (those related to events such stimulus presentation and behavioural responses) are generally uncovered by cancelling out unrelated signals through summation and averaging of multiple trials. A real concern when moving into mobile data settings is that it may be impractical (and in some cases unnatural) to record the required numbers of repetitions of a specific event. On the other hand, a distinct advantage of real-world mobile methods is the ability to record data over longer periods (e.g., during home-based monitoring of patients), making collection and characterisation of larger scale single participant data sets a real innovation.

The example of high-density recording as a solution to current challenges also flags up the issue of fully equipped participants' appearance potentially defeating the purpose of increasing ecological validity - by rendering subjects more self-conscious about the experiment and affecting their real-world interactions. Mobile EEG systems using dry sensors may be a convenient and user-friendly solution to reduce preparation time, which could make mobile EEG more accessible to patient and consumer based applications (Chi et al., 2012; Dias, Carmo, Mendes, & Correia, 2012; Zander et al., 2011). However, state of the art dry electrodes EEG systems still do not match electrodes with conductive gel applied in terms of data acquisition quality, and are less comfortable for the subjects (Oliveira, Schlink, Hairston, König, & Ferris, 2016b). From an aesthetic and convenient point of view, recent studies have proposed in ear EEG sensors (Goverdovsky, Looney, Kidmose, & Mandic, 2016; Kidmose, Looney, Jochumsen, & Mandic, 2013; Looney et al., 2012; Mikkelsen, Kappel, Mandic, & Kidmose, 2015), around-the-ear electrodes grids (Bleichner, Mirkovic, & Debener, 2016; Debener, Emkes, De Vos, & Bleichner, 2015; Mirkovic, Bleichner, De Vos, & Debener, 2016), or a baseball cap fitted with electrodes (Bleichner et al., 2015). Future developments in mobile brain imaging should therefore aim to increase the ease of use, discretion and comfort of the sensors while maximizing data quality in order to be successfully applicable in real-world settings.

Given their high temporal resolution, ERPs have been invaluable in the investigation of the time-course of cognitive processes involved in the integration of sensory inputs and motor output in the face of a dynamic reality. The major practical issue with mobile ERPs lies in the acquisition of accurate timings of such events, time-stamping the EEG trace based on stimulus presentation and behavioural responses. Whilst the time-locking of events of interest has been facilitated through the use of computerized paradigms in laboratories settings, acquisition of the precise timing of events of interest is much more complex in a natural environment. This issue is of critical importance since event-related components are investigated at a millisecond scale. A recent study by Jungnickel & Gramann (2016) demonstrates the feasibility of recording brain activity time-locked to physical interaction with dynamically moving objects. In this case the definition of movement onset was based on velocity features of behavioural responses, recorded through motion capture. The results revealed faster behavioural response times and increased neural response (P300 following target stimuli) during physical pointing, in comparison to a classic button press condition. Jungnickel and Gramann interpret these results as suggesting dynamic integration of perceptual inputs, along with the execution of complex motor outputs, lead to higher computational efforts related to embodied cognitive processes.

Another classic approach in EEG research is the investigation of changes in the frequency domain. Through spectral density estimation methods, it is possible to characterize frequency bands contribution to recorded data. Power Spectral Density (PSD) estimation methods (e.g. variants of Fourier Transform) characterize frequency bands contributions to whole epochs signals. However, this stationary approach poorly represents dynamic changes over time, central to mobile EEG. More recently however, time/frequency analyses have given insights into Event-Related Spectral Perturbations (ERSP) allowing the characterization of power spectral modulations in the time domain (Makeig, Debener, Onton, & Delorme, 2004). In addition, the characterization of interactions between remote cell assemblies could provide insight as to how different parts of the brain work together to bind multimodal information to create a coherent perceptual experience. Travelling waves analyses assess the propagation of brain signals in terms of mode and velocity, to uncover local networks connections from global fields activity (Nunez & Srinivasan, 2006). For example, recent evidence from human electrocortigraphy (ECoG) supports the idea that theta oscillations related to working memory are travelling waves, showing a spatial propagation across the hippocampus (Zhang & Jacobs, 2015). Based on a theoretical connectionist model of cognitive functions, travelling waves applied to data acquired during natural behaviours may yield insight about brain-wide cognitive networks underlying everyday life cognition.

Given the range of analytic techniques that could be applied to real-world data an important development will be the synchronization of concurrent behavioural measurements to brain dynamics in mobile settings, such as simultaneous recording and integration of mobile EEG and eye-tracking data. Merging of eye-tracking data (along with first-person audio-visual recording) would provide information about the actual timing of engagement with real-world stimuli. For example, initial fixations on an object or person can in principle be used to generate post-hoc timestamps for the analysis of EEG data. To our knowledge, there is currently no scientific publication reporting such integration of mobile eye-tracking and EEG data in a real-world environment. Even though eye-movements related potentials have been used in laboratories settings, specific technical challenges inherent to mobile eye-tracking and mobile EEG might still impede the integration of both techniques. Eye-tracking data acquired in laboratories setups is usually based on a fixed reference frame (e.g. computer screen) which allows for the segmentation of this two-dimensional frame in pre-defined Regions Of Interests (ROI). This segmentation facilitates the quantification of gaze dynamics across meaningful parts of the visual display. In the case of mobile eye-tracking recording, this frame of reference is dynamically affected by the subject's displacement across the three-dimensional planes of the environment. Therefore, the definition of ROIs in mobile environment is a significant challenge to the analysis of mobile eye-tracking data. Current options to address this issue reside in the use of optical pattern barcodes (i.e., QR codes) or infrared-based markers placed in the environment to delimit ROI. However, this approach requires ROI to be defined *a priori* and any gaze dynamics recorded outside these areas still have to be annotated and processed manually. A potential solution for the processing and analysis of mobile eye-movement data is the use of automatic mapping of the video stream through object recognition algorithms (Brône, Oben, & Goedemé, 2011). Even with these solutions to ROI definition, recording eye movements in a three-dimensional environment also requires accounting for depth, which has not been resolved yet by current mobile eye-tracking systems. Since the calibration procedure is performed on arrays of elements presented at a predefined distance, eye fixations on elements beyond the range of the calibration are usually poorly tracked by current systems and represent another major issue in the study of visual exploration in natural contexts.

As the preceding discussion highlights, there are real practical challenges in developing mobile approaches. We anticipate that the mobile cognition approach will make such multi-methods data collection more attractive across a range of measures, allowing the study of natural behaviours (Gramann, Ferris, Gwin, & Makeig, 2014) in context and thus providing greater ecological validity in the process (see Figure 1.3). The development of mobile brain imaging methods follows the same dichotomy as the current state of mobile brain imaging literature. While the initial push towards mobile neuroimaging sensors was largely driven by brain-computer interfaces applications aiming to maximize the online classification of signal components at minimal cost in terms of data acquisition requirements, a considerable number of mobile brain imaging studies have turned towards mobile systems with more sensors, in order to record the high-dimensional data required to perform advanced signal analyses. Consequently, there is now a large spectrum of hardware and software solutions, which vary in terms of their ease of setup, quality of data acquisition and cost. While the on-going competition between manufacturers may be regarded as a healthy drive in the improvement of mobile brain imaging technologies, it also seems likely that discrepancies in terms of conceptual and methodological standards (related to both data acquisition and data analysis) may slow down the progression of the field towards standard practices.

One important attempt at developing standardized frameworks for mobile technology comes from open-source initiatives designed to support the processing and analysis of mobile brain and body imaging data and facilitate their integration (e.g., MoBILAB; Ojeda, Bigdely-Shamlo, & Makeig, 2014 and Lab Streaming Layer; Kothe, 2014). While these frameworks allow for the recording and processing of multimodal data, the exact synchronization of data streams remains problematic due to current hardware limitations. For example, differences in terms of refresh rate across mobile techniques can lead to inconsistencies (or jittering) in the time-stamping of EEG data. Notably, even though current mobile eye-tracking devices now offer up to 120 Hz sampling rates, this is still insufficient to define the onset of visual events in the EEG trace with enough precision to carry milliseconds scale analyses in the time domain. Thus, whilst existing data processing schemes offer clear benefits for a mobile cognition approach, at present, the acquisition of events markers remains a non-trivial challenge to the investigation of cognition in the real-world.

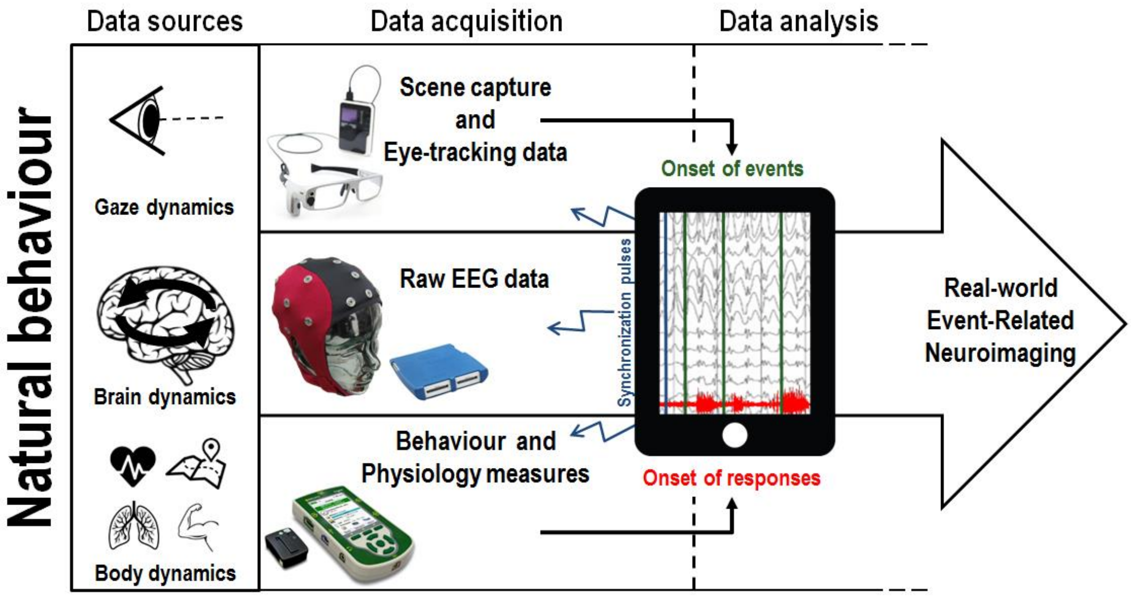

Figure 1.3. An illustration of one potential implementation of the mobile cognition approach to real-world brain imaging. Natural behaviour provides multiple sources of data, recorded concurrently, allowing the integration of mobile eye-tracking and body dynamics measurements with mobile electroencephalography (EEG). A concrete example of the application of this integrated approach can be found in a shopping situation where fixations on target objects will be use to timestamp the EEG and proceed to the classification of brain responses. We note one significant technical challenge associated with this multi-methods approach: in practice the simultaneous synchronisation of data acquisition across devices is non-trivial because each individual measure has typically been developed and used in isolation.

Besides the increased noise that inevitably accompanies cognition in motion, controlling for confounding variables will also be a significant challenge in everyday environments. Due to the rich and unpredictable nature of the outside world, inconsistencies may arise across conditions and between subjects. Whilst resolution of most of the aforementioned issues will build upon future technical improvements of the techniques, inventive experimental designs and methodological compromises will also be of critical importance to translate cognitive research into the real-world.

1.5. From proof-of-concept to cognitive research

Given the novelty of mobile technologies it is perhaps unsurprising to discover that the current state of the literature mainly consisting in proof-of-concept experiments assessing the feasibility of brain imaging in motion. Most published studies have worked towards the validation of mobile techniques through the replication of paradigms known to reliably elicit specific neural signals, such as well-known ERP components. These technically oriented studies have provided evidence that portable brain imaging can reach comparable levels of accuracy as traditional stationary devices within the same stationary laboratory setup (De Vos, Kroesen, Emkes, & Debener, 2014; Dias et al., 2012; Gargiulo et al., 2008; Liao et al., 2012), and also during treadmill walking (Gramann et al., 2010; Lin, Wang, & Jung, 2014; Severens et al., 2012). This body of research has pinpointed technical (e.g. ensuring the necessary sensor connectivity during whole-body movements), methodological (e.g. time-stamping of events in real-life situations) and mathematical questions (e.g. tackling motion artifacts) posed by mobile brain imaging (for a review, see Reis, Hebenstreit, Gabsteiger, von Tscharner, & Lochmann, 2014). Hardware and software solutions have been developed in response to these issues of concern (e.g., MoBI; Gramann et al., 2014), providing a solid framework to progress to the next step: addressing actual cognitive questions in natural environments.

Interest in mobile cognition can be found across a number of different fields in neuroscience – the relevance of real-world cognition has been highlighted for sport (Cheron et al., 2016; Park, Fairweather, & Donaldson, 2015), ergonomics (Mehta & Parasuraman, 2013), dual-task paradigms (De Sanctis, Butler, Malcolm, & Foxe, 2014a), spatial cognition (Mavros, Austwick, & Smith, 2016) and mental imagery (Kranczioch, Zich, Schierholz, & Sterr, 2014). Increasing numbers of studies are investigating cognitive processes during full-body motion in the real-world. Perhaps the clearest example to date is provided by Debener and colleagues (Debener, Minow, Emkes, Gandras and de Vos 2012), who used an auditory oddball task to elicit P300 ERP effects. The P300 is a well-characterised and much studied EEG marker found during the presentations of a series of frequent distractors versus infrequent odd-ball targets (discussions regarding the functional role of the P300, its interpretation and experimental paradigms used to elicit it will be discussed in more details in Chapters 3 & 4). Debener and colleagues (2012) recorded the P300 in a seated-indoor condition versus an outdoor-walking condition. An attenuation of the P300 ERP amplitude was reported in the walking condition in comparison to the sitting condition. While classification rates of single-trial ERPs were above chance levels for both conditions, the signal-to-noise ratio (SNR) was lower in the walking condition, suggesting an increased amount of noise in that condition. Whether these differences were a consequence of residual noise or due to a reallocation of cognitive processing resources in the outdoor-walking condition remained open for future investigations. A follow-up study compared outdoor-walking with being seated outdoors, finding equivalent P300 effects in each case (De Vos, Gandras, & Debener, 2014). Importantly, a similar degree of noise was found in walking and seated conditions, suggesting that the muscular activity involved in walking did not result in increased movement-related noise. Furthermore, Zink et al. (2016) have reported a decrease in P300 amplitude during an outdoor cycling condition in comparison to a fixed bike conditions. The increased cognitive load related to natural real-life behaviours appeared to be a major factor contributing to the difference observed in ERP waveforms between conditions.

Why these natural behaviours (i.e. walking, cycling) should reduce attention (as indexed by changes in the magnitude of the P300) compared to being seated indoors remains unexplained – is an important question for future research. Regardless, and more relevant here, the studies by Debener and colleagues demonstrate the feasibility of truly mobile EEG recording in the real-world. Whilst there is relatively little published data thus far, existing studies have aimed primarily at testing and validating mobile cognition methods using traditional well-established paradigms from the lab setting as benchmarks (Oliveira et al., 2016b). Critically, the evidence to date provides strong proof of concept regarding the basic feasibility of a mobile cognition approach (e.g., Figure 1.4.). It is important to recognise however, that whilst the demonstration of proof of concept was necessary and provides confidence in the mobile methods going forwards, it did not directly contribute to further our understanding of real-life cognition, *per se*. Moreover, Kingstone, Smilek, & Eastwood (2008) argue that the legacy of laboratory-based practices and experimental protocols may induce bias in the capture of the expression of human cognition in complex environments. For further progress to be made, future mobile cognition research must not focus solely on mimicking lab-based research, but should also investigate human cognition from an embodied, integrated and ecological perspective – assessing more naturalistic real-world behaviour (e.g., Figure 1.5.).

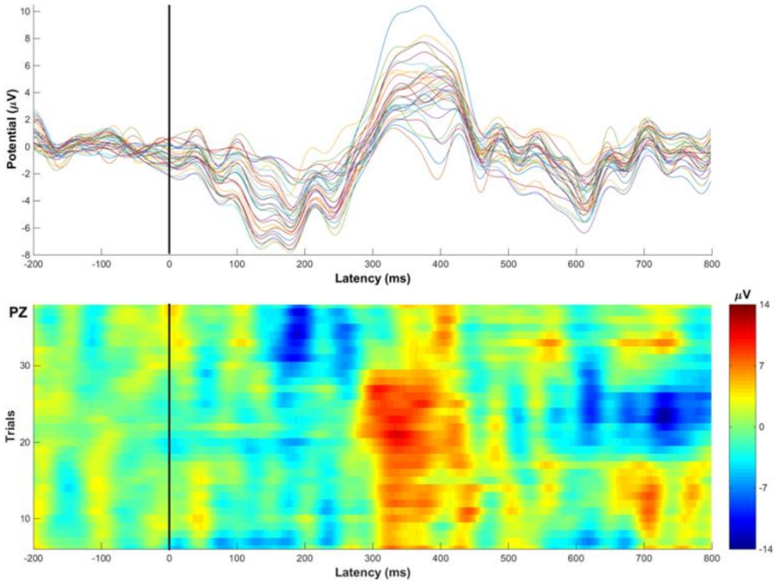

Figure 1.4. Illustrative single-subject ERP example recorded while the participant walked around the corridors of Stirling University performing an auditory oddball task (eliciting the classic P300 Event-Related Potential). Top: Average ERP waveforms across 32 channels, the P300 amplitude is most prominent at mid-parietal electrode sites, showing the classic P300 scalp distribution. Bottom: 36 single-trial Event-Related Potentials of target stimuli classically recorded at Pz electrode displaying consistent amplitude peaks 300ms after stimulus onset. Examples of mobile EEG findings can be found in the literature (e.g., Debener et al. 2012; Zink et al. 2016). This figure of single-subject raw data provides a visual demonstration to show that ERPs can be reliably recorded across trials and electrodes during locomotion in the real-world.

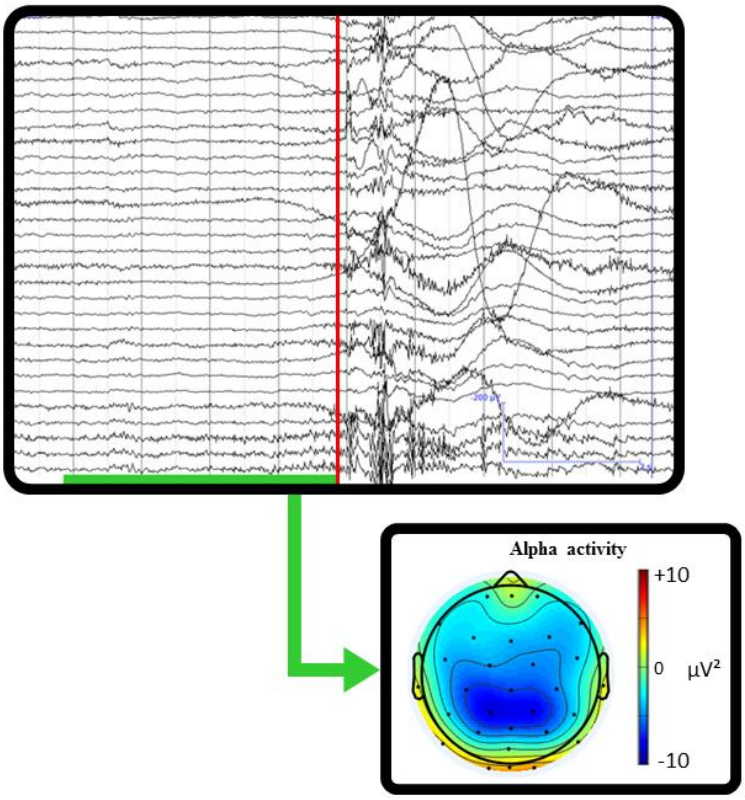

Figure 1.5. Single-subject real-world example of mobile EEG recording while taking a penalty kick. The red line marks the timing at which the ball was hit. The green underlined time interval represents where the participant is mobile, stepping up to kick the ball. The topographic scalp map shows the averaged alpha activity during the pre-shot interval before kicking the ball. This example recording illustrates how the integration of behavioural markers with mobile brain imaging could allow insight into cognitive processing related to natural behaviours. The quantification of changes in power spectral activity related to the execution of goal-oriented actions would provide information about the cognitive aspects related to real-world sporting behaviours.

1.6. Implications

The vision of a mobile cognition approach has the potential to add considerable value to existing laboratory based cognitive neuroscience: indeed, there are many research questions that can only really be sensibly addressed in real-world contexts. Take, for example, the study of spatial navigation. To date, in humans, the examination of neural correlates of spatial cognition has been limited to a small subset of the questions that are examined in non-human animals. Many studies in rodents allow free-movement through space, whereas human studies typically do not – for example, they employ fixed location map reading tests, or at best, Virtual Reality (VR) devices to simulate the exploration of an environment while offering the experimental control of a laboratory setting. However, we already know that the act of moving is central to navigation. For example Ehinger et al. (2014) have shown that the integration of vestibular and kinaesthetic information (provided through the navigation of the physical body in the environment) modulates brain activity in the alpha frequency band. These findings demonstrate that sensory and vestibular feedback are essential parts of spatial navigation that are neglected in lab-based navigation experiments. As a result, an obvious application of the mobile cognition approach is the study of the how we explore and navigate in real-world environments. We envisage participants navigating around complex environments (maze like corridors of large buildings, or around parks or city centres), performing route-finding tasks in the real world, whilst wearing a host of mobile cognition sensors. Such an approach would allow researchers to see whether there are human analogues of the phenomena seen in rats (e.g., place, head direction and speed signals), which to this point have only been assessed in virtual navigation tasks (Maguire et al., 1998; Ekstrom et al., 2003; Doeller et al., 2010; Jacobs et al., 2010; see Taube et al., 2013 for a critical review).

The mobile cognition approach is also particularly suited to investigating attention. Current understanding of attention is mainly based on visual exploration studies that have used static scenes (or at best moving images), while participants are stationary themselves. These studies necessarily place participants in a relatively passive spectating perspective, potentially over-emphasising top-down influences on visual exploration. Indeed, the artificial nature of the stimuli or the task, and the restriction of participants' behaviour, all inevitably lead to a very specific context that does not involve the same interaction between perception and action that can be found in complex and dynamic environments. The deployment of (visual) attention in the real-world may therefore be more sensitive to bottom-up influences, emphasising the dynamic integration of information coming from multiple external and internal sources. Consider, for example, the role of attention when shopping: a large amount of information must be attended to in real-time – providing feedback that allows us to reorient our attention on elements of our surroundings that matter at that very moment, and allows us to adjust our movements to satisfy our goals. In this context, the interdependence between perception, cognition and action is clear, and forces attention to be considered alongside the integration of sensorimotor information, during interaction with our environment. Whether existing theoretical accounts of attention produced within laboratory settings can accommodate the varieties of attention found in real-world settings remains to be seen.

Moving towards a mobile cognition framework will also lead to changes in the way that problems are approached. For example, in the context of motor cognition, we predict a move away from stereotyped, relatively narrow, response options, towards more complex, self-generated and spontaneous movement. On this basis, the investigation of sporting behaviour can move away from examining the impact of sporting expertise on the performance of abstract laboratory-based tests (e.g., demonstrating that the P300 elicited by auditory oddballs is larger in elite athletes). Instead athletes can be examined whilst performing real sports behaviour (cf. Park et al., 2015), in real-world environments. Such an approach is more likely to deliver correlates of predictive value. Laboratory performance may not produce effective predictors of sporting performance, while mobile cognition should capture the highly adaptive and integrated complexity of sporting behaviour, producing models with far greater applied relevance. Similarly, for health science, a mobile cognition approach could add considerable value by producing evidence-based interventions of real societal application. For example, we may be able to better predict (and therefore help prevent) falls in the elderly if models fully capture the multi-modal, integrative and environment-based nature of the problem – evident in the act of getting up from the chair to answer the door (for example, Nieuwboer et al., 2007). Equally, for rehabilitation following brain injury such as stroke, or when considering the consequences of dementia, it seems particularly important to have an understanding of the cognitive processes in the complex, dynamic, modality integrated reality of real-life settings.

The potential of a mobile cognition approach in terms of clinical applications is particularly likely to be far-reaching. One obvious first step is to examine problem behaviours, such as falls in the elderly, using real-world monitoring to capture the physiological and neural precursors of relatively rare but critical behavioural errors. Monitoring brain states of patients at home may yield crucial information to devise and adjust informed medical decisions (e.g. stroke and epilepsy patients; Askamp & van Putten, 2014). The possibility to record brain activity during whole body motion and the related processing methods to handle motion artefacts allow to study populations that experience difficulties to remain still such as children and patients suffering from motor impairments (e.g., ALS, Parkinson's disease). In the future, mobile techniques may be integrated to cognitive rehabilitation strategies under the form of neurofeedback and the online acquisition of cognitive biomarkers metrics could be used by medical practitioners as tailored and ecological assessment tools to assist in the diagnosis and rehabilitation processes of patients affected by various neurological aetiologies.

Venturing away from highly controlled laboratories-based experiments opens up a range of new research questions, adding value to the traditional cognitive neuroscience approach. The work presented in this thesis capitalizes on recent technological breakthroughs to investigate aspect of human cognition under real-world circumstances. It is important to note that even though the present thesis has been focusing on the application of mobile EEG technology to investigate embodied aspects of human cognition, the vision of a real-world approach to study human cognition is nevertheless not restricted to that particular research method. Moreover, despite the fact that an important part of the initial work had to be dedicated towards addressing conceptual and methodological issues related to the acquisition of real-world EEG data, the main focus of this research concerns the study of cognitive processes in natural contexts.

In this general introduction, the rationale, challenges and implications relative to the application of a real-world approach to the study of human cognition have been discussed. The next chapter will document the solution development process required to address the specific issues related to the acquisition and analysis of real-world EEG data. The resulting processing pipeline used within this thesis will be detailed, and rationale underlying its design will be provided at the light of a critical review of signal processing state of the art. The following empirical chapters will report the application of a real-world approach developed through series of studies across which brain dynamics associated with cognitive functions were recorded during natural behaviours in real-world environments. This body of work present technical, conceptual and theoretical implications. First, it provides proof-of-concept demonstrating the feasibility of recording real-world EEG during active behaviour.

Secondly, the conceptual implication of the work is that cognitive markers recorded in real-world environments are different than in laboratory settings. Because such evidence of the singularity of real-world cognitive markers could not be demonstrated before, the work offers an innovation on traditional EEG research and has significance for both the understanding of human cognition and the application of technologies of brain and behaviour in the real-world. Theoretically the work further contributes to our understanding of the mind as embodied. These implications are discussed in the general discussion, as well as the limitations of the work and future avenues for real-world cognitive sciences research. Thirdly, this is of theoretical significance as it demonstrates embodied aspects of human cognition. Finally, the General Discussion will provide a summary and make connections between findings issued from the different studies while critically addressing the limitations of the presented research. The theoretical implications of the presented findings will be examined at the light of previous literature and future directions for cognitive research in the real-world will be discussed. Moreover, the potential of a mobile cognition approach within the frame of real-world applications will be developed and illustrated by examples of clinical interventions based on extensions of the present findings.

Chapter 2: Solution development for the recording, processing and analysis of real-world EEG dynamics

Mobile brain imaging methods offer exciting new research prospects, allowing the exploration of previously uncharted territories of human cognition. In practice, however, the acquisition and interpretation of electrophysiological signals during the execution of whole-body movements, in natural settings, presents many methodological and conceptual challenges. This chapter will detail the problem-solving process developed within the frame of the present thesis to address the unique challenges of EEG data recorded in the real-world. Due to the novelty of recording brain activity during active behaviours, innovations in how brain signals were acquired, processed and analysed were required to ensure the validity and high quality of the data upon which interpretations are drawn. The present chapter will therefore introduce issues relative to real-world EEG recordings and propose solutions to address those issues. As this chapter essentially focus on the specific problems relative to the recording of mobile cognition data, generic steps that are not specific to mobile EEG (e.g., material, recording preparation, experimental setup procedure) or that are related to a specific study (e.g., experimental design) will be detailed in methodological sections of the corresponding empirical chapters (see Figure 2.1). The structure of the present chapter reflects the progression from the acquisition to the analysis of the data. The implementation of solutions to address the issues relative to real-world EEG data will therefore be presented following a chronological order throughout the stages of data acquisition, data processing and data analysis.

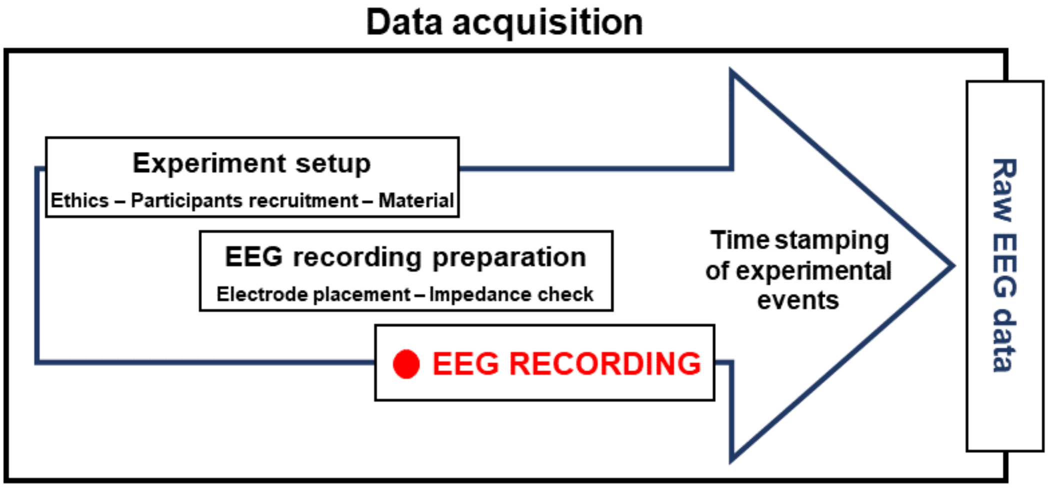

Figure 2.1. Timeline of the different procedures involved prior to data acquisition.

2.1. Methodological challenges of mobile EEG

Traditional lab-based EEG studies secure good signal-to-noise ratios (which is critical for the collection of high quality data), by carrying out experiments in highly controlled environments (i.e., laboratory and clinical settings). Moreover, traditionally, subjects were required to perform as little movement as possible, including being instructed to refrain from swallowing and blinking during recording sessions. These pre-emptive measures yield good results in increasing the signal-to-noise ratio, for example by reducing the occurrence of muscle and eye movements related noise observed in the EEG trace. However, their validity has been questioned, for example with regards to the additional cognitive workload involved in suppressing natural reflexes and behaviours. In effect, such procedures represent a secondary cognitive task, leading to the undesirable recruitment of inhibitory mechanisms that contaminate the cognitive processes that were meant to be under investigation.

One of the drivers of the present research is to depart from the confines of the laboratory and fully exploit the portability of modern technology. The aim is to apply brain imaging methods directly to real-world situations, with the ambition to capture ecological measurements of human cognition. In this context, traditional compromises such as restraining participants behaviour and neutralizing variability found in real-world environments are not adequate solutions to address signal-to-noise issues because they inherently prevent the capture of human cognition in its most natural and ecologically valid expression. Therefore, alternative options and novel techniques have to be considered to deal with unconventional (but natural) sources of noise in EEG data. The main methodological challenges related to the acquisition of real-world EEG data concern the definition and how to acquire event-related brain signals but also how to ensure the validity and high quality of the data recorded.

2.1.1. Acquisition of event-related brain signals in the real-world

2.1.1.1. Problem context

In contemporary laboratory-based EEG research, the timestamping of the EEG trace has become a trivial issue thanks to the development of computerized stimulus presentation software that directly communicates the onset of events to the recording amplifier. By contrast, acquiring such information represents a significant challenge within the frame of mobile brain imaging. Indeed, the occurrence and timing of meaningful events during the capture of real-world brain activity may be partially out of control of the experimenter and participants reactions latencies may be unpredictable. As the implementation of computerized paradigms may not always be suited for the purposes of mobile brain imaging experiments taking place in real-world environments, the acquisition of events timings is a challenging issue to address. Therefore, other informative sources are required in order to retrieve information related to experimental events with enough temporal precision to allow for accurate EEG time-domain analysis.

2.1.1.2. Potential solutions

One solution to the problem of time stamping is to rely on other measurement methods to provide information about the time course of concurrent body dynamics (e.g., increase heart rate, muscle contraction, pupil dilation, gait cycle and other body kinematics). For example, eye movement data acquired from an eye-tracker could therefore provide information about the timing of visual events in the real-world. Motion sensors and electromyogram (EMG) could be used to track the onset of movements related to the task. EEG could then, in turn, provide insight regarding the electrocortical activity related to gait cycles, motor execution during complex movements, or displacement of visual attention in real-world environment.

While the aforementioned methods are all associated with hardware that have followed the trend of miniaturization with portable solutions available, technical limitations still impede their successful synchronization with EEG. A first requirement is to be able to align the different data streams. For this purpose, it is necessary to have a means of communication between recording devices, to send triggers that will be registered by each system internal clocks to align and synchronize the data streams. A second requirement is the need for equivalent high temporal resolution in each of the complementary data streams. To carry out analyses of brain dynamics at the milliseconds scale, it is crucial to have a highly accurate measure of the timing of events onset. Indeed, any discrepancy between the timing of experimental events and their markers will lead to lagged ERP features, which will likely invalidate the analyses. Furthermore, variance in the timing of event markers will not only invalidate any interpretation of ERP components latencies, but also lead to a reduction or even complete disappearance of effects, because the jittered signals will no longer be phase-locked, rendering their representation in the time-domain invisible. While consistent lag can be corrected post-hoc (assuming that the magnitude of the delay is known), any unknown variance in event marker timing cannot be accounted for and therefore adds additional temporal variance to the measured neural response resulting in changes to both the timing and magnitude of the measured effect.

In practice, temporal resolution is directly linked to the sampling rate of the recording device, and should reach a minimum of 250Hz for time domain EEG analysis purposes. This requirement does not pose any issue for most physical and physiological contingent measures. For example, EMG and ECG systems, which typically sample data over 1kHz. By contrast, mobile eye-tracking devices do not currently present sampling rates higher than 125Hz for pupil position tracking, and 60 frames per seconds for video recording from the mounted cameras. This lower temporal resolution implies that synchronization of data streams may involve an unaccountable lag of tens of milliseconds (comprised within the interval between two data points of the slowest recording). As a result, the timestamping of every event recorded through the lower temporal resolution device would therefore induce unquantifiable lag, introducing trial-to-trial latency variability.

2.1.2. Motion artifacts and other noise during natural behaviour

2.1.2.1. Problem context

In EEG recordings acquired in controlled environments, non-brain signals are easily identified because they exhibit characteristic topographies and significantly larger amplitudes than genuine brain signals (e.g., eye movement related activity prominently recorded at frontal electrode sites). As discussed in the General Introduction, natural behaviours and their increased muscular activity pose unprecedented challenges in terms of signal processing for human brain electrophysiology research. Indeed, in the case of mobile EEG, a wide range of muscle and movement-related sources of noise occur in addition to the artifacts usually found in lab-based EEG data. For example, when recording the brain activity of subjects navigating the environment, while enjoying complete freedom of movements introduces motion-related artifacts that were usually cautiously avoided. Moreover, because these kinds of artifacts have rarely been documented, effective solutions to deal with these novel sources of noise in the EEG remain scarce. Even through sporadic manifestations, artifacts can have a substantial impact on the measures computed from the data, leading to significant errors in interpreting the data. Given the problems with artifacts described above, it is imperative to cleanse EEG data of as much non-brain artifacts as possible, so that meaningful interpretation can be drawn from the resulting signals.

2.1.2.2. Potential solutions

The following section presents solutions that address the unique challenges posed by mobile brain imaging methods in terms of data processing and analysis. Current solutions to deal with brain imaging data recorded during natural behaviours are critically reviewed. The data processing pipeline used within the frame of the empirical work presented in this thesis is then detailed, and its current limitations are acknowledged at the light of the critical review.

2.2. Processing pipeline for mobile EEG data

This section outlines the signal processing methods that have been included in the pre-processing pipeline developed in the present thesis to deal with the inherent challenges of mobile EEG data. The following sections present the different processing steps involved in disentangling non-brain activity from brain signals and subsequently characterising relevant properties of cleaned data to address the specific research hypotheses of each study. Each of these steps will be introduced, and the logic of their implementation within the processing pipeline will be discussed (see Figure 2.2 for a schematic representation). EEG recordings offer a complex and multidimensional data. To extract meaningful information from the raw data, researchers have the choice between a wide range of signal processing methods. Furthermore, each of these processing methods can be adapted to address the specificities of the data. Therefore, researchers face a multitude of choices throughout the processing of EEG data, which can have significant implications on data analyses outcomes, with incorrect practice likely invalidating any interpretation of the data (Luck & Gaspelin, 2017). It is therefore necessary to carefully select effective and adequate signal processing methods to ensure the validity of analyses outputs. Theoretical considerations that have informed the design of the processing pipeline will be discussed. In practice, parameters employed in the processing of each study was tailored to the data properties and the research question under investigation. The rationale behind the objective selection of specific parameters will be discussed along with their implications on EEG data.

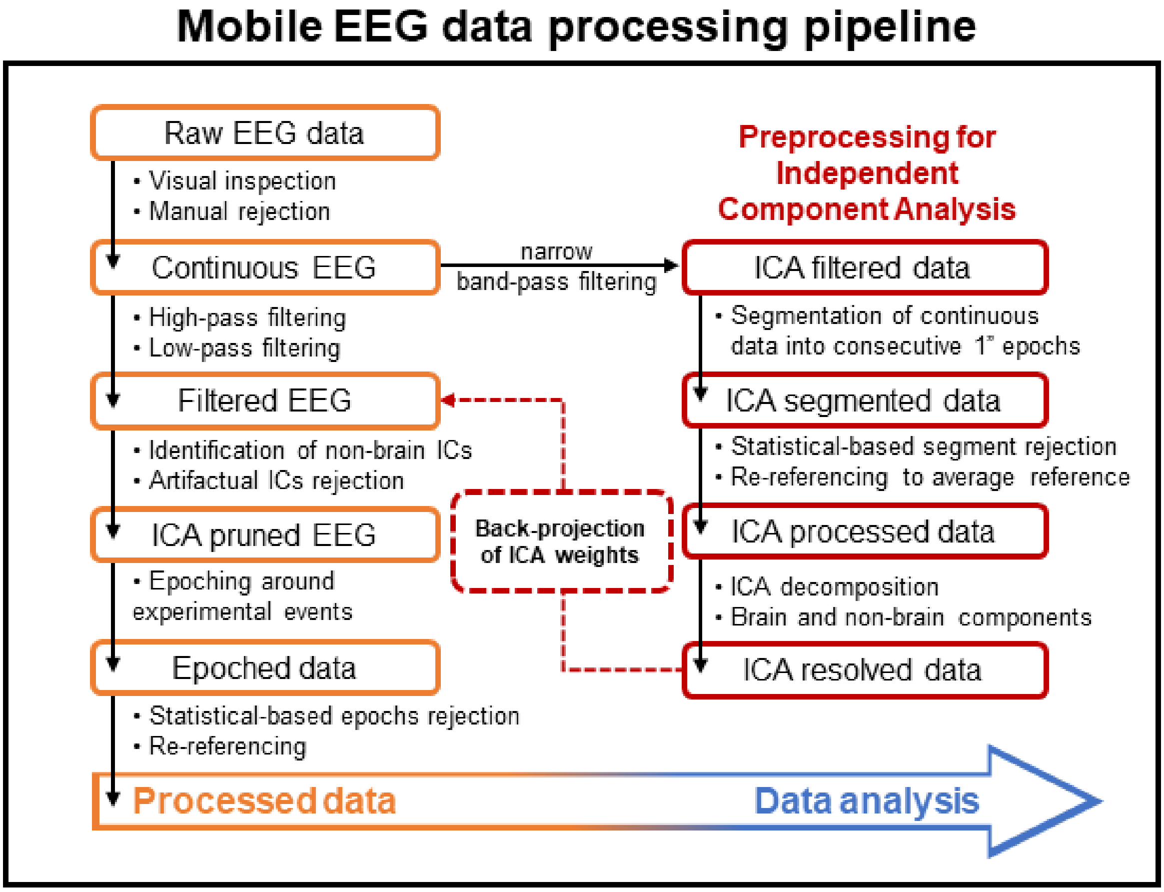

Figure 2.2. Schematic representation of the different steps included in the EEG data processing pipeline applied to the data collected within the frame of this thesis. The orange rectangles represent the different stages of the main processing procedure applied to the data. Following an initial inspection, noisy portions of the raw EEG are manually rejected. The EEG continuous data undergo parallel processing procedures. The processing steps represented by the red rectangles detail an "aggressive" preprocessing approach that aims to optimize ICA decomposition by reducing the complexity of the signals. Once both the normal filtering (orange) and the parallel ICA procedure (red) are completed, the weights of independent components contributing to the signal are back-projected to the normally filtered data. The advantage of such procedure is that independent components are extracted with greater sensitivity without compromising data dimensionality. Artifactual components are then identified and rejected. The pruned continuous data is then epoched around experimental events upon which statistically-based rejection methods are applied. The processing is concluded by the re-referencing of the epoched data accordingly to the dynamics investigated. The processed data is then subject to data analysis.

2.2.1. Filter design

Mobile EEG data displays a range of noise across the lower end of the frequency spectrum (e.g., slow channel drifts oscillations at seconds scale) but also at higher frequency (e.g., signal response saturation across channel during muscular contractions). The contribution of noise specifically affecting the ends of a certain frequency range can be effectively attenuated through the use of band-pass filters. The following paragraphs introduce filtering and review critical aspects to consider within the frame of filter design. The filtering solutions applied to the data included in this thesis are then presented and their efficiency in reducing real-world EEG noise is discussed.

When dealing with Alternating Current (AC) signals, frequency filtering is a ubiquitous preprocessing step commonly used to attenuate noise, while preserving signals of interest. The application of filters reduces the contribution of spectral activity outside of the boundaries of frequencies of interest, highlighting the unfiltered frequency range. Filtering of EEG data can help remove high-frequency noise (e.g., muscle activity above 30Hz, see Brown, 2000 and Brown, Salenius, Rothwell, & Hari, 1998) through low-pass filters (which only attenuate higher frequency activity). In addition, filtering can remove low-frequency drifts (e.g., power at the “0Hz” DC component, impedance variations due to sweat or micromovements of sensors) through high-pass filters (which only attenuate lower frequency activity). The combination of low and high-pass filters is commonly referred as band-pass filtering (see Figure 2.3). for an example of band-pass filtering implementation). In contrast, notch filters (i.e., a filter that only attenuates a very specific range of frequencies) are commonly used to attenuate electrical line noise from mains currents; typically at 50Hz (in most parts of the world) and 60Hz (in the US and in few Asian/North American countries).

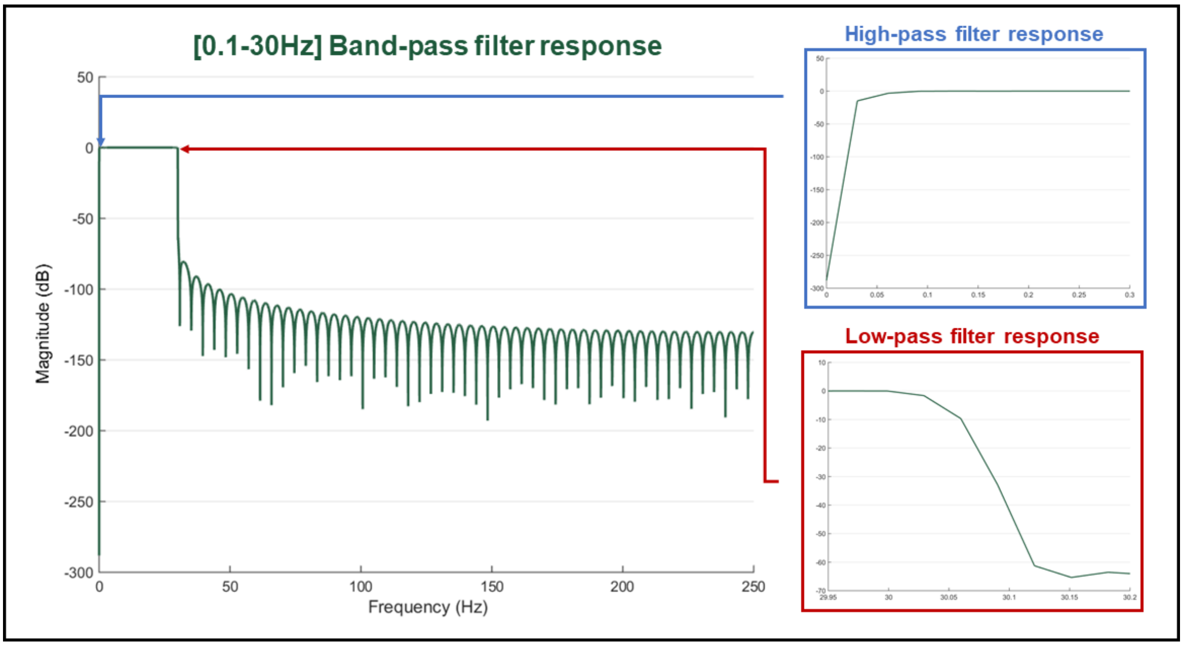

Figure 2.3. Filter responses following the application of a 0.1-30Hz zero-phase Finite Impulse Response band-pass filter. The figure highlights the effect of the high-pass (blue) and low-pass (red) filters, illustrating their consequences at the transitions bandwidths. Cut-off frequencies were adjusted for each filter (respectively 0.05Hz and 30.05Hz) with regards to the steepness and width of the filters, so that the lower and higher edges of the pass-band would match the selected pass-band boundaries.

Even though the choice of filters used during pre-processing is primarily determined by the frequencies of interest and is therefore relative to the aim of the experiment (i.e., hypothesis-driven, based on cognitive processes and brain structures under investigation), technical aspects in the selection of filter parameters also need to be considered during their implementation. An accurate understanding of the theoretical consequences of filtering is important to avoid adverse side effects, such as distortions of the signal and the introduction of filter artifacts (Rousselet, 2012). In the context of real EEG data, where noise and genuine brain signals may present overlapping activity at certain frequencies, filtering can result in the incidental attenuation or distortion of the signal of interest (Tanner, Morgan-Short, & Luck, 2015).

Throughout every step of filter designing, researchers face a trade-off between aggressive filtering parameters that could potentially alter the signal of interest and softer filtering parameters that would not attenuate as much noise. This dilemma is a longstanding and unresolved source of discussions between researchers within the field of human brain electrophysiology. Indeed, the appropriate approach to the selection and implementation of adequate filtering parameters can have significant impact on an experiment's outcomes. For example, some authors argue against high-pass filtering of EEG data because it can lead to systematic bias of some signal components (Acunzo, MacKenzie, & van Rossum, 2012; Luck, 2014; Maess, Schröger, & Widmann, 2016). Equally, other authors warn against low-pass filtering that may invalidate the interpretation of some aspects of filtered data in the time-domain (VanRullen, 2011).

Ideally, filters should be designed in such a way that none of the spectral component of the signal of interest is attenuated, but at the same time, as much noise as possible is removed. The design of frequency filters usually involves selecting which frequencies to include/exclude to define the band-pass thresholds, indicating a) what type of filter (i.e., Infinite Impulse Response (IIR) versus Finite Impulse Response (FIR); gaussian versus plateau shaped filters) will be applied, and b) the filtering strength (i.e., how much the filtered frequencies will be attenuated). The filter roll-off (i.e., the width of the transition band between the frequency being allowed versus removed by the filter) has particularly important implications. Filters with a steep (i.e., fast) roll-off will introduce distortions of great magnitude over only few neighbouring frequencies. By contrast, shallow (i.e., slow) filters will introduce less signal distortions, but in a wider range of frequencies neighbouring the filter cut-off.

An important aspect of filter design to take into consideration is that changes induced by filtering in the spectral domain have direct consequences in the time domain. Indeed, any alteration (i.e., attenuation or delay) of the frequency spectrum of a signal will inevitably lead to changes in its temporal domain, because both representations of the signal are co-existent dimensions that are coupled together by the Fourier Transform (Widmann, Schröger & Maess, 2015).

In practice, many of the processing steps carried on raw EEG data act as filters. For example averaging trials in the time-domain acts incidentally as a low-pass filter for frequencies that are non-phase-locked (i.e., most frequencies above 15Hz tend to be non-phase-locked, see Widmann & Schröger, 2012). Nonetheless it is useful to apply low-pass filters when computing time-domain ERPs to reduce remaining aliasing effects (i.e., different spectral features of the signal cannot be distinguished from each other when sampled in the time domain) induced by high frequency activity of the signal. By minimizing residual high-frequencies noise, low-pass filtering smooths the averaged waveform (i.e., anti-aliasing by under-sampling), which further facilitates the extraction of component features based on peaks (e.g., peak amplitude, peak latency) and reduces the probability that high frequency noise (e.g., spikes) would be classified as such peaks.

Another crucial aspect to take into account when designing filters is their implementation in the temporal domain. Epoched data usually consist of short segments (e.g., one second time windows) of the continuous recording and can be susceptible to edge artifacts introduced by low-pass filters (e.g., a 0.1Hz high-pass filter may distort up to 10 seconds of the following data). While epoch filtering is sometimes used online within the frame of Brain-Computer Interfaces installations, alternatives introducing lesser edge artifacts are usually preferred for offline EEG data processing purposes. To avoid edge artifacts, all filters were applied to continuous EEG data at early stages of the preprocessing procedure.

Finally, it is important to note that the frequency filters designs used in the present thesis were adapted with regards of the specific hypotheses under investigation. Parameters were adjusted to improve the signal-to-noise ratio of components of interest, while introducing minimal distortion. For time-domain analysis of ERP (Studies 1, 2, 3 and 7), FIR filters were implemented with cut-offs at 0.1Hz for the high-pass filter, and 20Hz for the low-pass filter, with a -6dB roll-off. In studies looking at spectral dynamics of ERP (Studies 4, 5 and 6), FIR filters were implemented with cut-offs at 0.1Hz for the high-pass filter, and 125Hz for the low-pass filter, with a -6dB roll-off. Filters were consistently implemented at early stages of the preprocessing pipeline and prior to segmentation of the continuous data into epochs.

2.2.2. Parsing non-brain signals from real-world EEG data

As the traditional pre-emptive ways of avoiding sources of noise by restraining participants behaviour are not relevant within the frame of ecologically valid real-world brain imaging, alternative solutions are required to address issues of noise artifacts contaminating the EEG data. Frequency filtering in itself is merely used to attenuate frequencies outside the range of current investigation. In practice, however, there may be overlap between brain and non-brain signals across the frequency spectrum and the selection of ever narrower bands may lead to distortions of the original data, eventually biasing the interpretation of the data collected. Therefore, filtering cannot be considered as a sufficient processing step on its own, not least because it does not directly parse non-brain noise from signals originating from brain sources.

2.2.2.1. Limitations of statistically-based data rejection

Another commonly used signal processing method to deal with noisy segments of electrophysiological data has been the rejection of segments containing out-of-bounds values. Single or even multi-channel data comprising unlikely patterns of oscillations in the frequency domain or abnormal voltage peaks in the time domain, may be selected and removed because they are considered to reflect non-brain signals (e.g., signals originating from eye movements or muscular activity). This straightforward statistically based rejection approach of discarding entire sections of the EEG trace presenting abnormal values has been widely used in traditional human brain physiology research. Importantly, however, the definition of thresholds used to delimit sections of data considered to be non-brain signals are based on statistical properties of the continuous EEG recording (i.e., computed across the entire data). This method therefore relies heavily on the assumption that the continuous EEG data is free of non-brain signals (for the most part) and that noise only occurs sporadically. While this might hold true for recordings acquired in highly controlled environment, it is less likely to apply to EEG data recorded during natural behaviour where periods of absolute stillness – free of motion artifacts – may be rare or even non-existent. Moreover, the statistical rejection approach also implies discarding of any data outside the parameters used, which can lead to a loss of a considerable proportion of the data in the case of recordings presenting high variability of the features used to define the threshold boundaries.

Arguably the selection of parameters used in statistical based rejection methods may not be entirely objective and could therefore eventually lead to bias. Similar to frequency filtering, statistical-based rejection methods are merely a mean of reducing the prevalence of noise in the data without disentangling brain from non-brain signals. As a result, statistical rejection methods must be implemented carefully, because their incorrect application may lead to threshold boundaries that are too lenient, in which case the processed data will still contain abnormal signals. Equally, thresholds may be too strict, which may result in an insufficient number of epochs remaining after rejection for the performance of analyses based on trial averaging. In mobile EEG data, the prevalence of noise originating from movements and eye movements is likely to be higher than in lab-based experiments. It is important to recognize that effective data processing requires a compromise between the identification and removal of noise, and the potential for loss of real brain signals. The methods are ineffective if the underlying data contains too much noise. In this context, relying on strict thresholds to reduce noise in the data at later processing stage may lead to the rejection of the majority of the data. By contrast, if data is relatively clean and previous processing steps have substantially reduced noise prevalence and data variability, it is unlikely that the application of stringent thresholds to the cleaned data would lead to incorrect classification of brain signals as noise.

Within the frame of mobile EEG recordings, the amount of data recorded is not the sole resort of the experimenter but also highly dependent on the nature of the experiments. For example, in most of the studies reported in this work, the participants had to walk through long corridors for extended periods of time (trial duration was therefore mostly dependent on the length of the corridors as the natural walking pace was found to be highly consistent across participants). As a consequence, the number of trials had to be defined considering physical and mental fatigue related to continuous walking over long period of time that could alter the cognitive processes investigated and related issues such as the increased risk of sweat during long recording of active behaviours that would result in channel saturations. These practical considerations effectively limited the total amount of data that could be recorded while maintaining sufficient data quality. Considering the inherent limited number of trials recorded in real-world EEG studies and the prevalence of noise, it is therefore not advised to apply statistical rejection to the raw mobile EEG data in order to discard non-brain signals, as only few epochs would survive the rejection criteria.

In order to address the issues regarding the loss of signal of interest using traditional filtering and statistical data rejection approaches, modelling techniques can be used to selectively discard improbable signals from mobile EEG data. Thus, in the present thesis, intermediate processing steps were included in the processing pipeline to further reduce variability of the data related to non-brain sources, before successful application of standard rejection methods.

As mentioned previously, while frequency filtering and rejection of statistically outlying data may help attenuate noise and therefore help reducing its impact in later analysis of the epoched data, these methods do not provide a definitive solution to characterizing and quantifying residual noise, nor to isolating its sources. In addition, the pervasiveness of noise in mobile EEG data is an issue that cannot be dealt with solely by mere rejection of noisy segments and attenuation of a selection of frequency bands considered at fault – because the majority of the continuous data includes artifacts that contaminate an extended range of the EEG spectrum. Therefore, additional methods for detrending and selectively attenuating the contribution of artifacts to the signal are especially necessary for mobile EEG recordings.

Before outlining modelling approaches in detail, here we first briefly highlight how filters and statistical rejection methods were applied in the current thesis. Criteria used for the epochs rejection are based on properties of the channel participant data, channel-epoched data kurtosis distribution, absolute power and voltage thresholds, as implemented in the EEGlab toolbox. Whenever a value was identified as an outlier (above 5 standard deviations around the mean of all trials for the current subject), the corresponding epoch was automatically marked for rejection. Confidence intervals were computed for each recording session, for each participant, in order to account for intra-subject differences and potential variability across conditions that could result from impedance changes following recapping procedures. Relatively lenient boundaries were employed for the rejection thresholds, because of the trade-off between discarding further noise and the loosing higher number of trials.

2.2.2.2. Principles and relevance of Independent Component Analysis for the processing of real-world EEG data

Independent Component Analysis (ICA) is a model-based approach that decomposes patterns of activity based on maximal differences in terms of topography, spectral activity and time course (Makeig, Bell, Jung & Sejnowski, 1996). The concept underlying ICA decomposition can be practically illustrated by the analogy of a concert. During the live performance, people in the public are dancing and talking to each other while musicians are playing. Two microphones are placed in the concert hall, one at the front of the stage where the musicians are playing and one further away, at the back of the room. Unwanted noise coming from the audience along, and the intended signal from the band playing are contributing to the signal that is recorded by both microphones. However, the strength of their contribution to the recorded signal depends on the location of the microphones. The microphone in front of the stage will provide the clearest recording of the musicians' performance, while only slightly picking up the noise from the crowd. By contrast, the microphone placed closer to the audience will not provide as clear a recording of the music, as it will be covered by the much more prominent noise coming from the spectators. The recording from each microphone will capture a different mix of the two sources, based on their spatial relationships. Indeed, the further away the two microphones are from each other, the more distinct will be contribution of the different sources in the two recordings. Critically, the difference in the recordings allows the separate signals to be identified and separated, such that spectators noise can be selectively removed from the live recording.

Similarly, EEG sensors placed on the scalp record signals arising from multiple different sources. Based on the electrode locations and the projection of the signal sources, each source will present a distinct spatial and temporal pattern that can be used to identify the different sources within the recording. By discriminating patterns of activity in the EEG signal that present maximal differences, ICA decomposes the signal into independent sources that contribute to the recorded data in their own specific way. Importantly, ICA allows the separation of noise from signal, through the identification of different sources of noise in the signal. For example, in the context of the concert analogy, musicians playing different instruments will be classified as independent sources contributing to the music. Moreover, if two trumpetists are playing different parts or if they play the same part but from distinct locations on the stage, they can be identified as independent components. In contrast, if two musicians play in unison close to each other, both of their signals will be decomposed as a unique component (e.g., in EEG data blink related activity is captured most prominently across all frontal electrodes and usually decomposed into one component). Using this modelling approach, continuous data can be linearly transformed into Independent Components (ICs) that are estimates of the contribution of statistically different sources to the initial signal.

ICA is a model-driven representation of the EEG data, highlighting maximally distinct sources of activity contributing to the signal. Applied to EEG data, ICA is a powerful tool for the identification and parsing of non-brain signals (artifacts) from cortical activity. Indeed, ICA can isolate prominent sources of variance in the data, such as eye-movement related artifacts, based on their distinctive spectral, temporal and topographical features. Critically, the use of ICA means that other data cleaning methods (e.g., data rejection) can be minimised. In practice, as the ICA algorithm makes progress through the different dimensions of EEG data, prototypes of ICs are progressively built. Through many iterations (limits vary between algorithms, for example due to trade-offs between computation speed and accuracy), the ICA algorithm calculates a model of independent sources that explains as much of the variance in the data as possible, while preserving high levels of independence between components. The EEG signal is then allocated weights reflecting the similarity between the channel-based signal and every prototypical independent component. Since the ICs are a simple linear transformation of the data, the resulting model accounts for the entirety of the variance of the initial signal, and there is no loss of data following ICA decomposition. Furthermore, switching back to the initial channel-based representation of the data either in the spectral or time domain is conveniently done through the multiplication of ICs weights computed for each channel to the inverse weights of every components.

Theoretically, ICA decomposition of EEG data offers a model-based method to estimate distinct patterns underlying the signals recorded. Practically, these independent patterns of EEG features can then be characterized in isolation, and non-brain signals can be removed from brain signals through a data pruning process. For example, IC associated with high proportion of variance during artifactual signals (e.g., blinks and lateral eye movements are presented in Figures 2.4. & 2.5. respectively) can then be subtracted from the EEG on the basis that they reflect noisy signals that originate from non-brain sources. For the studies presented in the present thesis, ICA decomposition has been included in the processing pipeline and used to detrend non-brain activity from signal of interest by discarding components clearly associated with artifactual activity. It is, however, important to keep in mind that noise presenting a recurrent pattern in the EEG is likely to be classified as an individual IC, while artifacts associated with varying source location (e.g., muscular activity associated with head movements) or presenting high variability will likely be decomposed into several distinct ICs. Moreover, it should be noted that ICA decomposition, as with any signal processing method, produces better outputs when applied to good quality data, in the sense that ICs computed will reflect more of the total variance from artifactual origins and incorrectly remove less non-artifactual signals (false positives).

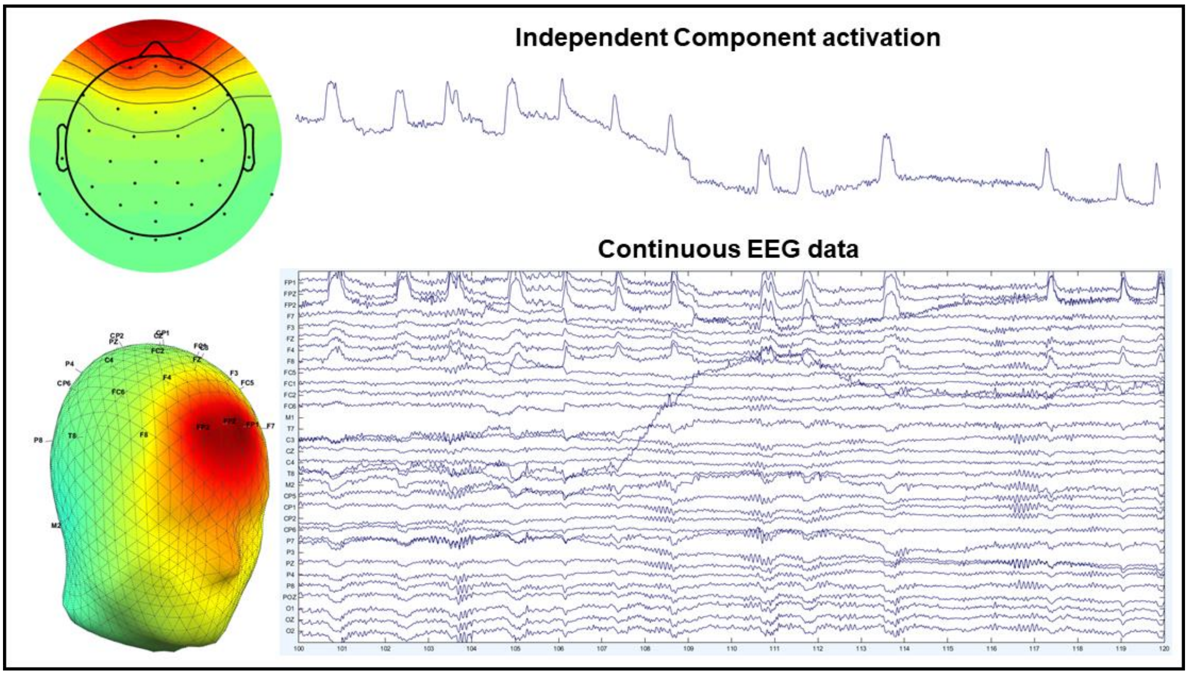

Figure 2.4. Independent Component Analysis decomposition of eye blinks related artifacts. The Independent Component activation is plotted on top of the corresponding continuous EEG data. Typical spatial (as shown on the 2d and 3d topographical representation) and temporal (as shown on the time series) patterns of activity related to eye-blinks have been decomposed into a single component. The 20 seconds of single-subject continuous data presented in the graph is part of the first ERP study presented in Chapter 3.

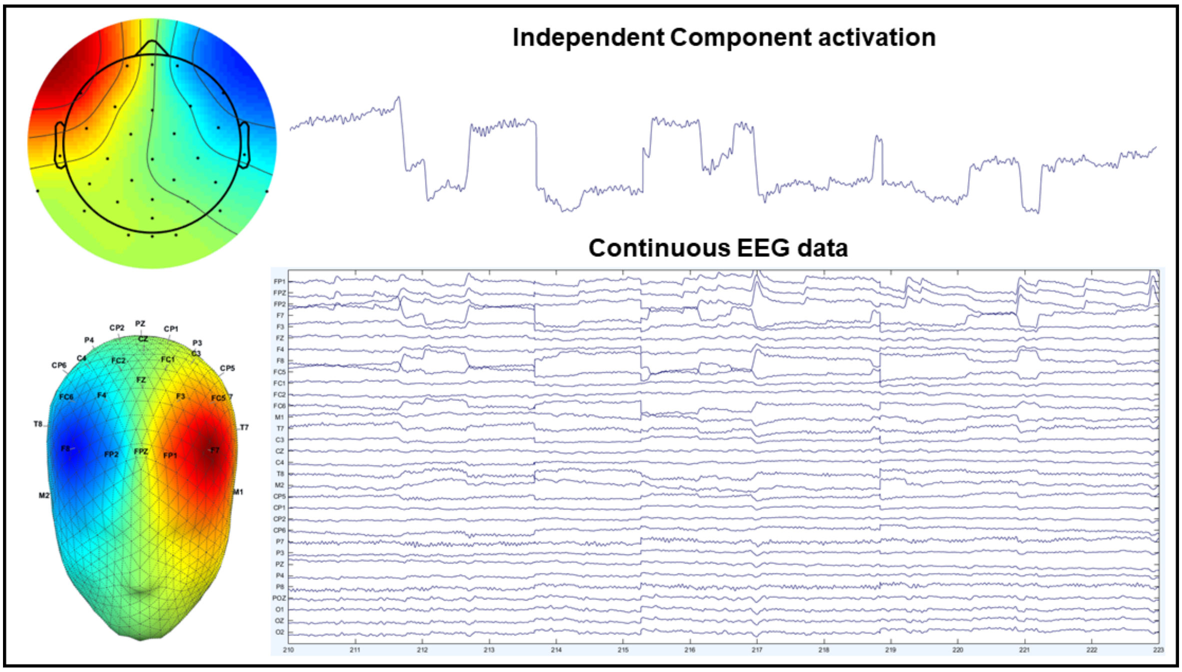

Figure 2.5. Independent Component Analysis decomposition of lateral eye movement related artifacts. The Independent Component activation is plotted on top of the corresponding continuous EEG data. Typical spatial (as shown on the 2d and 3d topographical representation) and temporal (as shown on the time series) patterns of activity related to lateral eye-movements have been decomposed into a single component. The 20 seconds of single-subject continuous data presented in the graph is part of the first ERP study presented in Chapter 3.

EEG data acquired during motion includes a wide range of noise sources which expression in real-world EEG signals includes more variance, which is particularly challenging for the ICA decomposition algorithm. Moreover, ICA decomposition of real-world EEG data may in turn be less accurate as the boundaries between noise and brain signals become less clear. Practically, the imperfection of ICA decomposition means that a component reflecting a large proportion of an artifact activity may also account for a proportion of the signal of interest. Moreover, the subtraction of independent components contribution also reduces the dimensionality of the data, which can be useful for interpretation purposes because it reduces the complexity of the data, (e.g., by distinguishing non-brain from brain signals), but also increase the artificial nature of the output data (which is no longer real recorded data, but instead is a product of a linear transformation). In some areas of EEG research (such as BCI, Brain Computer Interface), the isolation of signals of interest into a small number of components is desirable because it allows all other components to be discarded, thereby optimizing the signal-to-noise ratio. By contrast, for the experimental data presented in the current thesis, the critical aim was to accurately identify noise artifacts. In this context, reliance on prominent ICs risks ignoring artifactual components that are less consistent in the continuous data. Taken together, these considerations argue strongly for the adoption of a conservative approach to the selection and rejection of artifactual ICs.

As should be clear from the foregoing discussion, ICA decomposition provides a highly effective way to parse typical artifacts from the data and is a powerful method for EEG data cleaning. However, it can be argued that the manual selection of artifactual ICs to reject is not sufficiently objective considering the impact of this step in the processing of EEG data. As mentioned previously, rejection of IC has implications in terms of data dimensionality reduction and can have significant impact on the outcomes of analyses. Given these concerns, efforts have been made within the EEG community to provide tools that would automatically select ICs based on thresholds applied to a series of features. Unfortunately, however, the effectiveness of these tools remains highly questionable. For example, automatic approaches typically yield a high rate of false positive and a disappointingly low rejection rate even for some of the most obvious artifactual components (e.g., blinks). While community-driven solutions based on machine learning of large-scale shared data are under development, which should ultimately allow for impartial and online rejection of artifactual ICs, current removal approaches require clear definition of inclusion and exclusion criteria to ensure good practice in EEG research. In the present thesis, given the need to provide objective rationale for the selection of ICs in mobile EEG data, complementary solutions to the identification of artifactual ICs had to be considered. Because of its potential to provide objective criteria for the selection of artifactual ICs, the application of source estimation was considered. The following sections present and discuss the relevance of source-localization for mobile EEG data as both a processing and analysis tool. The following section provides the rationale and details regarding the implementation of source estimation as a complementary method to identify non-brain components. A second section will discuss the limitations of cluster-based analyses of source estimates within the frame of low-density EEG data.

2.2.2.3. Implementation of ICA decomposition in the processing pipeline

As previously mentioned, ICA yields better, more accurate results when applied to clean data. Although the quality of the data used as input for ICA is the predominant predictor of the decomposition output, the quantity of data and the nature of it are also important. Inputting a higher number of artifacts through the ICA decomposition will most likely result in the classification of more consistent pattern of signals into ICs, that will better explain the variance within the different artifacts subtypes, accounting for a more representative population of artifacts.

In the present thesis, therefore, raw EEG data was subjected to aggressive cleaning process in preparation to ICA decomposition. In a first preprocessing step, the continuous data was visually examined and portions of the EEG displaying extreme levels of noise (e.g., channel disconnections) were manually discarded. The datasets were then filtered with a low-pass filter of 20Hz and a high-pass filter 1Hz, narrowing the pass-band of the EEG signals in comparison to the filters described in the filtering section. The continuous EEG was then split into consecutive epochs of 1 second. Epochs presenting abnormal values were pruned based on statistical criteria (greater than three standard deviation from the mean) as implemented in EEGLAB toolbox. This process removes segments of data that present abnormal values, which would reduce the quality of ICA decomposition. Then, an extended Independent Component Analysis (ICA, Bell & Sejnowski, 1995) was performed and the resulting Independent Components (ICs) decomposition matrices were saved. In a second step, the initial continuous datasets were Finite Impulse Response filtered accordingly to the frequency range under investigation (−6 dB cut-off, filter order 16500 at both lower and higher ends), and ICs features obtained during the first step of the preprocessing procedure were then back-projected to the filtered data. Moreover, ICA decomposition was not performed on epoched data because the inclusion of epochs edges can lead to the generation of additional and prominent artifactual artifacts, or to the classification of ERP features under investigation as individual ICs.

2.2.2.4. Relevance of source-localization and clustering methods as data-driven approaches to the identification of artifactual independent components

An elegant alternative to the issue of subjectivity in the selection of artifactual components lies in the grouping of ICs based on objective parameters. Indeed, ICs can be clustered based on feature similarities, such as their overall power spectra, their respective contribution to epoched data dynamics (e.g., ERPs), or even their estimated source localization. The resulting clusters allow subsets of ICs presenting some degree of similarity to be examined together, and allows their respective contribution to brain dynamics to be investigated (see Figure 2.6). As artifactual ICs typically present high variability and raw values that are significantly different from any actual brain component, such artifactual components will be clustered separately from brain components.

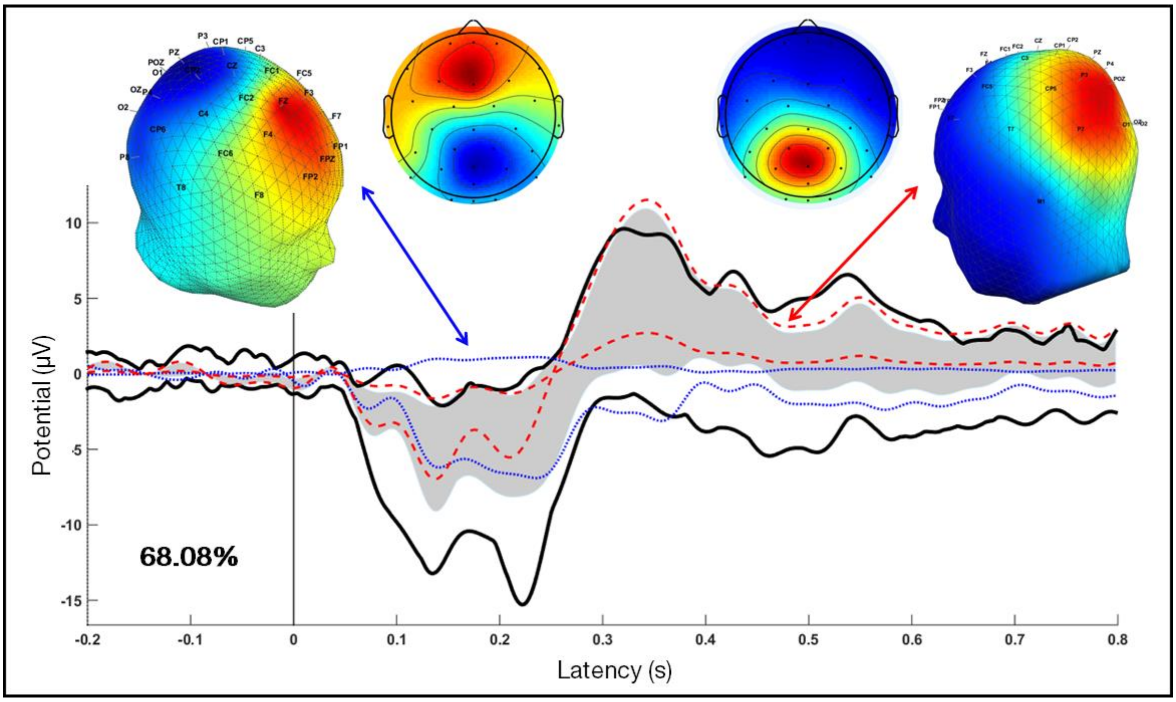

Figure 2.6. Representation of the two independent components contributing most variance to the ERP waveform. The black line indicates the ERP envelope (i.e., minimum and maximum of all channels at every time point). The dotted lines represent the respective ERP envelope of the left (blue) and right (red) Independent Components. Both components are represented using 2d and 3d topographical maps. The percentage displayed on the bottom left of the figure indicates the percent variance accounted for by these two components within the post-stimulus interval (0-800ms). While single components may not be sufficient to explain ERP waveforms dynamics, they convey information regarding different sources of activity contributing to ERP features such as peaks. In the present example of a single subject performing a P300 elicitation task, the two dominant components present different spatial and temporal patterns of activity. The blue IC reflects negative activity over frontal electrode sites within a 100 to 200ms time period after stimulus onset. This first pattern is in line with the N100 and N200 ERP components associated with early sensory processing. The red IC reflects positive activity over parietal electrode sites from 300 to 500ms after stimulus onset. This second spatial-

temporal pattern of activity is typical of a P300 ERP component, associated with attentional processing of stimuli.

Although source generators localization was not the main purpose of the current work, here we briefly describe the basic logic of source estimation and its relevance for the identification of artifactual ICs. It is important to recognize that ICA decomposition does not inherently provide any spatial information relative to the origin of ICs activity; the ICs simply reflect the weighted contribution of activity at each recording channel. However, when coupled with source-localization methods, ICA has been successfully used to uncover the respective contribution of different neural sources to EEG. Dipole fitting (Scherg, 1990) of ICs offer a source-estimate representation that can be applied to a wide range of EEG analysis, such as ERP peaks in the time domain, and frequency de/synchronisation and phase coherence in the frequency domain (Makeig et al., 2004).

In the present thesis, source estimates of ICs have been used as a complimentary approach to the assessment of topographical distribution (pattern of signal activity across channels) and spectral features (power over different frequencies) for the selection and rejection of artifactual components. Due to the nature of artifactual signals in the EEG data, source solutions are likely to be estimated outside of the head, and forward solutions estimated on the basis of these signal origins are likely to present improbable projection patterns (see Figure 2.7). This additional information can therefore be used to confirm that some ICs are related to artifactual activity. It is important to note, however, that estimated ICs sources should not be used to perform clustering of EEG data, nor should source localization of EEG signals be subject to quantitative analyses; rather, they are only used to provide qualitative information informing the classification of ICs. In essence, the aforementioned outputs of ICs source localization are solely used to identify prototypical non-brain sources of noise contributing to the EEG.

2.2.2.5. Limitations of components clustering and source-localization based analyses with respect to low-density mobile EEG data

The accuracy of EEG source localization solutions largely depends on the acquisition of sufficient spatial and temporal sampling of the EEG potential field, implying a complete and evenly distributed sensor coverage of the scalp (Song et al., 2015). Moreover, providing accurate solutions to the inverse problem (i.e., calculating the exact set of neural sources from where observed signals originate) posed by EEG source localization essentially depends upon honing an accurate representation of each participants' head and how signals propagate from the source to the recording EEG sensors. Individual differences in terms of skull thickness, cortical folding and gyri morphologies, can all lead to inaccuracies in volume conductivity estimates, and are therefore necessarily detrimental to the accuracy of source estimations (Acar & Makeig, 2013). These issues can be addressed to some extent through the use of tailored head models acquired through brain imaging methods, providing high spatial resolution images of cortical and subcortical neural structures (i.e., co-registration of EEG electrodes with structural MRI scans).

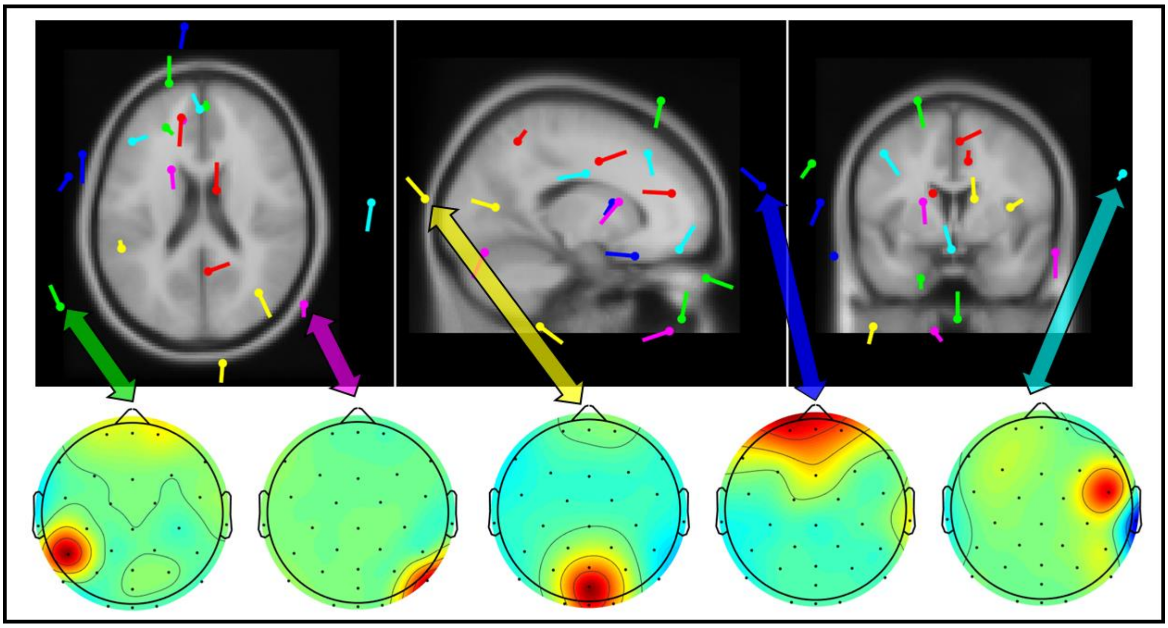

Figure 2.7. Example of ICA decomposition and dipole fitting of ICs of EEG data recorded while the participant was navigating through the corridors of the University of Stirling. Top: Dipole fitting of Independent Components under top, sagittal and coronal perspectives computed from a single subject dataset (30 minutes mobile EEG recording). Bottom: Topographical representation of artifactual components. Coloured arrows link the different representations of artifactual component produced by the model (top) to the associated channel-based topographical effect (bottom).

In the present thesis, however, the distribution of the electrode arrays was relatively sparse (32 electrodes), in contrast to high-density EEG recording (120+ electrodes) used in static recording settings. The choice of using an easy-to-cap, and comfortable-to-wear, but low-density EEG system was driven by the ambition of recording brain dynamics in the real-world. Moreover, structural MRI was not used, preventing any plausible co-registration of neural anatomy to model signal propagation on single subject basis. As discussed in the previous section, using low-density EEG without resorting to additional brain mapping techniques highly limits the application of source localization methods. Nonetheless, recent open-source code libraries have become available that allow source estimation of ICs through dipole fitting based on predefined standard head models, providing rough estimates of ICs localization. Even though these methods can only ever provide imprecise estimates of cortical activity sources (i.e., are invalid as a basis for strong anatomical interpretations of the data), they nevertheless provide useful information regarding the localization of potential artifactual ICs. In this context, therefore, the decision was made to limit the application of source-localization methods to the identification of non-brain components and not as a basis for the analysis of spatially clustered brain components.

2.2.3. Limitations of channel interpolation with respect to low-density mobile EEG data

One common issue in EEG recordings is the loss of individual electrodes (e.g., due to wire breakage or gel drying out). This issue is particularly relevant to mobile EEG data, as the risks of channel disconnections are increased during the performance of active behaviours. When this occurs, interpolation processes can be used to estimate data from noisy or missing channels based on the activity of neighbouring electrodes. Interpolation algorithms therefore reconstructs the data from spatially-weighted metrics, based on signals recorded at other electrode sites. Within the EEG literature, interpolation is typically applied to channels that have been disconnected for substantial parts of the recording, present noise that cannot be effectively dealt with through other methods, or would require large segments of data to be discarded, complicating averaging-based analyses. The quality of the reconstruction of a channel is a direct function of the number and proximity of electrodes used in the interpolation. Moreover, the quality of the signal recorded by the channels on which the interpolation is based significantly affects the interpolation result.

In principle, the more electrodes are included, the better will be the estimation of the interpolated channel. While high-density EEG recordings of more than 128 channels provide a rich neighbouring environment, data collected from 32 sparsely distributed electrodes is less reliable for interpolation purposes. Moreover, conceptually, interpolation involves a linear (or spline)-based reconstruction of data based on signals recorded in a local area. It can be argued, therefore, that the interpolation process leads to the production of artificial data that inherently possess a high spatial correlation (due to the nature of the algorithms employed). Given the fact that interpolation is poorly suited to low-density EEG recordings, and the signal produced is artificial, the processing pipeline for mobile EEG data did not including channel interpolation.

2.2.4. Considerations regarding the selection of reference channels within the frame of mobile EEG data

In EEG data, the signals recorded at every electrode are relative to the values recorded to a “reference”. Therefore, the voltage values recorded at each electrode are inherently dependent on the activity measured at the reference electrode because they consist of the difference between the two electrode measures. The choice of reference electrode location is not trivial, because activity recorded at the reference site (including noise) will be reflected across all the other channels. Using a single reference located on one side of subject scalp introduces lateral bias, with high differential values more likely to be located on the opposite side. Also, electrodes located close to each other will likely produce only small differences, which may render the comparison of signal features across multiple conditions less sensitive. For these reasons, the ideal reference(s) location should combine several qualities, including a) being evenly distributed (either a central-midline reference, the average of all electrodes or bipolar locations), b) free of noise, and c) at maximal distance from the electrodes investigated and/or capturing minimal signal of interest activity. The latter quality makes the choice of reference location dependent on the paradigm used and the research hypothesis. Typically, earlobes or the average of the mastoids have been used as references for the study of midline effects. The average activity across all electrodes is also commonly applied to high-density EEG recordings and to the investigation of lateralized effects. Taking these guidelines into considerations and based on previous literature, the present studies have used an averaged mastoids reference for the quantification of P300 ERP (Chapters 3,4 & 5) and the average reference for the investigation of spectral changes in the frequency domain (Chapters 6, 7 & 8). The first series of experiments (Chapters 3 & 6) highlighted the issue of mastoids electrodes being prone to disconnect during whole body movements, eventually resulting in loss of entire datasets from five participants. This issue largely reflected the design of the system whereby mastoid electrodes were crafted within the cap fabric. Practical solutions were found using drop-down mastoid electrodes, offering greater flexibility during capping and more reliability during data acquisition. Moreover, a second generation of mobile EEG caps was developed in collaboration with the manufacturer, addressing most of the remaining issues related to the loose ends of the caps. These changes resulted in a higher retention rate of datasets, with only one participant excluded from the analyses of the second series of experiments (Chapters 5 & 8) due to mastoid electrode disconnections.

2.2.5. Epoching: extraction of event-related dynamics

2.2.5.1. Non-stationarity of brain dynamics and its implications

Electrophysiological data can be recorded and examined over many different time frames. For example, the inspection of continuous EEG data has proven to be useful in medical contexts, where background EEG monitoring is applied to epilepsy episodes and sleep-cycles disorders. Similarly, resting-state EEG analyses are performed on extended time series data while subjects are supposedly maintaining a specific cognitive state. Such extended timeframes of EEG recordings have provided insight into brain properties related to tonic states (e.g., the seminal finding of alpha-locking during sleep by Hans Berger, 1929). Over the following decades of brain physiology research, evidence has grown in support of the assumption that our brain dynamically reacts to the surrounding environment on a moment-to-moment basis, to organize and optimize our behaviour. This view has engendered interest in the characterization of phasic brain responses related to transient, short-lived, cognitive experiences. Arguably, emphasis on the highlight of non-stationarity properties of brain activity acted as a catalyst for the explosion of brain imaging studies, and largely contributed to the establishment of Event-Related Potentials as a prominent research method in cognitive sciences.

2.2.5.2. Segmentation of time series data

Henceforth, continuous brain imaging data has been segmented into relatively short epochs, defined around experimental events. The use of short time series was originally dictated by the limited computational resources available to perform analyses. Even though modern computers allow the manipulation of longer time series of multidimensional EEG data, this practice has, however, vastly influenced the landscape of ERP literature by leaving behind a legacy of specific components elicitation paradigms that were characterized by low inter-stimulus intervals. The extraction of segments of EEG relative to events of interest allows the identification and characterization of brain signals related to specific cognitive processes. Conceptually, the continuous data is segmented into epochs around timestamps that mark the onset of stimulus presentation and/or the registration of behavioural response, depending on the paradigm and the nature of the task. Epoching is commonly the final step concluding the preprocessing of EEG data, before proceeding with further signal analyses.

2.3. Data analysis

The previous sections focused on detailing how the challenges of mobile EEG data were addressed throughout the different stages of data acquisition and processing within the frame of the present work. Methodological solutions to acquire and process event-related signals within the frame of real-world EEG recordings were critically reviewed. Relevant solutions were integrated in a processing pipeline specifically adapted to mobile EEG data. The following sections will introduce how meaningful signals are extracted from epoched data, with respect to the research questions investigated and the dimension of brain dynamics examined (see Figure 2.8). EEG analyses methods used within the frame of the empirical work presented in the following chapters will be introduced in terms of the rationale and concepts underlying their application. Then the implementation of such analyses will be discussed, along with considerations regarding the choice of parameters employed.

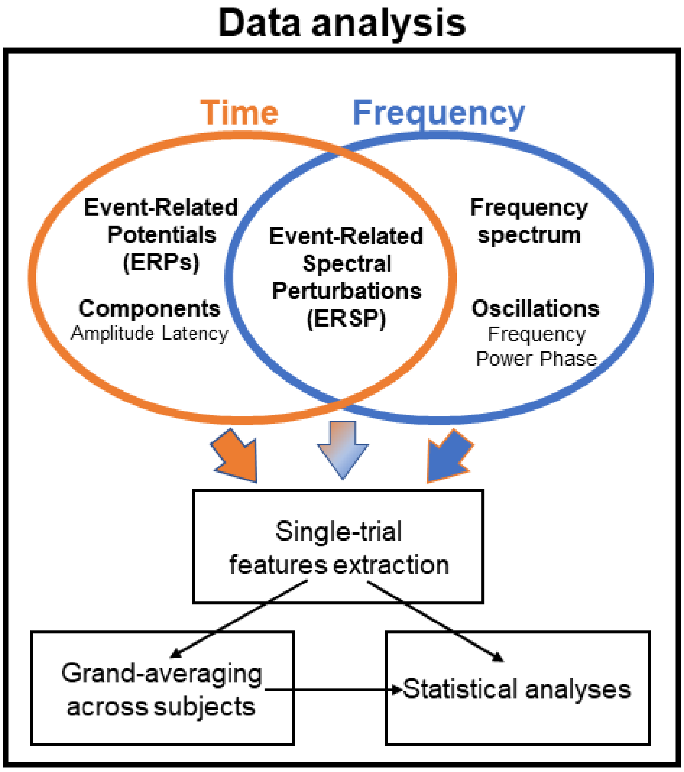

Figure 2.8. Schematic representation of the analyses applied to the EEG data. Depending on the research hypothesis the analyses either focus on characterising the temporal (orange) or spectral (blue) dimension of the data. It is important to note that time-resolved spectral dynamics of the data have also been subject to analysis (represented at the intersection of the ellipses). Following the extraction of the relevant features to address the experimental hypothesis, these measures are then grand-averaged across subjects and subject to statistical testing.

2.3.1. Preface to EEG analyses methods

Since the seminal report of alpha spectral activity related to sleep (Berger, 1929), EEG has been used extensively to explore brain dynamics in the frequency-domain. The emergence of computerized methods has enabled the systematic extraction of information from the EEG trace, which facilitated the characterization of EEG activity in relation to experimental events in the time-domain. Most research in experimental psychology and cognitive science using electroencephalography have classically involved either describing ‘evoked’ peaks highlighted through averaging of Event-Related Potentials (ERP) in the time domain, or changes ‘induced’ by experimental manipulations in the EEG power spectrum (Karakaş & Barry, 2017). Over the last decade, interest has grown in the study of spectral features (oscillations characterised in terms of frequency, amplitude and phase), over time, in relation to experimental events (Makeig et al., 2004). The execution of such time-frequency analyses was originally relatively demanding in terms of computational resources, due to the consequent number of convolution iterations that were applied across time bins, frequencies and sensors dimensions. Their implementation has benefitted from the optimization of convolution-based transforms (i.e., Fast Fourier Transform), and advances in computing speed. The contribution of these complementary dimensions of EEG data as time-frequency perturbations or Event-Related Spectral Perturbations (ERSP), offer novel and more comprehensive insight on the event-related dynamics of EEG data. The following sections will present the different analyses involved in the extraction of Event-Related features of the epoched EEG data. Analyses of three complimentary dimensions of EEG data will be discussed in the following order: a) Characterization of ERPs in the time-domain, in terms of peaks, amplitude and latency, b) Discrete power spectral decomposition of event-related signals, and c) Time-frequency analyses, in terms of event-related perturbations relative to baseline activity.

2.3.2. Time-domain analyses: Event-Related Potentials

Event-Related Potentials (ERPs) are averaged EEG signals highlighting brain activity related to experimental events. Capitalising on the high temporal resolution of the EEG, ERPs offer a way to capture the timing of brain dynamics related to cognitive processes. ERPs have been used to investigate a wide range of research question in cognitive science and experimental psychology, ranging from low-level perception to attentional processing, memory and motor planning. The averaged time-locked neural responses translate into waveforms whose deflections are characterized in terms of magnitude (voltage measured in "µV" microvolts) and timing (latency relative to experimental events measured in "ms" milliseconds).

Consistent deflections observed in the ERP waveforms elicited through experimental manipulations have led to the documentation of a large library of ERP components. Most of ERP components have been referred to following their voltage index (positive or negative power) and the time at which they typically occur (e.g., N100 for the negative deflection occurring 100 milliseconds after stimulus presentation). Through a large body of research robust ERP features elicited by specific paradigms have been linked with specific aspects of cognition. Quantitative measurements of ERP components are examined as a function of experimental manipulations and thereby associated with behavioural and other physiological measurements. Differences in terms of components amplitude and latency between experimental conditions are statistically tested. Significant differences then shed light on brain dynamics related to the experimental manipulation employed and provide insight about the time course of cognitive processing. This averaging process reveals the signal of interest, highlighting any consistent event-related brain dynamics in the time domain and removing residual noise. The logic of averaging is simple: based on the premise that noise fluctuations are randomly distributed around 0 µV, averaging over many trials ultimately results in a cancellation of non time-locked activity. Importantly, however, background brain activity unrelated to the events must also be removed through baseline normalization of the data (see Section 3.5).

The computation of ERPs requires the averaging of single-trials, time-locked to a specific category of experimental event. Mean ERP waveforms can be defined as:

$$\overline{ERP}(c,t) = \frac{1}{n}\sum_{k=1}^{n} A_k(c,t)$$

Where n is the total number of trials, and $A_k(c,t)$ is the amplitude of the signal recorded by channel c at the time point t for trial k.

The metrics used to characterize ERP features are often based around the peak (maximum voltage recorded within a specific time window). Most ERP studies either examine a single time point at which the maximum voltage was recorded (maximal peak amplitude) or measure the average amplitude recorded within an *a-priori* time window (area amplitude) (e.g., ranging from 250 to 500ms after stimulus onset for the P300). However, several studies have reported substantial interindividual differences in terms of P300 component topography, especially regarding its latency (Polich, 2007; Doppelmayr, Mainz & Klimesch, 2016). Furthermore, there are important discrepancies in the P300 ERP literature in the definition of the time window investigated. While the rationale behind the definition of these time window is rarely discussed in empirical papers, it is however an important aspect of the analysis that has significant impact on the interpretation of data. Indeed, using a narrower or larger time window can lead to statistical differences in terms of amplitude quantification and therefore the somewhat arbitrary definition of time windows can potentially lead to significantly different results based on the same data. Due to the wide range of time windows that has been reported in the literature in relation to the P300 component, the entirely objective selection of an *a-priori* time window is practically impossible. Therefore, in the present thesis, for these combined reasons of accounting for interindividual variability, and addressing the concerns related to the objectivity of analyses used, the definition of time windows used to quantify ERP components amplitude has been data-driven. The P300 component time-window was defined based on an interval of two standard deviations around the average of single-trials P300 latencies, across all subjects.

First, the latency at which maximum voltage was recorded was defined for each single-trial, within an extended *a-priori* window, through the following equation:

$$P_k(c) = \max_{250 \leq t \leq 500} A_k\,(c, t)$$

Where $P_k(c)$ is defined as the maximum peak amplitude A, recorded at channel *c*, within the time range *t* (from 250 to 500ms after stimulus onset) for trial *k*. The resulting array returns a single-value that represents peak latency over each channel and every trial. In addition, the mean latency of P300 peaks can also be computed across trials:

$$\bar{L}(c) = \frac{1}{n}\sum_{k=1}^{n} P_k(c)$$

Where *n* is the total number of trials across all subjects, $P_k(c, t)$ is the peak latency recorded at channel *c*, at the time *t*, for trial *k*. The resulting array returns the mean peak latency values for every channel.

These values where then used to calculate the P300 period interval, defined as two standard errors around the mean peak latency, as follows:

$$t_{[l,h]} = \bar{L}(c) \pm \left(2 \times \frac{\sigma_L}{\sqrt{n}}, 2 \times \frac{\sigma_L}{\sqrt{n}}\right)$$

Where *n* is the total number of trials across all participants, σ_L is the latency standard deviation, $\bar{L}(c)$ is the mean latency of peaks recorded at channel *c*. Latency standard deviation was also computed, through the following equation:

$$\sigma_L = \sqrt{\frac{P_k(c) - \bar{L}(c)}{N - 1}}$$

Where $P_k(c)$ is the peak latency recorded at channel *c*, at the time t, for trial *k*, and $\bar{L}(c)$ is the mean latency of peaks recorded at channel *c*. *N* is the total number of trials across all participants.

Given these calculations, the mean P300 ERP amplitude could then be computed across channels, through:

$$\overline{P300}(c) = \frac{1}{n}\sum_{k=1}^{n} A_k(c, t_{[l,h]})$$

Where *n* is the number of trials, A_k is the amplitude *A* recorded at channel *c*, within the time range $t_{[l,h]}$, for trial *k*. P300 ERP amplitude is then computed as a single value, for each experimental condition, for each subject. The resulting values can then be subjected to statistical analyses.

The aforementioned approach presents the advantages of providing an objective delimitation of P300 ERP time window boundaries, through statistics, while accounting for interindividual differences in P300 latency. To address reasonable concerns about the subjectivity of standard deviations used, the results obtained using two standard deviations were compared to those computed using a narrower time window (defined using one standard deviation around the mean of single-trials latencies). This comparison assessed the impact of using a more or less inclusive time window length on the quantification of P300 ERP features and their effect on statistical analyses applied to the comparison across experimental conditions. While significant differences in terms of the raw P300 ERP amplitude value were found between larger and narrower time windows (Studies 1, 2 and 3), these differences did not lead to different pattern of results when testing for statistical differences between experimental conditions.

Although the pattern of results was not affected by using different time windows, statistical differences between experimental conditions were more reliable using a narrower time window. This finding can be interpreted as a magnification of the amplitude resulting from the inclusion of fewer time points around the mean peak latency, as commonly observed in studies extracting ERP component amplitude based on a single-point representing the maximal absolute voltage. One consequence of opting for a narrow time window, is the potential to miss differences between waveforms that are part of the ERP component, even though they are not comprised in the immediate peak neighbourhood. This issue is particularly relevant to the P300 ERP component because its peak latency variability is much larger than what is seen for early ERP components associated with sensory processing (P100, N100). For these reasons, therefore, the P300 effect is measured more accurately using a more comprehensive (and thus larger) time window.

An additional complication that must be considered when analysing the P300 ERP component is that the amplitude is negatively correlated to latency variability (Polich & Martin, 1992). This relationship mostly originates from the averaging nature of ERP component quantification, which necessarily involves computing the mean of single-trials that may present some variation in their peak latency. At a single-trial scale, latency of the P300 peak has been related to task difficulty (Polich et al., 1997; Polich, Howard & Starr, 1983), and interpreted as an index of attentional processing timing (Verleger, 1997; Verleger, Jaśkowski & Wascher, 2005). Unlike sensory processes displaying a very consistent time-locking, attentional processing is inherently subject to more variation in the time domain. Therefore, the outcome of averaging signals with latency jitter will likely result in a shallower and widened curved waveform, reducing incidentally the amplitude of peaks (Michalewski, Prasher & Starr, 1986). These additional considerations provide further justification for the use of a wider time window based on two standard deviations around the mean.

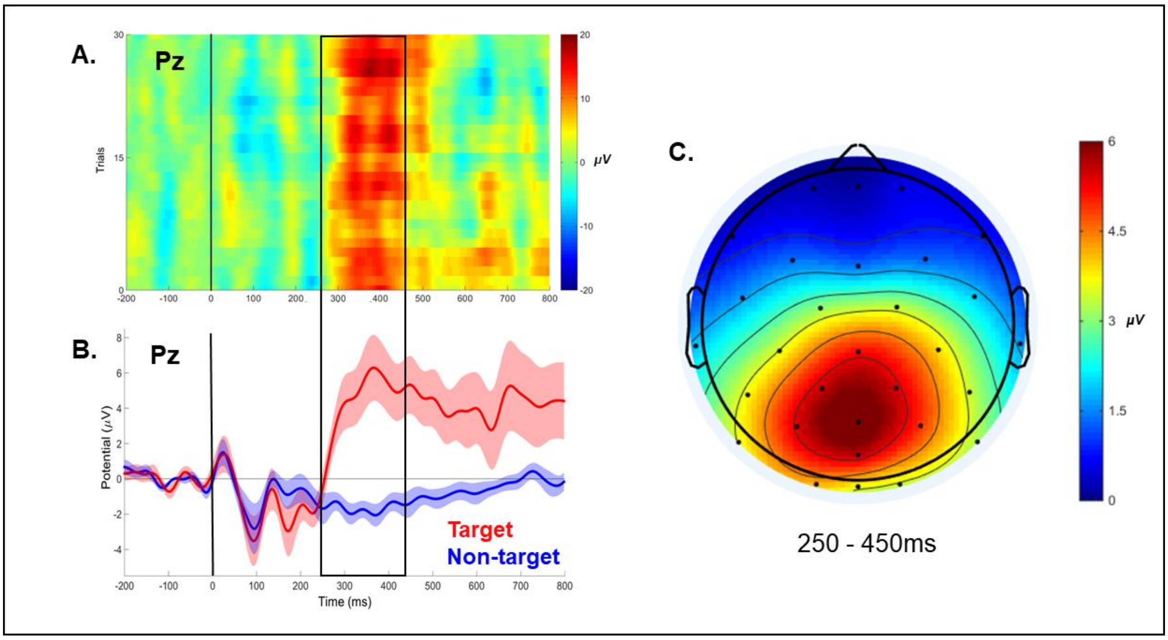

Figure 2.9. Single-subject and averaged EEG data recorded during navigation in a real-world environment. Twenty-four participants were asked to silently count the number of target tones amongst non-target tones (i.e., perform an auditory oddball paradigm designed to elicit the P300 Event-Related Potential) while walking. A. Thirty single-trial Event-Related Potentials of target stimuli recorded at Pz electrode site in a single subject. The target stimuli elicited consistent amplitude peaks 300ms after stimulus onset. B. Grand average (N=24) Event-Related Potentials waveforms of target and non-target stimuli at Pz electrode site. C. Topographical map representing the distribution of the difference between target and non-target stimulus types within the P300 ERP time window (250-450ms after stimulus onset). The P300 amplitude is most prominent at mid-parietal electrode sites, showing a prototypical P300 scalp distribution.

Within the frame of P300 effect analysis, non-target ERPs are subtracted from ERPs elicited by target stimuli (see Figure 2.9). The resulting difference waveform highlights the specific topographic distribution of the measured ERP effect, which allows the pattern of activity to be differentially identified as a P300 effect relating to attentional processing of target stimuli (in contrast to irrelevant information). Moreover, spatial analyses can be carried out on ERP features by comparing differences in the spatial distribution of the waveforms recorded at different electrode sites. Even though this kind of spatial analysis of the P300 was not statistically reported in the present thesis, topographical maps within the P300 time window very clearly display the stereotypical distribution expected of the P300 ERP effect. Moreover, by design, the paradigm employed to elicit the ERP effects is well-documented as producing reliable P300 effects. The statistical analyses reported here have therefore focused on the comparison of ERP amplitude across recording conditions, in order to investigate consequences of the manipulations embedded in the experimental design.

2.3.3. Frequency-domain analyses: Quantifying EEG power spectrum

2.3.3.1. Frequency, power and phase

Electrophysiological recordings are commonly represented as rapidly changing waveforms, displayed on top of each other. The EEG trace, as used for clinical monitoring of epileptic patients, is a typical time-domain representation of raw data, displaying a continuous flow of spikes and waves. In reality, however, the time series of EEG signals, results from the sum of a whole set of brain waves each oscillating at different rhythms. These oscillations reflect fluctuations of neuronal populations excitability, changes that occur across both spatial and temporal planes (Buzsáki, 2006). While the alternation between states of excitation and inhibition is a major mechanism involved in the production of brain oscillations, neural networks that are either purely excitatory or inhibitory also contribute to the modulation of brain waves.

In essence, brain oscillations index both short-term modulations and long-term potentiation of neural networks, each of which can be informative regarding the transient and long-lasting effects induced by experimental manipulations and related to cognitive experiences. The rhythm of these oscillations ranges from infinitely slow to very fast and is usually characterized as a range of frequencies in hertz (Hz), which corresponds to the number of cycles per second of an oscillation. A wide spectrum of frequencies contributes to the complex EEG signal observed in the time domain. This spectrum ranges from 0.01Hz (the Direct Current, as “0Hz” DC component is pre-filtered by most EEG data acquisition systems) to the Nyquist frequency, a frequency defined by the sampling rate/2. Frequencies above the Nyquist limit suffer from aliasing (i.e., a minimum of two data points per cycle is required to recover frequency activity at different phase stages of the oscillations) due to the lack of a minimum of 2 data points per cycle). Each frequency within the recording spectrum can therefore be seen as a sine wave of *n* cycles per second. Moreover, a key feature of brain rhythms is that they can be quantified independently, isolating the signal related to a specific frequency.

As well as their frequency, oscillations can also be characterized in terms of their amplitude and phase. The amplitude of the oscillation reflects the amount of energy (power is computed as the squared amplitude of the oscillation) present in this specific frequency band. The contribution of different frequencies to the time-domain signal will therefore depend on their respective power at a given time. The prevalence of brain oscillations is best illustrated by a famous example of a spectral effect that can be observed in the unfiltered EEG trace; namely, increased power in the alpha frequency range when subjects close their eyes (Berger, 1929). The increased power within the alpha band of frequencies (8-12Hz) is reflected through high amplitude and relatively slow waves in the continuous EEG data.

The phase indexes the angular position of a specific frequency signal along the sine wave, at a given (temporal or spatial) point, which is measured in radians or degrees. Oscillations are conceptually represented in the form of sine waves (see Figure 2.10) that perform a complete cycle (i.e., returning to an initial value) at the rate of 1/f (where f defines the frequency of the oscillation). Throughout a cycle, the sinusoid will reach maximal amplitude in both positive and negative polarities before returning to the initial position. Considering the initial position as 0 degrees/radians, the sinusoid will perform a full cycle in 360 degrees (or 2π radians) and half of a cycle (therefore returning back to the origin) at 180 degrees (or π radian). It is important to recognize that phase and amplitude are independent characteristics of oscillatory signals, but their interaction has implications for the interpretation of time-domain and frequency-domain data, as discussed in the following sections.

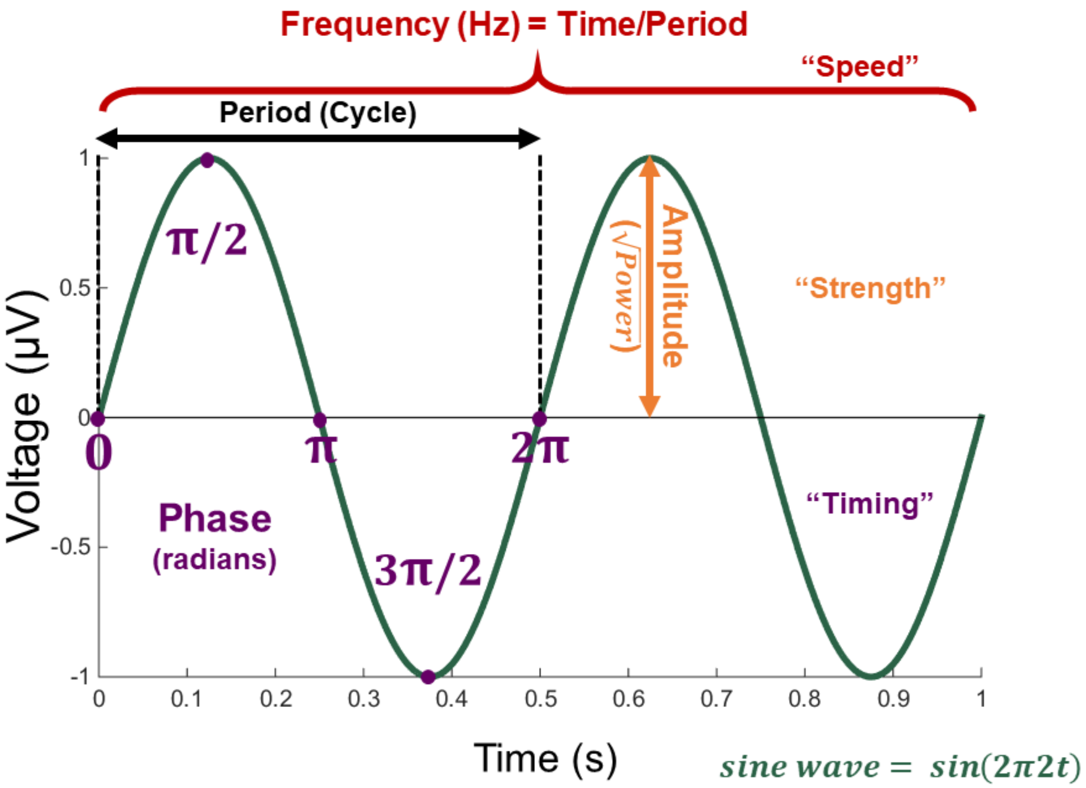

Figure 2.10. Illustration of the three-dimensional features characterizing oscillatory signals. Oscillations, just like any sine wave, are defined as $A\sin(2\pi ft + \theta)$, where A is the amplitude or the "strength" of the oscillation, f is the frequency or the "speed" at which the signal oscillates quantified in Hertz as the number of cycles per second, and θ as the phase of the oscillation indexing the "position" or "timing" at a given point in the oscillation cycle.

The characterization of frequency, power and amplitude features of brain oscillations provide additional measures to investigate EEG dynamics. The isolation of the different brain rhythms that simultaneously compose the EEG signal into a spectrum of frequencies allows researchers to characterize the oscillatory features of individual (or groups of) frequencies. Brain oscillations have been grouped into frequency bands ranging from delta (1-4Hz), theta (4-8Hz), alpha (8-12Hz), beta (12-30Hz), lower gamma (30-80Hz) and upper gamma (80-150Hz), up to omega (150+Hz). Cognitive processes have been mostly associated with frequency bands ranging from delta to gamma activity (2 to 150Hz), and sub-delta slow waves and high frequencies have been linked to sensory and cognitive processes (for reviews see Kopell, Kramer, Malerba & Whittington, 2010; Başar, Başar-Eroglu, Karakaş & Schürmann, 2000; Buzsáki, 2009). It is to be noted that individual frequencies are not bound to specific cognitive functions; activity within a frequency band can be modulated by cognitive processes of a very different nature. For example, working memory (Klimesch, 1999), visual processing of target stimuli (Voytek, 2010) and sentence processing (Lam, Schoffelen, Uddén, Hultén & Hagoort, 2016) have all been linked with power increases within the alpha band.

The interpretation of oscillatory activity is further complicated when interactions between different frequencies are taken into account. Cognitive phenomena may be reflected across the EEG spectrum. For example, frequency coupling of theta and gamma activity has been related to spatial information processing (see Lisman & Jensen, 2013). Classification of the functional role of EEG spectral activity is therefore dependent on the research question investigated and the paradigm used. Furthermore, EEG frequencies are typically characterized and referred to following their spatial features, either based on the source from where they originate (e.g., hippocampal theta in invasive recordings, see Buzsáki, 2002), or to the networks or brain structures they are related to (e.g., alpha oscillations involved in motor control network connectivity, see Westlake et al., 2012; Westlake & Nagarajan, 2011). The boundaries between bands may also be subject to small variations across studies because individual differences in peak frequencies have been observed in relation to age (Aurlien et al., 2004), genetic factors (Landolt, 2011; Linkenkaer-Hansen et al., 2007), brain structure and neurochemistry (Muthukumaraswamy, Edden, Jones, Swettenham, & Singh, 2009).

2.3.3.2. Discrete Fourier Transform: Computing frequency power spectrum

As explained in the previous section, EEG time series are made of a sum of superposed signals, each having a specific frequency, amplitude and phase. Information regarding frequency-band activity can be retrieved from the EEG signal through a series of computational procedures. Fourier Transform is a versatile mathematical tool that allows such alternation between time and frequency domain representation of an oscillatory signal. Applied to time series data, Fourier Transform decomposes the signal into its constituent frequencies. The output of a Fourier Transform consists of complex-valued coefficients for every frequency occurring in the initial time-domain signal: a real part of the coefficients reflects the amplitude, and an imaginary part reflects the phase offset of the respective frequency oscillation. In simpler non-mathematical terms, Fourier Transform can be seen as essentially returning the recipe and ingredients that exist within the time-domain signal. By running the signal through a series of frequency "filters", information can be extracted about the distinct ingredients (frequencies), their proportion (amplitude), and the timing at which they have been incorporated in the recipe (phase offset). These filters compare how similar the signal is to set of templates, which are a series of sine waves of different frequencies.

In practice, Fourier Transform involves the computation of similarity estimates between the signal and a series of sine waves representing the range of frequencies investigated. This degree of similarity is computed through the dot-product:

$$dot\ product_{sk} = \sum_{i=1}^{n} s_i k_i$$

The dot product consists of the multiplication of each data point of the signal vector *s*, with the corresponding data point of a kernel vector k (here as a sine wave of frequency *f*). Note that the calculation requires that both vectors have the same length. The length of the vectors will define the spectral resolution of the output. It is therefore possible to increase the frequency resolution by either increasing the length of the epochs (at the expense of time resolution) or zero-padding the original signal (artificial smoothing). All of the products are summed together to return a single dot product value, which indexes the degree of similarity between the signal and the kernel.

The dot product is then computed across frequencies. The discrete Fourier Transform computes complex coefficients of a time series signal, for a range of frequencies. The same time series data is then compared to:

$$S_f = \sum_{t=0}^{n-1} s_t e^{-i2\pi f(t-1)n^{-1}}$$

Where *n* refers to the length of signal *s* vector, S_f is the complex Fourier coefficient of the signal s for frequency *f*, and s_t is the signal value at time point *t*. Given this equation, it should be clear that the spectral resolution of the output of a Fourier Transform is directly related to the length of the signal subjected to the Fourier Transform.

Following the Fourier Transform, the amplitude of the signal at any given frequency *f* can then be extracted from the real part of the Fourier coefficient. These amplitude values are then squared, converting them into power. These values are then baseline corrected and normalized (as described in section 3.5), before being subject to statistical analyses. In the present thesis, modulations of power across frequency bands were investigated through multiple correlations. By contrast, however, the phase of the signals was not directly investigated in the present work.

In terms of implementation, power spectral decomposition was performed using Fast Fourier Transform Matlab function [fft = (signal, fftlength);], which is a computationally optimized alteration of the initial Fourier Transform. As mentioned previously, the length of vectors compared (here “signal” and “fftlength”) defines the spectral resolution the Fourier Transform output. Due to the requirement of vectors of same length to be compared, the window size of the Fourier Transform is by default the same size as the input signal. Nevertheless, the spectral resolution can be artificially increased by zero-padding (i.e., adding zero-valued data points at the edges of the time series signal) the signal. In the present thesis, the use of zero-padding was limited to graphical display purposes (e.g., smoothing power spectra plots). Amplitude (the real part of the complex values) is then squared to convert magnitude into power [power = (fft)^2]. Power values are then converted in decibels (dB) relative to baseline activity for visualizations purposes:

$$dB_f = 10 \times \log_{10}\left(\frac{signal\ power_f}{baseline\ power_f}\right).$$

It is important to note that the conversion from temporal to spectral representations of the data through Fourier Transform is a lossless and reversible decomposition of the initial signal, which can then be accurately reconstructed through an inverse Fourier Transform. Furthermore, representation of the data in the frequency domain allow the application of signal processing functions more efficiently (e.g., any frequency filtering-based signal processing).

2.3.4. Time-frequency analyses: Event-Related Spectral Perturbations

2.3.4.1. Quantifying brain oscillations in the time domain

We have seen previously that some properties of event-related EEG signal can only be characterized in the frequency domain, such as the contribution of different frequencies to the signal, and non phase-locked signals. By computing the power spectrum of event-related EEG data, as outlined in the previous section, a measure of spectral activity can be retrieved that reflects the energy power across frequencies for the entire duration of an epoch. This discrete characterization of power across the frequency spectrum has an inherently low temporal resolution. Moreover, its computation relies heavily on an assumption of stationarity of the data (i.e., oscillating patterns are repeating endlessly). Indeed, by comparing a series of prototype sine waves to the signal and examining their fit to the data, discrete Fourier Transform assumes that the data will continue to present the same pattern of overall activity over time (or at the very least for the entire duration of the epoched signals).

Although the assumptions underlying frequency analysis cannot be avoided, it is important to recognise their implications for the interpretation of the data. As discussed in section 2.4, brain imaging applied to cognitive sciences research has increasingly focused on the investigation of functional changes of brain dynamics. If human brain activity was indeed following the assumption of stationarity, it could be argued that our ability to adapt and learn from interactions with the environment would be severely compromised. Put simply, if this were the case, human brain physiology would mostly consist of a limited range of long-lasting resting-state activity. Thankfully, brain activity is highly non-stationary overall, reflecting rapid flexible changes in processing over time. From this perspective, a key aim of any analysis is to understand when a given experimental paradigm encourages changes in processing, allowing functional non-stationarity to be correctly accounted for.

Importantly, Fourier Transform can be used to retrieve spectral power decomposition of relatively short segments (50-200ms) of the EEG signal that are more likely to present higher degrees of local stationarity in comparison to longer epochs. Therefore, using discrete Fourier Transform on successive short segments provides a way to quantify changes in frequency power over time, providing the analysis with resolution in time as well as frequency. As described in the previous section, however, the length of the signal will define the frequency resolution of the Fourier coefficients. This trade-off between temporal and spectral resolution implies that the segmenting epochs into shorter time bins to increase the time resolution of the analysis, will largely reduce its frequency resolution (spectral leakages may then appear). Conversely, using larger time bins, while increasing spectral resolution will come at the expense of the temporal representation of spectral dynamics (increasing the risk of not capturing transient changes in spectral activity). The limitations of Fourier Transform in representing changes of frequency pattern over time have been resolved by Morlet wavelet analysis, through the replacement of sine waves of predefined length by a family of wavelets.

2.3.4.2. Wavelets convolution

A wavelet is the product of the multiplication of a sine wave with a gaussian window. Wavelets have the inherent advantage of acting as natural temporal filters due to their gaussian-shape. Indeed, wavelets amplitude reaches its maximum at their centre, before returning gradually to zero at the ends. Conceptually, when a wavelet is used as a kernel (i.e., a vector mapped onto the signal to compute the dot product), the band-pass filtering of the signal is progressively attenuated on both sides around the middle of the time series. As a result, the dot product between a signal and a wavelet will therefore be mostly influenced by the data points to which the wavelet kernel is centred on, while the influence of neighbouring data points tappers off. Wavelet-based dot-product therefore provide a local measure of spectral covariance in the time-domain. In contrast, a sine wave does not offer such temporal localization because its amplitude continues to oscillate over it’s the entire length.

Wavelet analysis is based on a similar principle to the basic Fourier Transform; wavelets of different frequencies are compared to the signal and a coefficient expressing their degree of similarity is computed. To capture the dynamics of the data in both the time and frequency domain, the wavelets are compared across the time series signal. The principle of such time-domain convolution is to slide the kernels across the signal and compute dot product for every data points. To retrieve complete dot products at the edges of the signal, a common practice is to zero-pad the signal time series with n-1 (where n is the length of the kernel) zeros on both sides. Capitalizing on the temporal localization property of wavelets, dot products of different time points are smoothed in the time and frequency domain, and mostly capture the local dynamics of the signal as a function of the length of the wavelets.

A group of wavelets sharing common properties is referred to as a family of wavelets, and the mother wavelet is the prototypical wavelet function that reflects the parameters defining the wavelet family. These parameters are the length and cycles of a wavelet, which are directly related to the temporal and spectral resolution of the time-frequency decomposition. The number of cycles within a wavelet is positively correlated with frequency resolution. Importantly, however, fitting more cycles within a wavelet increases their duration in the time domain. Moreover, in practice, the wavelet length serves to define the time-domain resolution of the time-frequency decomposition. Wavelets length is negatively related to time resolution, such that the shorter the wavelet, the higher the time resolution will be. Since the number of cycles and length are co-dependent defining properties of the wavelets, a trade-off has to be made between fitting more cycles and increasing the wavelets length. Therefore, the quantification of brain oscillations temporal dynamics involves compromises between the resolution achieved in the time and frequency domains. It is important to recognize that these trade-offs are not absolute, and must be considered relatively to the frequencies under investigation and the properties of the epoched data. Indeed, the length of the signal constrains the number of cycles at lower frequencies, especially for short epoch. Conversely, the lowest frequency will define the number of cycles possible to reach satisfactory temporal resolution. In practice, fewer cycles are better able to detect and characterize transient changes, while higher number of cycles are more sensitive to changes at specific frequencies over longer dynamics.

Morlet wavelets are created by multiplying a complex sine wave by a Gaussian window:

$$Gaussian\ window = \ ae^{-t^2/2s^2}$$

Where a refers to the amplitude (height of the Gaussian's curve), t refers to the time point at which the curve peaks (position of the centre of the curve) and s is the standard deviation (width of the window). The gaussian window properties determines the temporal resolution of the time-frequency coefficients computed. The gaussian window is multiplied to complex sine wave defined as follows:

$$complex\ sine\ wave(t) = \ e^{i2\pi ft}$$

Where f is the frequency and t is time. Therefore, complex morlet wavelets are created through the following equation:

$$complex\ morlet\ wavelet(t) = \ e^{-t^2/2s^2}e^{i2\pi ft}$$

Where the first exponential is a Gaussian function and the second exponential is a complex sine wave, f is the central frequency of the wavelet and s is the standard deviation of the Gaussian defined as $s = \frac{n}{2\pi f}$, where n is the number of wavelet cycles.

Applied to EEG data, the output of Morlet wavelets convolution returns a set of complex coefficients at the intersection of each time and frequency. Similar to the Fourier coefficients, the real part indexes the magnitude and the imaginary component reflects the phase angle of the signal at a given time-frequency. The following section will present how this information is extracted to characterize event-related spectral changes, as used within Studies 4,5 & 6.

2.3.4.3. Event-related spectral dynamics

Representation of averaged event-related dynamics has become a prominent research method in cognitive sciences. Some aspects of brain activity may not be visible in the ERP waveform, however, even though they are time-locked to experimental events. This is because another requirement for event-related brain activity to be represented in the ERP (beyond time-locking) is that the signal should also exhibit consistent phase-locking (Freunberger, Fellinger, Sauseng, Gruber & Klimesch, 2009; Kalcher & Pfurtscheller, 1995; Tallon-Baudry, Bertrand, Delpuech & Pernier, 1996). As previously discussed, the phase of an EEG signal refers to its position at a particular time on the sinusoidal cycle of a specific oscillation frequency. Therefore, even though brain activity might consistently arise (in terms of amplitude) at a certain time, discrepancies in terms of their position on the oscillatory cycle across trials will lead to the summation of polarity-varying neural responses. Inter-trials phase incongruence will result in either partial suppression, or complete extinction, of the responses in the time domain (due to phase cancellation during averaging procedures).

On this basis, a distinction has been made in the EEG literature between evoked potentials (time and phase-locked, observable in the ERP waveforms) and induced activity (time but non phase-locked, not fully captured in ERPs). The study of induced event-related dynamics of EEG data therefore requires the characterization of spectral features in the time domain. For example, Pfurtscheller & Aranibar (1977) have quantified the time course of power spectral activity in the alpha-band in relation to auditory stimulation while subjects were closing their eyes. A significant decrease of power across the alpha band was observed over time following the presentation of stimuli, a change in activity now known as Event-Related

Desynchronization (ERD). This term derives from the concept that background activity is perturbed by sudden cortical arousal and is therefore desynchronized from its stationary oscillatory mode (Pfurtscheller, Maresch, & Schuy, 1977). Initially referring to a depression in alpha-band power, the terminology has later evolved to distinguish event-related spectral power increases as Event-Related Synchronization (ERS; e.g., see Pfurtscheller, 1992). Following these initial demonstration in the alpha band, Makeig (1993) generalizes the concepts of band-defined ERD/ERS as the quantification of Event-Related Spectral Perturbations (ERSP) across the whole frequency spectrum.

Event-Related Spectrum (ERS) are calculated by computing the signal power spectral activity for short sliding time windows, across the epoch duration, through Morlet wavelet convolution for each trial. The complex Morlet coefficients are then squared to transform amplitude reflected by the real part of the coefficients into power value:

$$ERS_k(f,t) = |F_k\ (f,t)|^2$$

The resulting three-dimensional matrix returns complex spectral values at each frequency *f* and time point *t*, for single-trial *k*. The average across all trials is then computed through the following equation:

$$\overline{ERS}(f,t) = \frac{1}{n}\sum_{k=1}^{n}|F_k(f,t)|^2$$

where *n* is the number of trials, $F_k(f,t)$ is the wavelet coefficient at frequency *f* and time *t*, for trial *k*. The output of this computation is a matrix of mean ERS power estimates at the intersection of each *f* frequencies (power spectrum range) and *t* time points (relative to epoch length and sampling rate).

Event-Related Spectral Perturbation (ERSP) is a measure of change in spectral dynamics induced by experimental events, relative to the mean activity within a baseline period. Within the frame of the work presented in this thesis, this relative measure was computed by dividing the signal time-frequency power by the mean power in a baseline period:

$$ERSP(f,t) = \frac{ERS(f,t)}{\mu_B(f)}$$

Where $\mu_B(f)$ is the mean spectral power across the baseline time window. The ERSP output is therefore interpreted as a percentage change in signal activity, relative to baseline. ERSP was then converted to a logarithmic scale, indexing signal deviation from the baseline in decibels (dB):

$$ERSP_{log}(f,t) = 10\log_{10}\left(ERSP(f,t)\right)$$

Although this approach is widely used within the cognitive neuroscience field, it is important to recognize that other baseline normalization methods are valid and may also be applied to time-frequency event-related data, as discussed in the following section.

2.3.5. Baseline correction and normalization

Baseline correction refers to the rescaling of data relatively to signal acquired during a neutral "baseline" period. Ideally, a baseline period does not include any activity related to experimental manipulations, similar to resting state activity. Conceptually, baseline correction subtracts a combination of stationary background brain activity (that is unrelated to the cognitive processes investigated) and residual noise. Through this process, baseline normalization effectively increases the resulting signal sensitivity to event-related changes. In practice, however, the selection of the time window used as a baseline period has important implications for the resulting signal which may, in turn, lead to significant differences in the interpretation of the data. The appropriate definition of the baseline period interval is therefore paradigm-dependent.

Time-domain EEG data is often baseline corrected through a linear baseline subtraction, which is justified based on an additive model that assumes event-related brain activity linearly adds on top of background neural activity (Sauseng et al., 2007). A common practice in EEG studies is to average power data across trials and then perform a baseline normalization on the averaged data. Theoretically, applying baseline correction prior to averaging on a single-trial basis may help mitigate the impact of outlying trials (Grandchamp & Delorme, 2011). This assumption, however, relies on the presence of a reliable baseline period preceding every single-trial, which, in practice, may not always be the case. Applied to mobile EEG data, single-trial baseline correction may therefore be more detrimental than useful, because it may increase variance of trials presenting a noisy baseline. The implementation of baseline correction and data normalization may vary from one study to another because they are heavily dependent on the paradigm used and the type of analysis conducted. In the present thesis, ERP data (Chapter 3, 4 & 5) involved a relatively low inter-stimulus interval, potentially leading to overlap of elicited neural responses across trials that would contaminate the following baseline periods (depending on the previous trials stimulus type). The local variance induced by such single-trial discrepancies therefore discourages the application of single-trial baseline normalization. By contrast, in the frequency and time-frequency data (Studies 4, 5 & 6), inter-trial time periods were consistently longer and have been used individually as a baseline to account for changes of mean power across recording sessions.

Similar to baseline correction in the time-domain, EEG data in the frequency domain may be subject to various types of normalizations. The phenomenon of power decrease as a function of frequency means that power spectra are difficult to interpret (frequency analyses provide a 1/f skewed representation). Thus, to make peaks of power in faster frequency bands visible alongside (s)lower frequencies, and to allow quantitative comparisons of power across frequency bands, spectral data has to be normalized. This can be done through the computation of power relative to baseline activity, either a) as a raw quotient dividing the data of interest by the equivalent power during the baseline (scaled as a percentage, %, or logarithmically, in decibels, or b) as standard deviation (Z-Transform) and subtracting the relevant baseline. In the present thesis a decibel ratio was preferred because the properties of logarithmic scaling attenuate the incidence of single-trial noise, especially regarding outlier values that may contaminate lower frequencies.

2.3.6. Single-trial features extraction

The computational methods described previously have been applied to epoched data to investigate Event-Related dynamics. Single-trials features of ERP and ERSP were extracted to be contrasted across conditions through statistical analyses or used to inform the definition of range of interest. Time domain single-trials ERP features such as peak latency and peak amplitude were both used for statistical analyses purposes but also to define the time window used to compute specific components amplitude area. Within the frame of frequency power analyses, features characterizing single-trials power spectra were analysed such as peak frequency and power within a specific frequency band.

2.3.7. Statistical analyses

Statistical analyses were conducted using JASP open-source software for statistical analyses (JASP Team, 2017). Descriptive statistics summarizing datasets central tendencies (e.g., mean) and their variability (e.g., standard deviation) were performed. Classic statistical analyses based on parametric assumption models were carried out to investigate differences introduced by experimental manipulations on various measures derived from behavioural and brain imaging recordings. The reported studies have all used within-subject experimental designs. Therefore, repeated measures ANOVAs and paired-sample t-tests have been applied to the data, effectively providing probability values (p-values) of the null hypothesis (i.e., datasets compared are not different). These p-values were considered as reflecting significant difference between datasets at a threshold of 5% ($p < .05$) under which the null hypothesis was rejected. While reporting p-values is a common practice in quantitative scientific research, concerns have been raised about misconceptions in the usage and interpretation of these values (Wagenmakers, 2007), potentially leading to false positive discoveries (by wrongly rejecting the null hypothesis, type 1 error) or even false negative interpretations (by erroneously accepting the null hypothesis, type 2 error). The Bayesian statistical approach proposes an alternative to the shortcomings of the p-values (Dienes, 2011; Edwards, Lindman, & Savage, 1963). Bayes Factors aim to quantify the probability of a statistical model over another based on the data (Kruschke, 2010). In the present thesis, Inverse Bayes Factors (BF_{10}) were computed to assess the support for an alternative model (H1) in comparison to the null hypothesis (H0), assuming that both models are equally likely and using default Cauchy priors (based on Rouder, Morey, Speckman, & Province, 2012). Inverse Bayes Factors values above 1 indicate that the data is more likely to fit the alternative hypothesis (i.e., samples compared are different) than the null hypothesis, while values below 1 indicate that the data is more likely to fit the null hypothesis model. Several scales for the interpretation of Bayes factors coefficients have been proposed (Jarosz & Wiley, 2014). Within the frame of the present thesis, however, the interpretations scale proposed by Raftery (1995) was employed. Bayes Factors ranging from 1 to 3 suggest that the data provide weak evidence for the alternative hypothesis, BF_{10} ranging from 3 to 20 indicated positive evidence, and BF_{10} ranging from 20 to 150 were interpreted as strong evidence, and values beyond 150 were indicating very strong evidence for the alternative hypothesis.

2.4. Further considerations

Amongst the plethora of tools available to address noise in EEG data, only few have been applied to real-world EEG data. An important conclusion that can be drawn from this review of the signal processing literature is that the usage of such methods needs to be tailored to the specificities of the data they are applied to in order to be effective and not detrimental to the validity of the data. By contrasting the guidelines advocated by the signal processing literature to the common practices in EEG research, it appeared that some aspects of the implementation of these methods are often left unspecified in empirical reports despite their significance on the outcome of data analysis and eventually the interpretation of results. Due to the novel challenges brought by mobile EEG recordings in terms of parsing non-brain artifacts from brain signals, it is crucial to keep track of the methodologies used in order to build upon previous experiences and highlight current limitations. This approach aims to bring clarity about the methodology used within each study while acknowledging the limitations of processing methods in terms of both their effectiveness in dealing with noise but also the concerns of objectivity and validity related to the selection of parameters used. In this context, even though the processing pipeline described in the presents methodological sections has been applied throughout the studies presented in this thesis, the implementation of the different processing methods has been carefully adjusted to the specificities of the datasets. Therefore, the next empirical chapters include a methods section that will specifically focus on reporting variations in the parameters applied at the different stages of the data processing pipeline that has been outlined in the present chapter.

Chapter 3: Recording event-related signatures of attention in the real-world

3.1. Introduction

A fundamental first step towards the recording of neurophysiological markers of human cognition in everyday life contexts is to assess the feasibility of acquiring such measurements in a real-world environment. One objective of this study was therefore to explore whether mobile EEG data can be used to address research questions in cognitive sciences. For this purpose, we compared P300 Event-Related Potentials (ERPs), reflecting attentional processing of target stimuli elicited during an auditory oddball paradigm, while subjects were standing still in a quiet room versus walking freely in a real-world environment. The study assessed whether classic ERP components can be characterized in mobile EEG recordings, comparing ERP amplitude and latency between lab-based and real-world recording conditions.

The following sections will introduce the EEG marker investigated in this study, the P300 ERP component. The theoretical framework surrounding the P300 will be discussed, along with the cognitive interpretation of its features. These elements will shed light on the rationale for the selection of this particular neural signature of attention.

3.1.1. What is the P300 Event-Related Potential?

The P300 effect was originally reported following the presentation of infrequent-target stimuli amidst frequent non-targets (Smith, Donchin, Cohen, & Starr, 1970; Sutton, Braren, & Zubin, 1965). This component of the ERP waveform is characterized by a positive deflection, peaking between 250 and 500ms after the presentation of target stimuli (Picton, 1992). Even though initially demonstrated in the auditory modality, the P300 effect can also be elicited by visual discrimination tasks (Sayers, Beagley & Henshall, 1974). The activity related to the P300 ERP is most prominent at parietal electrode sites and typically presents a frontal/parietal polarized topography (Johnson, 1993). From a methodological viewpoint, the P300 ERP component is usually elicited through paradigms involving the presentation of target and non-target stimuli. While the traditional paradigm used two stimuli types (oddball targets and frequent non-targets), variants using a single stimulus type (only targets) whose rate of presentation can be manipulated, or even three stimuli types paradigms including the presentation of additional infrequent distractors, have all been used to uncover subcomponent features of the P300 (Polich, 2003). Participants are generally instructed to mentally or physically respond to the target stimuli only (Mertens & Polich, 1997). Therefore, Go-NoGo tasks (Verleger, Grauhan & Smigasiewicz, 2016), such as experimental tasks involving selective attention towards a specific type of stimuli, will therefore typically lead to increased activity over parietal electrode sites around 300ms following the presentation of target stimuli. Even though the original P300 elicitation paradigm involved the presentation of auditory stimuli, P300 has also been studied in visual (Struber & Polich, 2002) and somatosensory (Nakajima & Imamura, 2000; Satomi, Horai, Kinoshita, & Wakazono, 1995) modalities.

3.1.2. Theoretical interpretation of P300 ERP

The main theoretical accounts for the P300 component have been related to attentional processing and context updating in working memory (following the presentation of informative task-relevant stimuli). According to the context-updating theoretical framework, the P300 component indexes brain dynamics related to the assessment and revision of previously stored mental representations, changes that are induced by the presentation of new relevant stimuli (Donchin & Coles, 1988). Following initial early sensory processing of stimuli (as reflected by early N100 and N200 and P200 components in the ERP waveform), attentional processes compare the novel information to previous events stored in working memory. If a novel stimulus has been presented, attentional processes update the former representation stored in working memory, resulting in the observation of the P300 in the waveform. This theoretical interpretation of the P300 as mainly an oddball effect largely derives from early studies focusing on the manipulation of target stimulus probability.

This context updating account does not provide any explanation for why the P300 effect is sensitive to the task-relevance effect of target stimuli. By contrasting neural responses following presentation of oddball targets to oddball non-targets (distractors) in a three-class P300 elicitation paradigm, subcomponents of the P300 ERP have been uncovered (Squires, Squires, & Hillyard, 1975). The three stimuli variant has distinguished the contribution of two subcomponents to the P300 feature. The earlier subcomponent, P3a, indexes any alerting and/or rare stimuli. By contrast, the later subcomponent, P3b, is specifically sensitive to task-related stimuli. The P3a subcomponent has been interpreted as reflecting early neural inhibitory activity that would delimit the attentional processing of stimuli unrelated to the task. The P3b has been interpreted as an index of subsequent attentional resources mobilized to promote higher-cognitive operations involving task-related stimuli (Bradzil, Roman, Daniel, & Rektor, 2003; Polich, 2007b). Furthermore, recent studies have distinguished the higher cognitive attentional processes involved in task-related stimuli processing from low-level sensory processing related stimulus mismatch detection (Naatanen, Paavilainen, Rinne, & Alho, 2007). Taken together, these findings have contributed to a reformulation of the interpretation of the P300 component as a marker of both attentional processing and context-updating processes related to working memory.

Within the frame of the present study, a classic oddball paradigm (targets versus frequent non-targets) has been used in order to evoke neural responses related to attentional processing of task-related information. Therefore, both P3a and P3b subcomponents are expected to be elicited by target stimuli and contribute together to the P300 ERP component measured.

3.1.3. Measuring P300 ERP features

Similar to other components, the P300 ERP is quantified in terms of its peak amplitude and latency by contrasting the averaged neural responses of attended target stimuli from non-target stimuli. As previously discussed in the methodological section, the definition of both amplitude and latency varies across studies and their definition has evolved over decades of ERP research. In the frame of this work, mean amplitude of the P300 effect is calculated using an area measure within a data-driven time window. The P300 latency measure used here follows traditional definitions of maximal peak activity occurring after stimulus onset within an a-priori time window. The P300 ERP is a particularly robust effect that is well documented in the EEG literature, to the extent that the effect can be directly observed in the continuous EEG at a single-trial scale under specific filtering conditions (Farwell & Donchin, 1988). The reliability and consistency of P300 elicitation have partly motivated the choice of this component to assess the feasibility of mobile EEG recording.

3.1.4. Factors underlying P300 ERP amplitude and latency modulation

Experimental manipulations underlying changes in the P300 ERP features have been extensively investigated, leading to the cumulative documentation of a wide range of modulating factors. Target stimulus probability, and its saliency in contrast to non-target stimuli, have been highlighted as yielding the most significant impact on both the onset and the magnitude of the P300 component (Polich, 2007; Polich & Kok, 1995). A gradual decline in P300 amplitude has been observed in extended paradigms suggesting that attentional focus decreases as a function of task-related stimulus repetition (Kramer, Schneider, Fisk, & Donchin, 1986). This habituation effect has been interpreted as reflecting more efficient and less expensive attentional processing of target stimuli in terms of cognitive resources (Lammers & Badia, 1989; Polich, 1989). Furthermore, increasing the inter-stimulus time between presentation of target stimuli generally leads to an increase in P300 magnitude (Gonsalvez & Polich, 2002; Gonsalvez, Gordon, Grayson, & Barry, 1999). More broadly, fluctuations in the arousal state of subjects have also been found to explain a substantial portion of P300 variations. Changes of physiological arousal that either occur naturally (following circadian cycle) or are induced by environmental factors (fatigue, exercise, drugs), have an impactful effect on P300 morphology (Polich & Kok, 1995).

Higher levels of arousal increase the readiness of cognitive processes through physiological facilitation (neurotransmission thresholds) of information processing. More specifically, therefore, biological alertness appears to be a key factor in the generation of P300 ERP, and any decline of tonic state typically translates into delayed and attenuated neural responses. Furthermore, lower and higher ends of the arousal spectrum have been both found to be detrimental to the performance of cognitive tasks (task performance as an inverse U-shaped function of arousal, see Lambourne & Tomporowski, 2010). While low physiological readiness may reduce or slow down the processing of information, higher levels of alertness may lead to increased propensity for false positive responses. Therefore, the arousal state of participants should not be overlooked within the frame of P300 elicitation paradigm, because these biological determinants can have a significant impact on both the behavioural and the physiological measurements. Given the factors outlined above, although biological determinants were not the object of the present study, participants have been tested at consistent time of the day. In addition, participants were instructed to refrain from consuming alcohol and caffeine 24 hours prior to the experiment, and exclusion factors included any recent use of psychoactive or sedative drugs. Furthermore, during testing, breaks between experimental blocks and water were provided to counteract drowsiness related to the extended and repetitive nature of the tasks.

3.1.5. Cognitive capacity and dual-task paradigms

Dual-tasks studies have shown that the amplitude of the P300 ERP elicited by targets belonging to the primary task was dependent on the difficulty and intrusiveness of the secondary task (Wickens, 1984; Wickens, Kramer, Vanasse, & Donchin, 1983). Evidence suggests that the modulation of P300 amplitude reflects the proportion of attentional resources captured by the competing task (for a review, see Polich 2007). Moreover, P300 amplitude has been found to be positively correlated with task performance, which suggests that P300 amplitude indexes the effective processing of task-related information from target stimuli (Ruchkin, Johnson, Canoune, Ritter, & Hammer, 1990). These findings have led to wide agreement that the P300 ERP amplitude provides a reliable measure of processing capacity that can be used to investigate cognitive resources allocation, during both dual-task situations and following the manipulation of task difficulty (Kok,1998). P300 latency has been mostly interpreted as a metric of classification speed and has found to be highly correlated to reaction time (Magliero, Bashore, Coles, & Donchin, 1984). Moreover, P300 latency and task performance have been shown to be negatively correlated, such as that earlier peaks are associated with higher performance (Kramer & Strayer, 1988). These findings suggest that P300 ERP latency may be a good predictor of cognitive capacity and task performance. In summary, P300 component features that are informative with regards to cognitive capacity, indexing the amount of attentional resources allocated to stimulus processing and, at least in some circumstances, predicting task performance

3.1.6. Previous research on P300 ERP during natural movements

Recent evidence from studies using static EEG during treadmill walking suggested that brain dynamics can be captured during whole body movements (Gramann et al., 2011b), but also that human brain may switch to a different mode when subjects are actively engaged in natural behaviours (Gramann, Jung, Ferris, Lin, Makeig, et al., 2014). These first attempts to record brain electrophysiology during motion have highlighted different patterns of cortical activity in relation to various degree of physical engagement (e.g., similar visually evoked potentials found in stationary, slow walking and fast walking recording conditions, Gramann, Gwin, Bigdely-Shamlo, Ferris & Makeig, 2010). Even though these proof-of-concept studies were necessary incremental steps towards the development of mobile brain imaging techniques, these studies have typically focused on replicating well-documented effects of the EEG literature, either during motion in a laboratory environment, or during stillness in the real-world. While the recent developments in mobile biosensor technology offers exciting prospects of real-world application for BCI and neurofeedback purposes (Lotte, Fujisawa, & Touyama, 2009; Stopczynski et al., 2014), it is crucial to characterize brain dynamics under real-world circumstances. Therefore, another main aim of the present study was to investigate differences in ERP features between recordings acquired in natural settings and in traditional laboratory environments, using truly mobile EEG sensors.

Previous studies have reported differences in P300 ERP amplitude between sitting indoors and walking outdoors (Debener, Minow, Emkes, Gandras & de Vos, 2012), and between static outdoor versus walking outdoor conditions (De Vos & Debener, 2014). Both studies reported an attenuation of P300 amplitude in the walking condition in comparison to the static condition. Moreover, the static and walking conditions did not present any significant differences in terms of single-trial classification rate. The signal-to-noise ratio was found to be lower in the walking condition, but it was unclear whether this difference was due to increased artifacts in the walking condition (i.e., higher noise) or due to a reallocation of attentional resources during real-world navigation (i.e., lower signal). To address this unanswered question, the following experiment contrasts P300 ERP features recorded during an auditory oddball paradigm in both a static and a walking condition. P300 ERP amplitude and latency are quantified, along with measurements of residual noise for both conditions. Taken together, these comparisons provide insight into the nature of the differences between static and walking conditions previously reported and may shed light on the hypothesis of a reallocation of attentional resources during real-world behaviour.

3.2. Methods

3.2.1. Participants

Participants were recruited through the University of Stirling website. Sixteen undergraduate students took part in the study. The subjects did not report any of the exclusion criteria (neurological/psychological antecedents, use of psychoactive drugs at the time of the study, consumption of caffeine/alcohol within the 12-hour time period preceding data collection, presence of gait disorders or any form of motor/locomotion impairments). Written informed consent was obtained from all participants. Datasets affected by technical issues resulting in loss of EEG signals for a substantial part of the recording (mainly due to intermittent mastoid electrodes disconnections during movement, or desynchronization of event timestamping) were discarded. Furthermore, participants that did not follow the task instructions to count the number of pitch-deviant tones and displayed outlying performance results (greater than 2 standard deviations from the mean) were also discarded from further analyses. These combined criteria led to the exclusion of five participants, the following analyses reported here have therefore been performed on the remaining 11 participant data (N = 11; 6 female, age range: 18-51; mean = 22).

3.2.2. Experimental design

A repeated measures design was used to contrast standing still versus walking recording conditions (see Figure 3.1). Subjects were therefore required to complete an auditory oddball task while either standing still in a quiet office environment, or walking through corridors within a university building. The order of conditions was counterbalanced to account for potential training/habituation effects (Pan, Takeshita, & Morimoto, 2000) that may arise due to the length of the study. The real-world recording environment included considerable amount of auditory and visual noise and involved a moderate rate of human encounters.

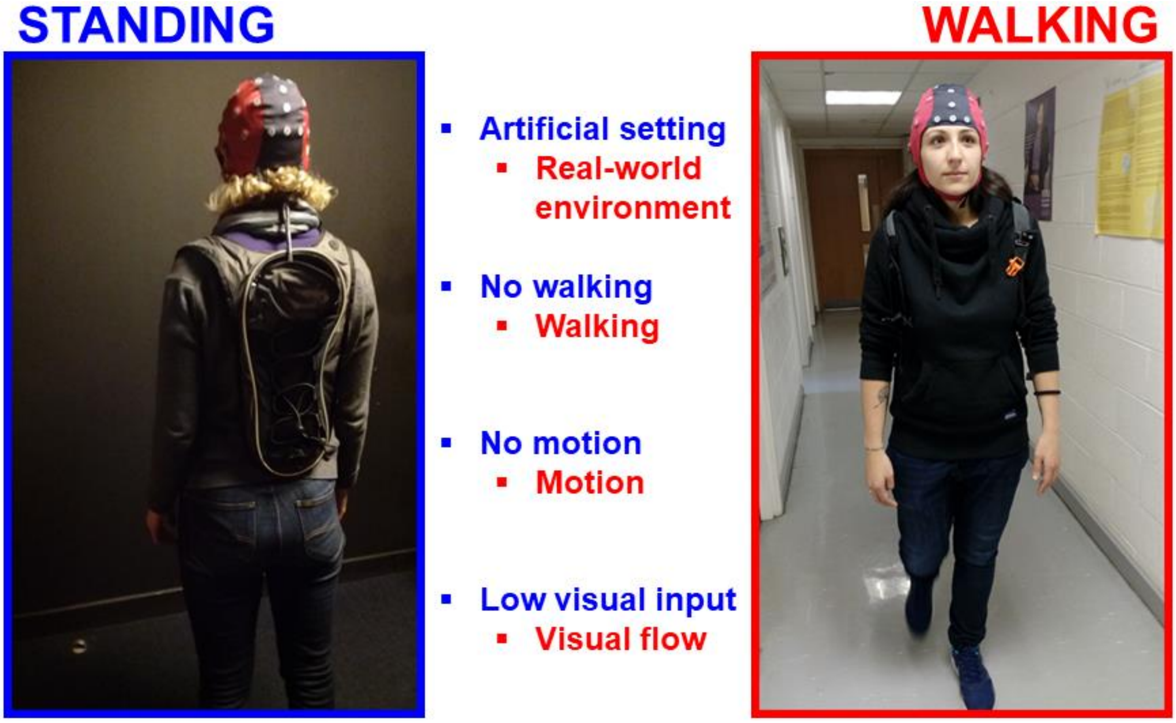

Figure 3.1. Illustration and comparison of the standing (blue) and walking (red) conditions.

3.2.3. Material

3.2.3.1. Mobile EEG system

EEG data was recorded through 32 Ag/AgCl electrodes located in an adaptable headcap and connected to a battery powered amplifier (ANT-neuro, Enschede, The Netherlands). The system digitized signals at a sampling rate of 500Hz, and prefiltered the data with a high-pass filter of 0.016 Hz and a low-pass filter of 250Hz (under Nyquist frequency). The 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 the ground placed on the AFz electrode position, and Cpz electrode used as common reference site (see Figure 3.2).

The communication rate of devices and software used to send event markers to the amplifier have been extensively tested through black-box testing (Black Box ToolKit Ltd., York, UK). Whenever consistent lag was found between the local timing of the external device sending triggers, and the registration of these as marker in the EEG trace, event markers latencies were corrected to account for the measured delay.

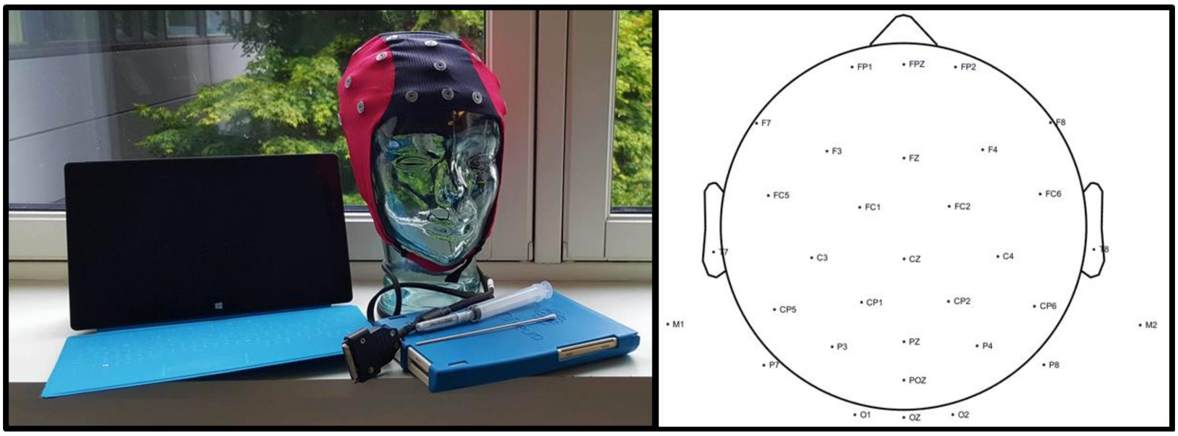

Figure 3.2. Mobile EEG system and electrode locations. Left: 32 electrodes EEG cap connected to a portable amplifier, transmitting wirelessly to a tablet displaying online EEG data acquisition. Both the amplifier and the tablet can be fitted in an ergonomic backpack. The entire system is relatively lightweight and does not constrain participants movements. Right: Channel locations according to the International 10-20 system. Three-dimensional electrodes coordinates were provided by the manufacturer.

3.2.3.2. Auditory oddball paradigm

The experiment used a classic auditory oddball paradigm consisting of the binaural presentation of two types of stimuli: frequent non-target tones (high pitch) and infrequent oddball-target tones (low pitch). The occurrence probability of oddball sounds was set to 20%. This oddball stimulus presentation ratio was selected as it presented a good compromise between the oddness of the stimuli (how infrequent the stimuli are, which is related to the magnitude of the oddball response) and the number of total stimuli presented per session (increasing the length of the task, which may have significant impact on participant’s performance to the task). This trade-off is further discussed in the following paragraph. A total of 300 trials were presented in each experimental condition in a pseudo-randomized order, avoiding the presentation of consecutive targets. Both stimuli types had a duration of 200ms and the inter-stimulus interval was fixed to 800ms. The tones were presented through USB speakers positioned on an ergonomic backpack that also contained the EEG data acquisition unit and the amplifier. The participants were instructed to silently count the target tones. Counting target stimuli involves working memory through a context-updating occurring when relevant information to the task (i.e., target stimuli) are presented. This context-updating element associated to the paradigm is reflected by a larger P3b effect (see Section 3.1). Each participant completed the task across the different experimental conditions following a counter-balanced design.

As discussed previously, target stimulus probability has a significant influence on P300 component features, especially in terms of amplitude (Johnson & Donchin, 1982). Reduction of target probability incidentally reduces the habituation effect that occurs when there are extended repetitions of task-relevant stimuli to attend. Moreover, the oddness of target stimuli is another key influence on P300 component features, dependent on both their dissimilarity with non-target stimuli and their low and unpredictable occurrence (Johnson & Donchin, 1982). Therefore, regular patterns of target stimuli presentation should be avoided as much as possible, so the participants cannot predict or expect the next occurrence of target stimuli (which would lead to false positive or delayed processing of such targets, see Polich, 1989). For these reasons, the presentation of stimuli followed a pseudo-randomized rule, defined by the avoidance of consecutive presentation of target stimuli. This constraint was used to reduce habituation effects, and to counteract the familiarisation to stimuli presentation patterns that usually occurs during ERP experiments (which occurs because many trials are collected to perform averaging-based analyses, see Sutton, Braren, & Zubin, 1965). Furthermore, while lowering the rate of target stimuli presentation appears as an attractive solution to maximize the oddness of such target stimuli, it comes at the expense that the total number of stimuli that must be presented to attain the same number of target stimuli has to substantially increase. This trade-off means that reducing target stimuli presentation rate will increase the length of each experimental block, incidentally meaning that participants would have to walk more (increasing potential physical fatigue across the recording), lowering the attentional engagement as the task becomes longer through both fatigue and habituation effects. Importantly, the P300 elicitation paradigm used within the frame of the following studies has been kept consistent across the different experimental conditions. Experimental condition order was also counterbalanced, in order to counteract practice effect inherent to the repetition of the task across conditions.

3.2.4. Procedure

Prior to the experiment, all participants were given general information regarding the functional and practical aspects of electroencephalography (EEG) recording in both verbal and written formats. While the nature of the experimental tasks was explained, the hypotheses were not disclosed until the end of subjects' participation. Moreover, participants were informed that the experiment was conducted in accordance with the guidelines of the University of Stirling Research Ethics Committee, that their data would be stored and treated anonymously, and that they had the right to end their participation in the study at any time without penalty. Participants were then invited to give their written consent to confirm their intention to take part to the study.

The participants were seated on a comfortable chair during the capping procedure. Measurements of participants head were used to setup the sensors according to the International 10-20 system (Jasper, 1958). The gap between the scalp and the electrodes was then filled with conductive gel, with the experimenter using a disposable blunt needle to increase sensor conductivity. Electrode impedance was measured prior to each recording session and maintained below 10 kΩ for each channel. Channel impedance was checked between experimental blocks and/or during breaks, in the case of extended recording sessions (i.e., every 30 minutes), to avoid slow drifts due to channel disconnections and sweat. Here we highlight one important consequence of this procedure for how the data was processed. In the event of actions being taken to lower the impedance of a channel, the continuous EEG data was subsequently segmented and each segment was subject to a separate Independent Component Analysis (ICA) decomposition. This processing stage was required to avoid aversive effects on the components classification. Indeed, discrepancies in the signal-to-noise ratio of specific channels, and potential displacement of sensors between different segments of the data, can have a substantial impact on the weighting of spatial relations between sensors computed during ICA. Careful logging of disruptions to the data analysis is therefore an important aspect of mobile data collection; failure to do so potentially invalidates the decomposition computed on unsegmented data.

Following the presentation of a short training block containing 10 trials amongst which two targets stimuli, participants were instructed to 'Please count the number of target stimuli throughout the duration of the experimental block, at the end of which you will be asked how many target stimuli have been presented'. In the case of the walking condition the participants were specifically asked to 'walk at a natural pace'. The participants were introduced to the route they would perform during the walking condition on a map representation of the building and then they would perform the route once with the experimenter. This familiarisation to the route was performed to ensure that the participant would know where to go during the actual experiment, and therefore avoid the engagement of spatial cognitive functions which would have acted as a confound. Moreover, the 'navigation' was further eased by the fact that the doors on the path were kept open (as opposed to other doors), to avoid the engagement of confounding motor preparation processes that would occur at every door encounter to open it but also that acted as a cue to further guide the participants.

Data was exported using the built-in data acquisition software (ASA, ANT-neuro). Continuous data was then stored on the Psychological Imaging Laboratory servers, before proceeding with further processing.

3.2.5. Data processing

EEG data were analysed using the EEGLAB (Delorme & Makeig, 2004) open source toolbox and custom MATLAB scripts (version R2014b, The MathWorks Inc.). In a first preprocessing step, the continuous data was visually examined and the portions of the EEG displaying extreme levels of noise (e.g., channel disconnections) were manually discarded. During the first stage of the processing procedure the datasets were filtered with a low-pass filter of 20Hz and a high-pass filter 1Hz. Then the continuous EEG was split into consecutive epochs of 1 second. Epochs presenting abnormal values were pruned based on standard statistical criteria (more than three standard deviations from the mean) as implemented in EEGLAB toolbox.

Following initial filtering and removal of noisy data, a first stage of artifact removal was carried out. An extended infomax Independent Component Analysis (ICA, Bell & Sejnowski, 1995) was performed on the remaining epochs and the resulting Independent Components (ICs) decomposition matrices were saved and back projected to the initial continuous datasets. In a second stage, the continuous datasets manually cleaned from noisy segments were finite impulse response filtered from 0.1 Hz to 20 Hz (−6 dB cut-off, filter order 16500). The IC features obtained during the first step of the preprocessing procedure were then back-projected to the filtered continuous data. The ICs indicating common artefacts such as eye blinks, eye movements and heartbeats were removed. After this ICA-based data pruning, the continuous datasets were then epoched around the onset of events (-

200 to 800 ms). The epochs dominated by artifacts were identified using the probability and kurtosis criteria implemented in EEGLAB toolbox (threshold greater than 2 standard deviations around the mean) and improbable epochs were discarded from further analysis. A baseline correction was then performed based on the mean EEG activity within the 200ms preceding the stimuli. The cleaned data was then re-referenced to the average of the mastoids (M1 and M2) and epochs were then split into the recording (standing and walking) and stimulus type (frequent and rare) conditions.

3.2.6. Data analysis

Averaging across epochs resulted in ERP waveforms for every channel, in each stimulus and recording conditions. The P300 amplitude was analysed by calculating the difference between rare and frequent ERPs waveforms. The P300 latency was analysed based on the maximal value recorded within the time window on a single-trial basis.

3.2.7. Statistical analyses

ERP amplitude, ERP latency, measures of residual noise, signal-to-noise ratios and task performance were all compared between the two recording conditions using paired-sample t-tests. Mean amplitudes from 256 to 448ms were analysed as a time window of interest for P300 ERPs analysis (based on a data-driven ERP component time window). This time window was also used to calculate the Signal-to-Noise Ratio (SNR), by dividing the ERP amplitude by the standard deviation in the prestimulus interval (-200 to 0ms). ERP analysis was limited to electrode channel Pz, where the oddball-P300 is most prominent (Alexander et al., 1996; Polich et al., 1997). Links between task performance and P300 ERP amplitude were assessed through Pearson’s correlations coefficients. The Greenhouse-Geisser correction was used when sphericity assumption was violated and adjusted degrees of freedom are reported whenever this was necessary.

3.3. Results

3.3.1. Event-Related Potentials

3.3.1.1. P300 ERP amplitude

Reliable P300 effects were recorded across both experimental conditions (see Figures 3.4 and 3.5), with target stimuli eliciting significantly larger neural responses than frequent non-target stimuli [standing, t(10) = 6.147, p<.001, d= 1.853; walking, t(10) = 5.027, p=.001, d= 1.516].

The P300 amplitude, calculated by subtracting frequent stimuli ERPs from the target stimuli ERPs, was significantly larger when participants stood still in a quiet office compared to when they walked down a hallway [Figure 3.3.; paired-sample t-test: t(10) = 3.286, p < .01, d= 0.991]. The P300 ERP effect was most prominent at parietal electrode sites, with maximal peaks recorded at Pz electrode site in both recording conditions (see Figures 3.4 and 3.5).

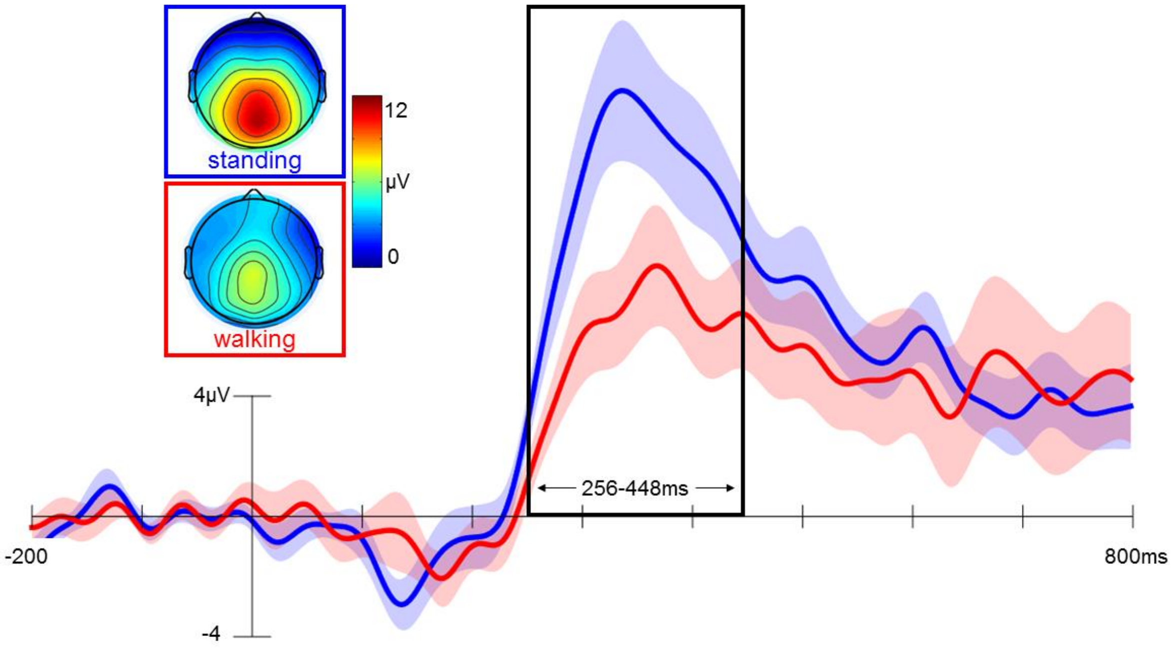

Figure 3.3. Mean Event-Related Potential waveforms (difference of activity evoked by target and non-target stimuli) in both recording conditions (standing in blue, walking in red) measured at the Pz electrode site. Topographic maps illustrate the distribution of the P300 effect within the analysed time window (256-448ms) for each condition.

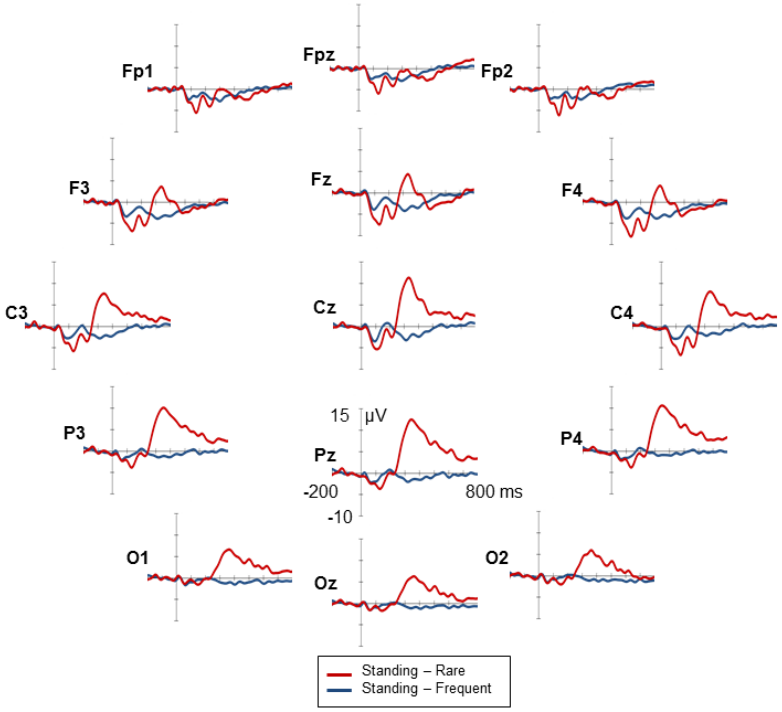

Figure 3.4. Distribution of P300 Event-Related Potentials grand-averaged (n=11) waveforms at midline and medial electrode sites for the rare target (red) and frequent non-target (blue) stimuli in the standing condition.

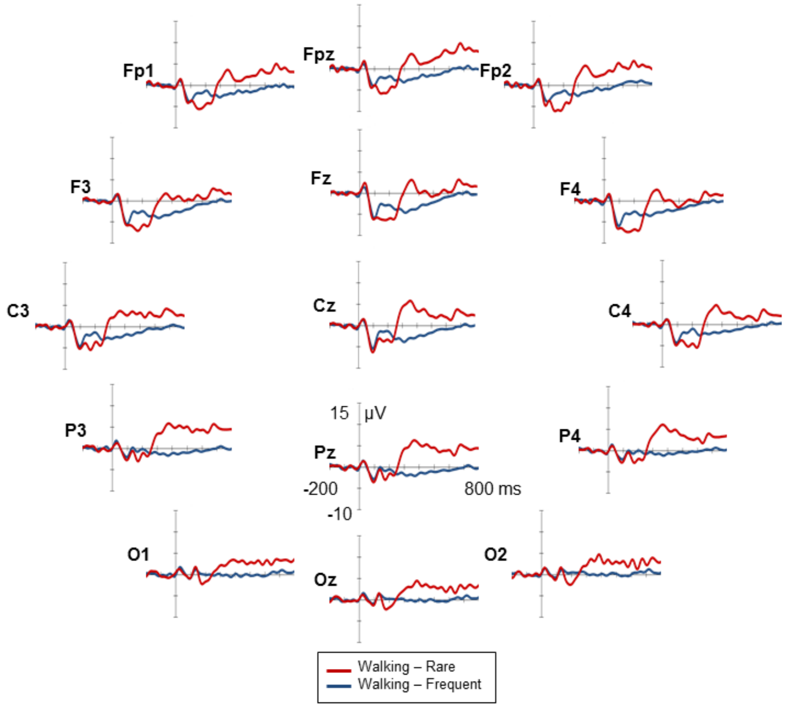

Figure 3.5. Distribution of P300 Event-Related Potentials grand-averaged (n=11) waveforms at midline and medial electrode sites for the rare target (red) and frequent non-target (blue) stimuli in the walking condition.

3.3.1.2. P300 ERP latency

There was no significant difference found in the mean peak latencies of the P300 ERPs between the standing (mean = 341ms, SD = 34ms) and walking (mean = 363ms, SD = 58ms) recording conditions [t(10) = 1.113, p = .292, d= 0.336]. Mean peak latency was not correlated across recording conditions [r = .058, p = .865, two-tailed]. The P300 time window was defined as two standard deviations around the mean peak latency computed from single-trials across both conditions (overall mean peak latency = 352ms, standard deviation = 48, interval = 256-448ms).

3.3.2. Behavioural results

Since the primary goal of the first study was to assess the classic auditory oddball P300 effect in the real-world, while participants were walking, we intentionally chose very distinct stimuli that could be easily discriminated from each other during motion in a potentially noisy environment.

Unsurprisingly therefore, participants correctly reported 98% (SD = 1) of targets stimuli presented in the standing condition and 96% (SD = 2) of targets that were presented in the walking condition. This near-perfect task performance observed across all participants suggest that the tones presented were consistently audible, despite the presence of external noise sources during the walking condition. Task performance was significantly higher for the standing condition than in the walking recording condition between recording condition [t(10) = 2.319, p < .05, d = .699, BF_{10} = 1.920]. Marginal correlations between P300 amplitude and task performance were observed between recording conditions [standing, r = .492, p = .124, two-tailed; walking, r = .595, p = .054, two-tailed].

3.3.3. Analysis of data quality

One of the main aims of this study was to shed light on the nature of the reduction in P300 ERP amplitude during walking and whether changes in the magnitude of this effect are a product of increased noise or decreased signal in the walking data (i.e., reflect methodological artifacts or an actual cognitive effect). For this purpose, different measures of noise were compared between recording conditions. First, variability in the prestimulus baseline data is examined. Then, the measures of baseline variance and signal strength characterised in previous ERP analyses will be used to compute signal-to-noise ratio (SNR).

3.3.3.1. Estimation of baseline residual noise

Pre-stimulus Root Mean Square (RMS)

There was no significant difference in prestimulus RMS (i.e., the arithmetic mean of the squares of a set of values) between standing (mean = 7.03, SD = 1.61) and walking recording conditions [mean = 7.22, SD = 1.82; t(10) = .453, p = .660, d= 0.137]. There was a significant (moderate) correlation of baseline RMS between both conditions [r_{10} = .652, p <.05, two-tailed], suggesting within-subject consistency in terms of residual noise across recording conditions (see Figure 3.6).

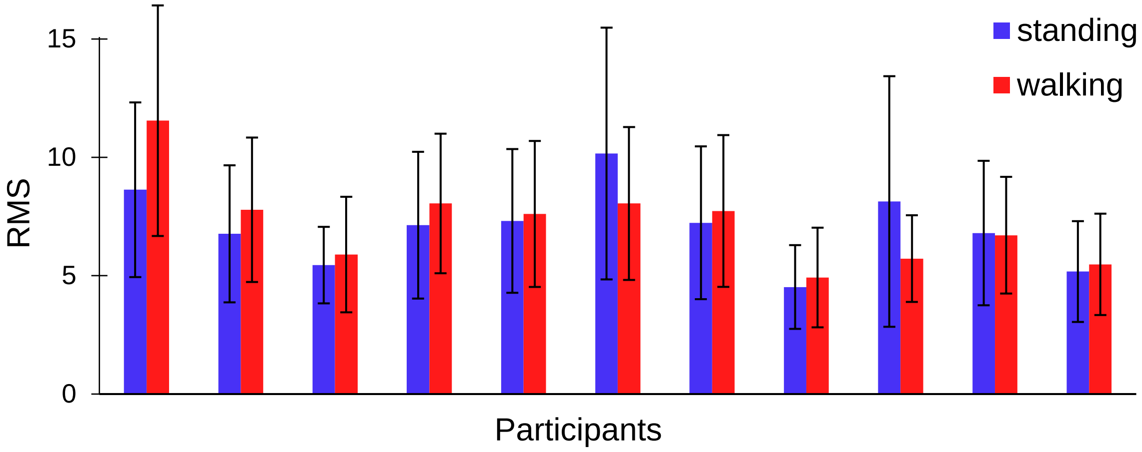

Figure 3.6. Root Mean Square (RMS) of the prestimulus baseline period activity [-200;0ms] recorded at Pz electrode across participants for both standing (blue) and walking (red) recording conditions.

Baseline standard deviation

There was no significant difference in prestimulus standard deviation between standing (mean = 1.40, SD = .51) and walking recording conditions [mean = 1.50, SD = .78; t(10) = .337, p = .743]. There was no significant correlation of baseline standard deviation between both conditions [r_{10} = -.004, .991].

3.3.3.2. Signal-to-noise ratio (SNR)

The signal-to-noise ratio (SNR) has been computed through slight variants of a quotient between a numerator reflecting signal strength and a denominator reflecting residual noise. Depending on the literature, different measures have been considered for both of these variables. The following paragraph reports and compares these measures across recording conditions. In each case, mean amplitudes from 256 to 448ms were analysed and used to calculate the SNR.

First, the SNR can be computed by dividing the P300 amplitude by the baseline RMS for each subject (Schimmel, 1967). Using this approach, a significant difference in SNR was found between standing (mean = 1.59, SD = .76) and walking [mean = .84, SD = .64; t(10) = 3.801, p < .01, d= 1.146] conditions. However, the SNR values did not correlate between conditions [r=.574, p =.065, two-tailed]. Second, the SNR can also be defined as the ratio of the peak amplitude for P300 and the averaged RMS (De Vos et al., 2014). A significant difference was present between standing (mean = 2.28, SD = 1.33) and walking (mean = 1.52, SD = 1.05) recording conditions [t(10) = 2.268, p < .05, d= 0.684]. Finally, SNR can also be computed by dividing the P300 amplitude by the baseline (-200 to 0ms) standard deviation for each subject (Debener, 2012). Using this method revealed no significant difference in SNR between standing (mean = 9.31, SD = 7.76) and walking [mean = 5.76, SD = 6.32; t(10) = 1.204, p = .256] recording conditions. There was no significant correlation between conditions [r_{10} = .045, p =.895, two-tailed].

3.3.3.3. Data rejection processing methods outcomes

Another important aspect aside of data quality aside from signal strength and residual noise variance is the proportion of data surviving the processing procedures. The number of single-trial epochs and Independent Components remaining after the application of artifact rejection methods provides information regarding the cost of such preprocessing of the data, and also whether the data have sufficient similarities in terms of trials and dimensionality to be validly compared across conditions.

Single-trials remaining after statistical epoch rejection methods

The total amount of trials remaining after rejection of time series epochs affected by noise was not significantly different across the recording conditions [F(1,10) = .626, p = .447, η^2= .059]. Moreover, there was no significant difference found between target trials remaining in the standing condition (mean = 34.181, SD = 5.58) and the walking condition [mean = 32.909, SD = 5.20; t(10) = .529, p = .608]. There was also no significant difference between frequent trials remaining in the standing condition (mean = 136.818, SD = 18.09) and the walking condition [mean = 132.363, SD = 22.05; t(10) = .729, p = .483].

Artifactual Independent Components manually selected

The number of artifactual Independent Components (ICs) manually rejected in the standing (mean = 2.545, SD = 2.20) and walking (mean = 3.4545, SD = 1.75) conditions was not statistically different [t(10) = 1.614, p = .138]. The selection of artifactual ICs for rejection was deliberately conservative in contrast to practice in BCI literature, where only few ICs related to the signal of interest are kept. The individual inspection of components sources estimates, power spectra and ERP-images features has raised suspicion about the presence of additional artifactual ICs for the walking condition. However, these components did not explain sufficient abnormal variance of the signal to justify their rejection. Indeed, while taking into consideration the trade-off in signal dimensionality implied by the rejection of a wider range of independent components, a conservative approach appears more suited. Moreover, artifactual ICs may include brain signals of interest to some extent (more details on this issue is discussed in the methodological section). Therefore, the diligent approach to the selection of artifactual ICs to reject employed within the frame of this thesis may explain the similarity in the number of ICs rejected across both recording conditions.

3.4. Discussion

Beyond providing further evidence confirming the feasibility of recording ERPs during natural behaviour, these results also highlight a significant difference in brain dynamics between laboratory and real-world settings. These results are consistent with previous research (De Vos & Debener, 2014; Debener et al., 2012) reporting an attenuation in P300 ERP amplitude during walking in a real-world environment. Moreover, the present findings partly address a pending question following these initial studies concerning the nature of the P300 attenuation. Both reallocation of cognitive resources and residual noise have been hypothesised as potential (non-exclusive) factors contributing to the observed differences in ERP waveforms. The latter explanation of reduced amplitude of ERP component due to increased noise was not ruled out because differences in signal-to-noise ratio between recording conditions were reported in their data.

In both of the aforementioned studies, signal-to-noise ratio (SNR) measures were used to assess and compare the proportion of noise across recording conditions. SNR measures are commonly used in methodologically focused studies aiming to assess the effectiveness of signal processing methods and within-subject recording reliability in relation to a specific paradigm. When used to contrast different approaches to handle artifacts in the data, the interpretation of the SNR as being purely an indicator of noise assumes that the numerator (signal strength) is consistent across conditions. This which is necessary for SNR comparisons to be informative, was not fulfilled in the present study, because the paradigm was contrasting environmental factors that could affect cognitive processes and therefore lead to changes in signal magnitude. Importantly, measures of residual noise were not found to be different between recording conditions, which refutes the interpretation of the attenuation solely on a reduction of signal-to-noise basis. Despite the fact that residual noise measures were found to be consistent across recording conditions, significant difference in signal-to-noise ratio was nevertheless found between conditions. Since the denominator (baseline noise) is consistent across conditions, this difference in SNR is directly related to difference in the numerator (P300 amplitude in this instance). The interpretation of SNR difference between conditions as a result of residual noise difference is therefore invalid within the frame of this study. Therefore, it can be argued that SNR is essentially flawed whenever differences induced by cognitive phenomena may arise between contrasted signals and that the interpretation of SNR data must be informed by careful consideration of both signal strength and residual noise measures individually.

Behaviourally, there was no significant difference in task performance between standing and walking recording conditions. This result is likely attributable to a ceiling effect in task performance related to the P300 elicitation task used. Indeed, the oddball paradigm aims to result in high accuracy discrimination of target stimuli through the presentation of unequivocal differences in the nature of the presented stimuli. Participants exhibited a near-to-perfect performance on the task in both conditions, confirming that target stimuli were correctly identified in both conditions. While task difficulty was not an independent variable in the present experiment, use of a more challenging task would be an interesting additional manipulation between the two conditions. Based on dual-task literature, cognitive performance declines as a function of the cognitive workload related to concurrent physical activity (Pashler & Johnston, 1998). Therefore, differences in task performance could have been observed between recording conditions in the context of a more sensitive paradigm or induced by a more cognitively challenging concurrent task. Despite this ceiling effect, there was a significant correlation between P300 amplitude and task performance. This relationship suggests that P300 amplitude not only indexes attentional resources deployed to the processing of relevant information for the ongoing task, but also that P300 amplitude can be used as a reliable predictor of task performance and an implicit measure of effective attentional processing.

Clearly, the observed reduction in the size of the P300 during walking cannot be accounted for by changes in the quality of recording (artifacts or loss of trials). The findings therefore raise the important question of what cognitive functions drive the reduction in the P300 effects.

One factor that could explain the difference in P300 amplitude is the increased power of slow brain rhythms related to walking activity. Indeed, it has been demonstrated that cyclic physical activities such as walking lead to oscillatory patterns of activity in the frequency range related to the cycle length (Gwin et al., 2011). It could be hypothesized that fluctuations of slow oscillatory patterns of brain activity related to walking would interfere with rhythmic activity contributing to the generation of P300 ERPs (delta, theta and low alpha range). It is plausible, even though unknown, that such fluctuation of activity across the theta band may have a significant impact on the recording of P300 ERPs. However, this assumption implies that brain activity related to gait cycles would be, at least partially, phase-locked to the onset of experimental events to consistently alter ERPs recorded. Unfortunately, gait dynamics were not measured within the frame of the present study, therefore such synchronization of strides to the rate of stimulus presentation could not be formally assessed. Regardless, the central aim of the present study was to compare ERPs from a classic auditory oddball paradigm in a lab-environment and in the real-world during walking. Clear and statistically robust differences in the amplitude of neural signatures related to attentional processing were found between recording conditions, highlighting an attenuation of cognitive resources deployed to task-relevant stimuli in the real-world walking condition. In the absence of difference in terms of residual noise between conditions, the reallocation of cognitive resources hypothesis underlying the observed difference appears more plausible. This result suggests that attentional processing in the real-world is different than in a laboratory environment. Moreover, this finding opens a new range of questions regarding the factors underlying the observed difference and which aspects of walking capture attentional resources. Despite the simplicity of its experimental design, the present study provides a foundation upon which following experiments can be based to further investigate aspects of real-world locomotion affecting cognitive processing. The following chapter will present a follow-up study that look into the contribution of the walking and motion factors potentially underlying the real-world walking effect using an incremental approach in the design of the experimental conditions.

Chapter 4: Factors modulating markers of attentional processing during real-world locomotion

4.1. Introduction

The previous study highlighted differences in neural signatures of attention recorded in the real-world compared to a lab-based environment. The lack of significant difference in terms of residual noise between the two conditions indicates that this difference was not a result of increased noise related to whole body movements. Moreover, this finding suggest that attentional resources may be reallocated towards cognitive aspects related to the experience of a real-world environment. Walking down a hallway and standing in an office differ in several ways, hence confounding variables have to be investigated to explore the underlying factors contributing to the observed effect.

The most obvious difference between the two conditions are the physicality of walking activity and the displacement through space necessarily involved during the traversal of corridors in the original walking condition. Both of these factors could induce a reallocation of cognitive resources that would explain the attenuation of attentional processing markers found in the walking condition. Therefore, a follow-up experiment explored the respective contribution of both walking and motion factors to the P300 ERP attenuation found in the previous study. For this purpose, a treadmill condition was introduced to allow walking without any physical displacement and a wheelchair condition where participants could traverse corridors but not be walking. These intermediate conditions were used to contrast the initial standing and walking conditions. If the diminished P300 response to an infrequent tone was due to the act of walking, it should be observed in the two walking conditions. In contrast, if the P300 effect was due to the additional sensory demands associated with movement through the hallway, then decreases should be observed in the two hallway conditions (walking, wheelchair) compared to the stationary conditions (sitting, treadmill).

4.1.1. Dual-tasking in the real-world

In real-life contexts, we are usually engaged in activities that require some degree of multitasking, essentially leading to a distribution of attentional resources between the primary task at hand and the processing of peripheral information (Kahneman, 1973). In order to reach our goals, we have to perform series of actions that will be readjusted based on the feedback acquired through interaction with the environment (Chiel & Beer, 1997). Conversely, the perception and understanding of our surrounding space shapes and transforms our intentions (Barsalou, 2008b). This recursive cycle plays an essential role in our experience and interaction with the surrounding world as embodied agents (Clark, 1999). On this basis, therefore, it can be argued that capturing brain dynamics during artificially isolated cognitive and motor processes may not reflect the real dynamics at work during real-world experiences. The interplay between sensory, motor and cognitive processes has to be accounted for in order to gain a better understanding of real-world human cognition.

According to the cognitive-motor dual task literature, the amount of cognitive resources allocated to a primary task will be largely affected by the demands related to concurrent motor tasks (Al-Yahya et al., 2011; Schaefer, 2014; Woollacott & Shumway-Cook, 2002). Since our cognitive resources are limited, we have to split them efficiently between the competing tasks at hand (Wickens, 1980). The P300 ERP component has shown to be sensitive to the division of cognitive resources within the frame of dual tasks paradigms (Isreal, Chesney, Wickens & Donchin, 1980; Polich, 1987). Indeed, the amplitude of P300 neural responses to attended stimuli of a primary task is largely affected by the amount of cognitive, and more specifically attentional resources, drawn away by the execution of a concurrent task (Wickens, Kramer, Vanasse & Donchin, 1983; Kramer & Strayer, 1988). Within this reciprocity framework, P300 sensitivity to the cognitive interference induced by a secondary task makes it a useful EEG marker to assess processing capacity (Polich & Kok, 1995). Moreover, P300 amplitude can be used to investigate the cognitive interdependence between simultaneous motor-cognitive tasks.

4.1.2. Motor-cognitive interferences during walking

Walking across the hallways could be considered to be a trivial and rather straightforward behaviour. Nonetheless, walking requires the concurrent integration of multimodal information and planning of motor sequences. Gait is dynamically controlled based on an incoming flow of information from vestibular, visual, auditory and proprioceptive systems (Assländer & Peterka, 2014; Rossignol, 2006). Walking is a pervasive behaviour that is often performed simultaneously with other activities such as navigating, conversing, listening to music, reading and sometimes all at once. Biomechanical aspects of bipedal walking have been extensively documented in healthy, ageing and neurologically impaired populations

(Beyaert, Vasa & Frykberg, 2015; Del Din, Godfrey, Galna, Lord & Rochester, 2016; Hausdorff, Yogev, Springer, Simon & Giladi, 2005). Under challenging multitasking circumstances (e.g., navigating while reading a map, or texting while walking), changes in gait dynamics can be observed in healthy subjects (Agostini, Lo Fermo, Massazza & Knaflitz, 2015; Schabrun, Den Hoorn, Moorcroft, Greenland & Hodges, 2014). Prior studies have shown differences across the lifespan in both neural and gait-postural dynamics during the performance of secondary tasks while walking, with the older adults presenting less flexibility in the allocation of cognitive resources to adapt to the demands of walking (Beurskens, Helmich, Rein & Bock, 2014; De Sanctis, Butler, Malcolm & Foxe, 2014; Malcolm, Foxe, Butler & De Sanctis, 2015).

The interference of walking on memory has been demonstrated in aging populations, where increases in walking speed and path complexity lead to slower and poorer recall (Lindenberger, Marsiske & Baltes, 2000). Moreover, Patel, Lamar & Bhatt (2014) have reported relationships between cognitive performance and walking pace. Under natural walking speed, an increase in cognitive-motor interference was reflected both by slower and poorer performance in cognitive tasks, and higher walking pace variability. Furthermore, by constraining the participants to walk at a slower pace than their preferred speed, the motor cost of walking activity was increased, exacerbating cognitive-motor interference. McCulloch, Buxton, Hackney & Lowers (2010) have reported a general trend of motor slowing in patients with acquired brain injuries as an adaptive strategy to optimize cognitive performance within the frame of cognitive-motor multitasking, effectively compensating for lower levels of attentional resource. Moreover, the cognitive-motor interference induced by walking has been shown to increase the sensitivity of neuropsychological assessment tools, allowing early diagnosis of the onset of cognitive decline and cognitive fragilities (Perrochon, Kemoun, Watelain & Berthoz, 2013).

Simoni et al. (2013) have shown that gait dynamics and cognitive performance (verbal working memory task) are more sensitive to cognitive-motor interference when subjects walk on a sensorized mat, in contrast to walking on a treadmill. This finding suggests that natural walking introduces a greater cognitive load than treadmill walking, however it remains unclear which aspects of natural walking underlie this difference in cognitive performance. In a recent study, Pizzamiglio, Naeem, Abdalla & Turner (2017) have shown that both gait performance and EEG dynamics were affected during walking whilst conversing and texting (in comparison to natural walking). Simultaneously walking and holding a conversation reduced gait performance and led to increases in theta and beta power at left-frontal and right-parietal electrode sites. Walking in a real-world environment while texting also reduced gait performance, and was associated with decrease of beta power over electrodes located at frontal-premotor and sensorimotor sites. These findings have been further supported by studies using fNIRS during upright walking that reported brain vascular dynamics associated with dual-tasking during locomotion (Holtzer et al., 2011, 2015; Maidan, Bernad-Elazari, Giladi, Hausdorff & Mirelman, 2017; Mirelman et al., 2014).

Taken together, these results highlight the interplay between brain and body dynamics during natural behaviour such as walking. Moreover, these studies demonstrate the relevance of dual-task paradigms for investigating cognitive-motor interference during natural behaviours in the real-world environment. The simultaneous recording of behavioural signatures and neural biomarkers offers a way to assess the impact of experimental manipulations on cognitive and behavioural functioning, in particular the distribution of cognitive resources that occurs when participants are under increased demands but have limited cognitive capacities.

4.1.3. Hypotheses

In the previous study, a significant attenuation of the neural signature of attentional processing was found when subjects were walking in contrast to standing still. Beyond the differences in terms of recording environment, the two conditions differ in many other ways: walking activity in itself, the implied motion related to displacement through the environment and the dual-task nature of the walking condition. These confounding variables make the interpretation of factors underlying the reallocation of attentional resources during real-world navigation unclear.

Is the P300 amplitude reduction found in the original walking condition explained by a reallocation of cognitive resources towards the completion of the concurrent motor task? Or, alternatively, was attention grasped by the dynamic flow of information brought by moving through the environment? To address these questions, the present study investigates which of these factors are driving the shift of attentional resources observed during walking in the real-world. For this purpose, the contribution of motion and walking activity on P300 ERP amplitude will be assessed in isolation. These measures will provide insights about embodied aspects of everyday life multitasking behaviours and their respective effects on cognitive resources distribution.

4.2. Methods

4.2.1. Participants

Twenty-four neurologically healthy participants (18 female, age range = 19-48, mean = 23) took part in this experiment. This sample of participants consisted in students at the University of Stirling where the experiment took place. The participants did not report any of the exclusion criteria commonly listed for EEG research on healthy population (listed in section 3.2.1), nor any physical impairment that could affect their ability to walk. Written informed consent was obtained from all participants. Fixing issues related to movement of wires in the EEG caps, described in Chapter 3, resulted in a better retention rate of datasets. One dataset had to be discarded due to missing events timestamps related to cable disconnections during data collection. An additional participant has been recruited to complete the experimental design and ensure proper counterbalancing.

4.2.2. Experimental design

This experiment aimed to isolate the factors underlying the attenuation of P300 during walking. For this purpose, two independent variables were manipulated: act of walking (in terms of pure physical activity) and motion (in the sense of displacement through space). The initial standing and walking conditions were contrasted with treadmill (walking but no motion) and wheelchair (motion but no walking) conditions. The use of these intermediate conditions allowed a 2x2 within-subject factorial design (see Figure 4.1). Order of conditions was counterbalanced across participants.

4.2.3. Material

For the wheelchair condition, participants were pushed along the corridors of the Psychology department. The wheelchair was adjusted accordingly to the height of the participants in order to ensure their comfort and safety during the experiment. Doors were pre-emptively fixed open along a predefined track to avoid interruptions during the course of the experiment.

The treadmill condition consisted of a 5 to 6 minutes’ walk on an electric treadmill (T900, Horizon Fitness Inc., USA) in a laboratory environment. Prior to data collection on the treadmill, the participants were put through a familiarization procedure in order to define their most natural and comfortable walking pace. The treadmill was positioned facing a blank white wall to prevent any visual distraction for the participants. Both walking and wheelchair conditions took place in a real-world recording environment that included considerable amount of auditory and visual noise and involved a moderate rate of human encounters. Tone volume was tuned prior to the experiment to ensure audibility and facilitate distinction between target and non-target stimuli.

An accelerometer was used to define the participants' natural walking speed prior to the experiment while freely walking in the real-world for 5 minutes. The treadmill pace during the treadmill habituation procedure was set based accordingly to this initial measure of natural pace. Based on participants' feedback, treadmill pace was adjusted to ensure a comfortable walking experience on the treadmill. The experimenter also referred to the participant's natural walking speed measure to adjust his walking speed while wheeling the participants through the corridors in order to keep a consistent pace across conditions.

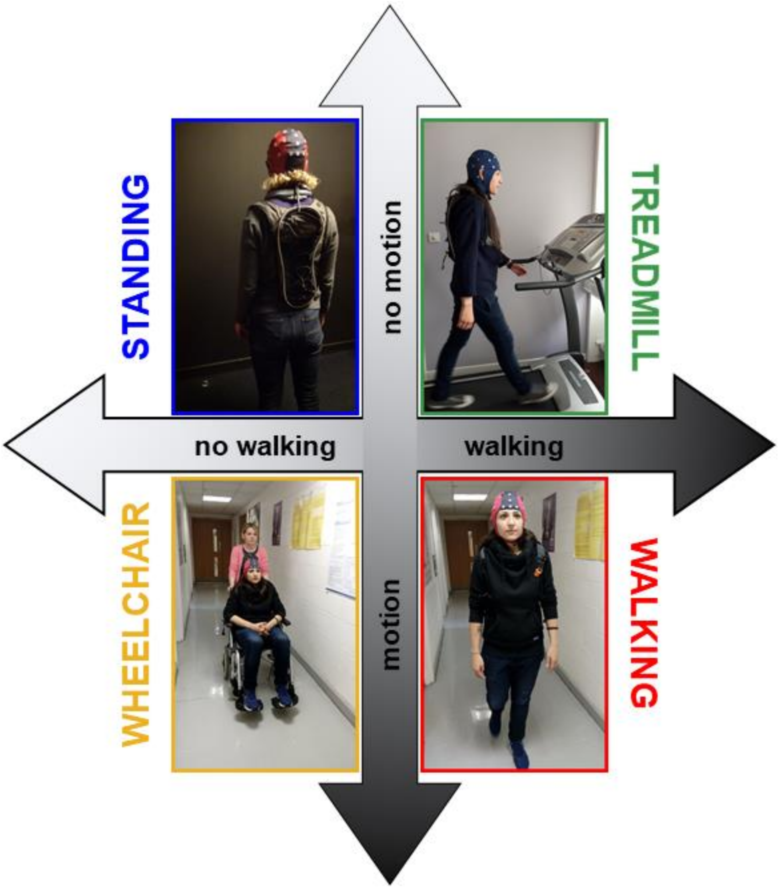

Figure 4.1. Illustration of the 2x2 experimental design used to investigate the effects of motion and walking activity on markers of attentional processing (P300 ERP). The standing condition (blue frame) did not involve either motion or walking activity to be performed and contrast with the walking condition (red frame) involving both motion and the physical of walking. The manipulation of the two independent variables resulted in the following intermediate conditions: the treadmill condition (green frame) where participants walked at a natural pace but did not actually move through the environment and the wheelchair condition (yellow frame) during which participants effectively traversed the environment without having to perform the physical act of walking themselves.

4.2.4. Data analysis

ERPs were analysed using a 2x2 repeated measures analysis of variance (ANOVA) comprising the factors of walking (absent, present) and motion (absent, present) and their interaction. Significant effects were followed by paired samples t-tests. The P300 time window was defined as two standard deviations around the mean peak latency of single-trial P300 ERP across all conditions (mean peak latency = 358, SD = 40). The mean amplitudes were therefore measured using a time window from 276 to 440ms for P300 ERPs analysis, and to calculate the signal-to-noise ratio dividing the ERP amplitude by the standard deviation in the prestimulus interval. ERP analysis reported here are limited to electrode Pz, where the oddball-P300 is most prominent. Bonferroni corrections for multiple comparisons were applied.

4.3. Results

4.3.1. Event-Related Potentials

4.3.1.1. P300 ERP amplitude

A main effect of the motion [F(1,23) = 16.717, p <.001, η^2 = .421] revealed differences between conditions involving displacement through space (walking and wheelchair) and stationary conditions (standing and treadmill). Moreover a significant interaction between walking and motion was found [F(1, 23) = 6.934, p < .05, η^2 = .219], but there was no significant effect of walking [F(1,23) = 2.329, p = .141, η^2 = .092].

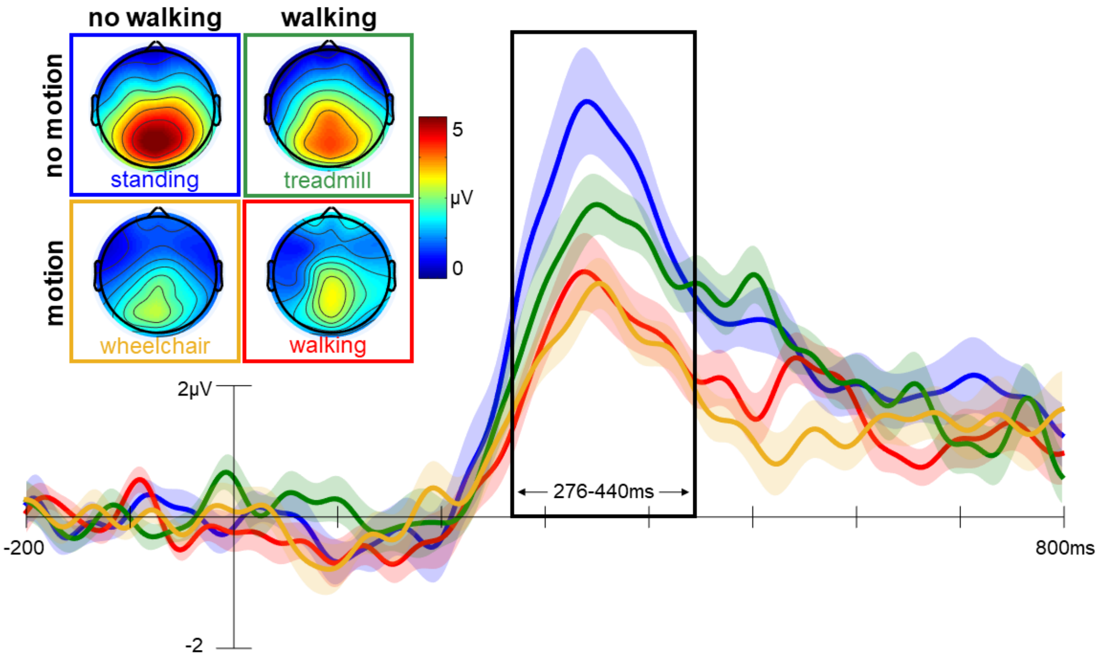

Figure 4.2. Mean Event-Related Potential waveforms (difference between frequent and infrequent tones) at the Pz electrode site during standing (blue trace), walking on a treadmill (green trace), walking down a hallway (red trace), and being wheeled down a hallway (orange trace). Scalp maps representing the topographical distribution of evoked activity within the P300 time window (276-440ms) across corresponding recording conditions.

Similarly to the first study, the P300 ERP amplitude recorded during the standing still condition (mean = 5.84, SD =3.08) was significantly larger compared with the walking condition (mean = 3.35, SD = 2.32; t(23) = 3.464, $p < .01$, d= 0.707). The treadmill condition showed larger P300 ERP amplitude (mean = 4.51, SD = 1.86) than both the wheelchair (mean = 3.14, SD = 1.36; t(23) = 3.289, $p < .01$, d= 0.671), and the walking condition [t(23) = 2.904, $p < .01$, d= 0.593]. While larger P300 amplitudes were found in the standing condition in comparison to the treadmill condition [t(23) = 2.766, $p < .05$, d = 0.565], no difference was found between the wheelchair and walking conditions [t(23) = .440, p = .664] (see Figure 4.2).

4.3.1.2. P300 ERP latency

Analysis of P300 peak latency revealed a significant interaction between walking and motion [F(1,23) = 5.650, $p < .05$, $\eta^2 = .197$], however, follow-up paired-sample t-tests did not reveal reliable differences between any condition. The walking condition (mean = 346, SD = 46) presented relatively earlier peaks than the wheelchair condition (mean = 368, SD = 41; t(23) = 2.048, p = .052, d = 0.418).

4.3.2. Behavioural data

The participants reported 98% of targets stimuli (SD = 1) in the standing condition, 95% of targets (SD = 3) in the walking condition, 97% (SD = 2) in the treadmill condition, and 95% (SD = 2) in the wheelchair condition (see Figure 4.3). Analysis revealed a significant main effect of motion on task performance [F(1, 23) = 32.547, $p < .001$, $\eta^2 = .586$]. Task performance during standing was significantly higher than during both wheelchair [t(23) = 4.664, $p < .001$, d = 0.952, BF_{10} = 253.772] and walking [t(23) = 4.449, $p < .001$, d = 0.908, BF_{10} = 157.125] conditions. There was, however, no significant difference in task performance between standing and treadmill conditions [t(23) = 1.802, p = .085]. Furthermore, task performance in the treadmill condition was significantly higher than in both the walking [t(23) = 2.511, $p < .05$, d = 0.513, BF_{10} = 2.780] and wheelchair [t(23) = 2.136, $p < .05$, d = 0.436, BF_{10} = 1.451] conditions. By contrast, there was no significant difference in performance between walking and wheelchair conditions [t(23) = .394, p = .697].

P300 amplitude and task performance was significantly correlated in both the wheelchair (r_{23} = .468, $p<.05$) and walking (r_{23} = .417, $p<.05$) conditions. The weak correlations between task performance and P300 amplitude found in both the standing (r_{23} = .298, p = .157) and treadmill (r_{23} = .367, p=.078) conditions most likely reflects a ceiling effect inherent to the nature of the task.

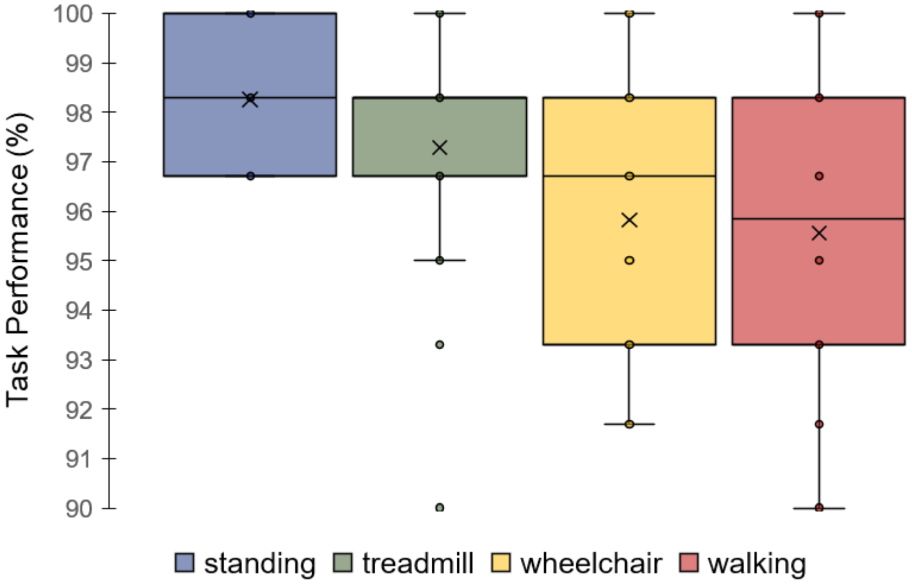

Figure 4.3. Boxplot representing task performance across recording conditions (standing in blue, treadmill in green, wheelchair in yellow, walking in red). Performance during the walking and wheelchair conditions was significantly lower than in the standing and treadmill conditions, however, no difference was found between wheelchair and walking conditions. These behavioural results suggest that performance is influenced by the demands associated with movement through space, rather than the act of walking.

4.3.3. Analysis of data quality

4.3.3.1. Root Mean Square (RMS)

There was a significant main effect of walking on the RMS in the prestimulus period [F(1,23) = 4.614, p < .05, η^2 = .167]. However, following paired-samples t-test did not reveal any significant difference in prestimulus RMS between recording conditions at the exception of walking (mean = 5.39, SD =1.04) and wheelchair conditions (mean = 5.92, SD = .71; t(23) = 2.077, p < .05). Single subject RMS was not significantly correlated across recording conditions.

4.3.3.2. Baseline standard deviation

Analyses of baseline standard deviation revealed no significant main effect of walking [F(1,23) = .033, p =.858, η2 = .001] nor motion [F(1,23)= .086, p =.772, η^2 = .004] on prestimulus variance. Paired samples t-test differences did not reveal any significant difference in terms of baseline standard deviation between conditions.

4.3.3.3. Remaining trials

Analysis of trial numbers revealed no significant main effects of walking [F(1,23) = .1.056, p = .315, η^2 = .044] or motion [F(1,23) = .093, p = .763, η^2 = .004] on the total number of trials remaining after processing. In addition, there was no significant effect of walking on the amount of frequent non-target trials remaining after processing [F(1,23) = 1.175, p = .290] and on the amount of infrequent target trials remaining [F(1,23) = .519, p = .478]. Similarly, there was no significant effect of motion on the amount of frequent bob-target trials remaining after processing [F(1,23) = .064, p = .803] nor on the amount of infrequent target trials remaining [F(1,23) = .200, p = .659].

4.3.3.4. Independent Components rejected

There was on average 6 (SD = 3) ICs rejected across all conditions. There was a significant effect of walking on the number of Independent Components (ICs) rejected, F(1,23) = 6.209, p < .05, η^2 = .213. However, there was no significant difference when comparing the number of ICs rejected between conditions.

4.4. Discussion

The present results suggest that movement through a hallway automatically captures attention, and thereby yields a diminished allocation of attention (as indexed by the P300 ERP effect). Both walking and wheelchair conditions led to a similar reduction in the neural correlate of attention. Consistent with the ERP results, walking activity did not reduce cognitive performance, rather motion led to a significant decrease in task performance. Data quality was consistent across recording condition, with slightly more prestimulus noise in the walking condition than the wheelchair condition, which does not explain the pattern of ERP results observed. The following paragraphs discuss the results in detail.

4.4.1. Cognitive demands related to walking activity does not reduce P300

As discussed previously, the complexity of the secondary task is a major factor driving the reallocation of cognitive resources under dual-task circumstances. For healthy subjects, walking represents a fairly implicit and automatic motor task that requires very little attention. Since our participants were not suffering from any gait disorder, or any neurological impairment that would hinder their mobility, it can be argued that the act of walking on the treadmill represented a very unchallenging motor task. The present findings, both support this prediction by showing that walking *per se* did not substantially reduce cognitive resources allocated to the primary task. The cognitive cost of natural walking activity in healthy, relatively young subjects can therefore be considered low under real-world circumstances. It is important to note, however, that in the present study, both the walking and the treadmill conditions consisted in walking at a natural pace on a plane surface. Therefore, it can be hypothesized that under more challenging circumstances, mobility may require a greater proportion of cognitive resources, which would translate into a significant reduction of P300 amplitude.

The dual-task literature has shown that manipulating walking speed, the presence of obstacles, or uneven terrains, will yield an impact on the performance of concurrent cognitive tasks, even in healthy subjects (Al-Yahya et al., 2011). These findings have received further support from brain imaging findings (EEG, fNIRS, PET) that report modulations of cortical areas indexing such interference between cognitive abilities and gait performance (Hamacher, Herold, Wiegel, Hamacher, & Schega, 2015). Furthermore, motor-cognitive dual task interference effects have also been found to be a major issue in the elderly and populations suffering from motor impairments, translating into poorer cognitive and behavioural performance (Amboni, Barone & Hausdorff, 2013; Holtzer et al., 2007; Holtzer, Epstein, Mahoney, Izzetoglu & Blumen, 2014). Applied to populations at risk, either due to cognitive impairments, decline in physical abilities, or a combination of both (e.g., Alzheimer’s, Parkinson’s diseases), the study of motor-cognitive interference may have important clinical implications. Diminution in cognitive performance, specifically in terms of executive functions, has been linked with higher risks of falls (T. Y. Chen, Peronto, & Edwards, 2012; Mirelman et al., 2012; Yogev-Seligmann, Hausdorff, & Giladi, 2008). Moreover, gait dynamics (e.g., cadence, stride length) have been found to be affected by cognitive load, with higher sensitivity in patients with motor impairments (McCulloch, 2007) and in the elderly (Rosano et al., 2008).

As a biomarker of attention, P300 effects may be a viable way to monitor and predict behavioural failures in clinical populations, suboptimal motor performance in the context of sport, or the effect of ergonomic design on cognitive processing related to motor planning and execution of complex series of movements. Each of these scenarios potentially involve assessment of cognitive errors that are likely to be substantially conditions involving walking (Schaefer, 2014).

The present results contrast with previous findings from De Sanctis et al. (2014) that highlighted difference in P300 ERP amplitude during a visual Go/NoGo task between sitting and treadmill walking conditions. The Go-Nogo data suggest an increase in cognitive load related to walking. It is important, however, to note that the paradigm employed in De Sanctis et al. (2014) study elicited P300 ERP reflecting inhibition control. Moreover, inhibitory tasks are, by nature, more challenging than attentional processing tasks as reflected by behavioural performances, with relatively high rates of false positive errors in Go/NoGo tasks compared to those reported during oddball tasks. This increased cognitive load during Go-Nogo tasks may therefore increase the sensitivity of this paradigm to motor-interference. Moreover, De Sanctis et al. used stimuli presented in the visual modality, which may change the nature of the cognitive-motor interference. Visual information is a crucial source of feedback for successful human locomotion (Chapman & Hollands, 2006; Jovancevic-Misic & Hayhoe, 2009). Therefore, the cognitive task and walking activity shared sensory and attentional processing in the visual modality, which might explain why the authors reported an increased interference effect. Finally, the authors casted doubt on the interpretation of P300 attenuation due to cognitive demands of walking. Indeed, they highlighted that increasing walking speed did not reduce P300 amplitude, and that no attenuation of the P300 effect was found when reductions in behavioural task performance were observed.

4.4.2. Displacement through a real-world environment reduces P300 amplitude

While the cognitive demands of walking did not substantially draw attention away from the primary task, the displacement through the environment significantly reduced P300 amplitude. Indeed, the wheelchair condition presented similar attenuation of P300 amplitude as the walking condition, in comparison to the standing still condition.

Scanlon, Sieben, Holyk, & Mathewson (2017) have reported no difference in P300 amplitude between cycling on a stationary bike and sitting. This is in line with the similarity of ERP waveforms observed between treadmill walking and standing still conditions, suggesting that physical activity in itself does not lead to a reallocation of cognitive resources towards motor task demands. Moreover, Zink, Hunyadi, Huffel & Vos (2016) have contrasted P300 waveforms recorded while peddling on a fixed bike, versus cycling freely in a real-world environment. They observed a significant decrease in P300 amplitude during the free outdoor cycling condition, suggesting that the complex nature of a natural environment is more taxing in terms of cognitive resources. This is in line with our finding of attenuated P300 amplitude during motion in the real-world. Furthermore, this finding provide evidence to update the interpretation of increased cognitive load related to natural walking (in contrast to treadmill walking) reported by Simoni et al. (2013); suggesting that increased processing demands related to the displacement in the environment rather than to increased motor control.

These findings open a new range of questions regarding which aspects of motion are responsible for the reallocation of attentional resources during displacement in a natural environment.

Chapter 5: Effects of visual and motion input on attentional processing

5.1. Introduction

The previous chapter identified the significant role that motion plays in capturing attentional resources during a motor-cognitive dual-task that involves the discrimination of target stimuli during real-world navigation. In contrast, walking related physical activity only had a limited effect on the modulation of the neural marker of attentional processing. The current study aims to further investigate the contribution of different aspects of motion that underlie the capture of attentional resources during real-world navigation. Two incidental factors related to motion have been hypothesised. A first explanation is the reallocation of attentional resources towards the processing of the visual flow of information encountered as a result of displacement through the environment. Alternatively, attentional resources could be drawn away from the primary task to process the increased amount of inertial information coming from the vestibular system (Ehinger et al., 2014). Indeed, the integration of multisensory information through a vestibular system (frontoparietal and hippocampal network) has been highlighted in animal studies showing specific patterns of brain activity under active spatial navigation as compared to static conditions (Andersen, 1997; Berthoz, 1997; Chen, 2013; Hamacher et al., 2015). The following study will therefore manipulate visual flow and vestibular information as independent variables, investigating their respective contribution to the P300 amplitude attenuation found during motion in a real-world environment. This incremental progression in the investigation of factors underlying the attenuation of neural markers logically leads to the investigation of cross-modality interplay during real-world navigation. The next section will review theoretical models of sensory and cognitive processing in the face of multimodal information.

5.1.1. Cross modality interactions in attentional processing resources

In daily life situations, information relevant to an ongoing task is often found in the middle of a lot more irrelevant information. In both previous chapters (Chapters 3 & 4), target stimuli were discrete auditory events that occurred sporadically amongst a continuous flow of information, in various modalities, that were not useful for the completion of the task. In order to successfully complete the task at hand, the limited amount of attentional resources available had therefore to be focused on the auditory processing of target stimuli.

The attentional capacity theory posits that information presented in any modality will be processed accordingly to the sensory resources available in that specific modality. For example, Rees, Frith, & Lavie (2001) presented non-task-related visual motion information during an auditory attentional processing task. Through manipulation of auditory stimuli discriminability (low, high), they investigated neural processing of visual distracting information under different selective attentional processing loads. Similar activation was found in visual areas sensitive to motion across both conditions, while auditory stimulus discriminability significantly impacted the magnitude of both neural responses and task performance. The authors suggested that attentional capacity is restricted within, but not between, sensory modalities. However, it can be argued that the independent modulations of visual and auditory neural responses observed by Rees et al. (2001) study may actually reflect selective sensory processing of task-relevant information, rather than the segregation of attentional resources. According to this theoretical model, increase of visual and vestibular information unrelated to the primary task should not reduce P300 effect related to the processing of task-related auditory stimuli because each modality has its own pool of attentional resources.

Deriving from the attentional capacity theoretical framework, the attention load theoretical account proposes that irrelevant information will be either suppressed at early sensory stages, or through inhibition at later processing stages, depending on the nature of the task (Lavie, 2005). If emphasis is put on perceptual processing (e.g., discrimination between easily distinguishable stimuli) then the irrelevant information will be discarded at sensory processing stages, before being subject to attentional processing. This sensory filtering is typically reflected by early frontal effects such as the N100 ERP component. However, if the stimuli are more difficult to distinguish, selection of relevant information may require additional cognitive processing and therefore irrelevant information will be filtered out through inhibitory cognitive control at later stages. According to this account, the introduction of irrelevant information will either modulate ERP components indexing early sensory or late attentional processing depending on the interference of the distracting information with the discrimination of target stimuli. Considering the high degree of distinctiveness of auditory target stimuli related to the nature of the task, it is therefore expected that irrelevant information would mainly interfere at early sensory processing stages and not at later cognitive processing stages.

5.1.2. Hypotheses

Based on the aforementioned premises, it is hypothesized that the interference of irrelevant information in visual or vestibular modality may only induce changes in early ERP components reflecting increased sensory filtering through early inhibition processes, but not in post-sensory processing EEG markers such as the parietal P300 ERP effect reported in the previous chapter. According to previous models, attentional resources are segregated between modalities. This account of modality-specific pools of attentional resources implies that cross-modality interferences should not impact attentional processing of relevant information post initial sensory filtering stages. In contrast, if the introduction of irrelevant information results in the reduction of attentional processing resources as indexed by the P300 amplitude, this would suggest that the concurrent information has a specific impact on attentional resources available for the processing of target stimuli and refutes the assumption of a modality specific segregation of attentional resources. Therefore, differences in ERP waveforms between conditions involving cross-modal interferences will shed light on the nature and effects of such interactions on sensory and attentional processing of auditory stimuli.

5.2. Methods

5.2.1. Participants

Twenty-four healthy participants (n = 24; 16 female; ages: 18-40, mean= 22.58) took part in this experiment. This sample of participants consisted of students at the University of Stirling where the experiment took place. The subjects did not report any of the exclusion criteria (listed in section 3.2.1). Written informed consent was obtained from all participants. One dataset had to be discarded due to missing events timestamps related to cable disconnections during data collection.

5.2.2. Experimental design

The aim of this study was to isolate the contribution of visual flow and inertial information to the P300 reduction observed during motion. To distinguish between these possibilities, a third group of participants was tested on the auditory oddball paradigm as they: 1) sat facing a grey wall, 2) sat and watched a virtual traversal of the hallway, 3) were wheeled down the hallway with vision obscured, and 4) were wheeled down the hallway with vision unobscured. This 2x2 within subject factorial design allowed the manipulation of visual information and inertial information as independent variables (see Figure 5.1). If visual flow diminishes the P300 oddball responses, then reduced P300 effects would be anticipated in the vision conditions (static virtual traversal; wheelchair + vision), but not in the conditions where visual flow is limited (facing the wall; wheelchair + obstructed vision). In contrast, if inertial senses are sufficient to capture attention, then a decreased P300 response would occur in both wheelchair conditions, but not in the stationary sitting conditions.

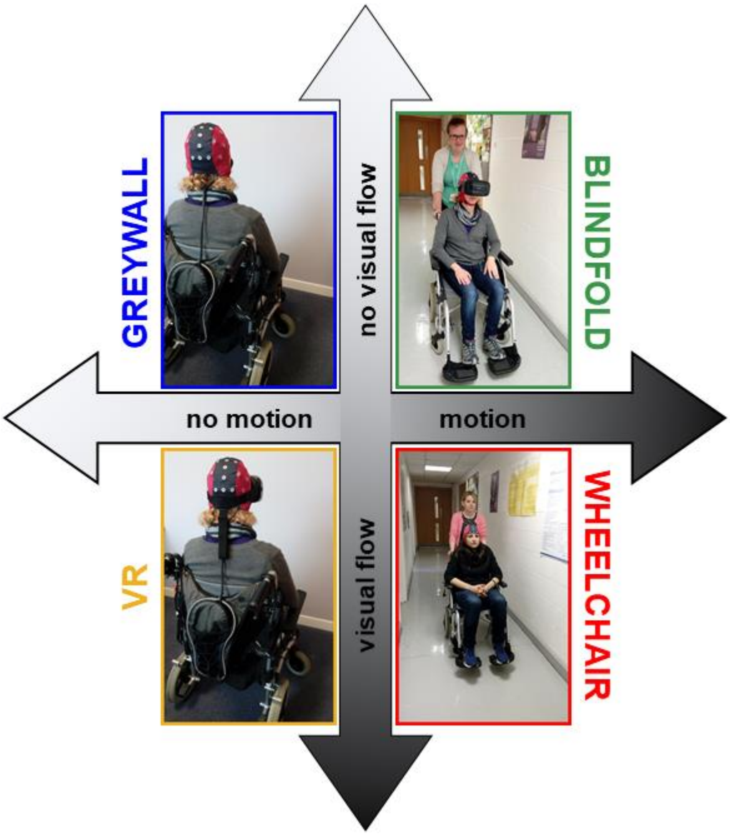

Figure 5.1. Illustration of the 2x2 experimental design used to investigate the effects of motion and visual flow on attentional processing. In the greywall condition (blue frame), participants were presented with a static visual scene while sitting still. In contrast, the wheelchair condition (red frame) involves both movement through the environment and continuous visual input. The manipulation of the two independent variables resulted in the following intermediate conditions: the blindfold condition (green frame) where participants are experiencing motion while the visual input is maintained low, and a VR condition (yellow frame) during which participants remained immobile while a first-person footage of someone being wheeled down the corridors, essentially replicating the "dynamic" visual experience of the wheelchair condition, was presented.

5.2.3. Material

Presentation of pre-recorded visual stimuli was achieved through the use of Virtual Reality goggles that were fitted to the participant head (carefully avoiding interaction with electrode sites). The visual obstruction used in the blindfolded condition consisted of the presentation of a static grey image for the entire duration of the block, using the same Virtual Reality goggles. The choice of a grey neutral background was motivated by a desire for consistency across conditions, as the wall used in the control condition was grey. Moreover, use of a black static image was avoided in the blindfold condition, because this could potentially trigger alpha locking at occipital recording sites, as is commonly observed when subjects have their eyes closed. The traversal speed in both conditions involving motion was matched to a normal natural pace that corresponded to the walking speed during the recording of the video used for the static virtual traversal condition (4.5km/h). The experimenter was equipped with a watch including online acceleration measures to maintain a consistent pace across conditions and participants.

5.2.4. Data Analysis

The ERP analyses described in previous chapters were applied to the data (see sections 3.2.6 and 4.2.4). ERPs were analysed using a 2x2 repeated measures analysis of variance (ANOVA) comprising the factors of visual flow (absent, present) and motion (absent, present). Significant effects were followed by paired samples t-tests. The P300 time window was defined as two standard deviations around the mean peak latency across all conditions (mean peak latency = 363.00, standard deviation = 41.40, 280.18 – 445.81, rounded to 280-446). The signal-to-noise ratio was computed by dividing the ERP amplitude by the standard deviation in the prestimulus interval. ERP analysis reported here are limited to electrode Pz, where the oddball-P300 is most prominent.

5.3. Results

5.3.1. Event-Related Potentials

5.3.1.1. P300 ERP amplitude

Analysis of the data using ANOVA with factors of visual flow and vestibular input revealed that both visual flow [$F(1,23) = 36.293$, $p < .001$, $\eta^2 = .612$], and inertial senses [$F(1,23) = 23.387$, $p < .001$, $\eta^2 = .504$] contribute to a diminished P300 response. No main interaction effect was found between these factors [$F(1,23) = 0.000$, $p = .998$, $\eta^2 = .000$]. The highest responses to the oddball stimuli were observed when participant sat facing a wall in comparison to sitting, watching virtual traversal [$t(23) = 4.901$, $p < .001$, $d = 1.000$], being wheeled without vision [$t(23) = 3.255$, $p < .01$, $d = 0.664$] and being wheeled down the corridors with vision unobstructed [$t(23) = 7.105$, $p < .001$, $d = 1.450$] (see Figure 5.2). The second largest P300 amplitude was observed when participants were wheeled down the hallway without access to visual flow, which showed significantly larger P300 amplitude than both conditions involving visual flow; wheelchair with unrestricted vision [$t(23) =$

5.833, p < .001, d = 1.191] and sitting, watching virtual traversal [t(23) = 2.265, p < .05, d = 0.462].

The largest decrease in P300 responses to oddballs was found when participants were wheeled down the hallway with unrestricted vision, where the responses were smaller than those associated with stationary sitting and observing a virtual hallway traversal [t(23) = 5.098, p < .001, d = 1.041]. Moreover, the independent effects of vestibular input and visual flow on P300 ERP amplitude were found to be additive (see Figure 5.3).

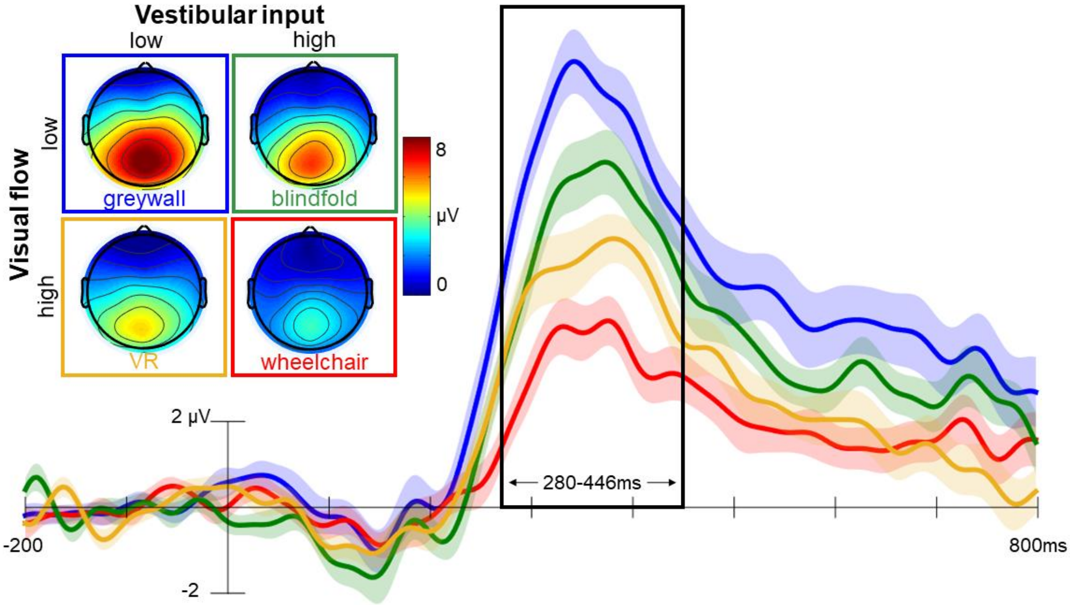

Figure 5.2. Mean Event-Related Potential waveforms (difference between frequent and infrequent tones) at the Pz electrode site while sitting in front of a grey wall (blue trace), being wheeled down the hallway with vision obscured (green trace), sitting and watching a virtual traversal of the hallway (yellow trace), and being wheeled down the hallway with vision unobscured (red trace). Inset: scalp maps representing the topographical distribution of evoked activity within the P300 time window (280-446ms) in each of the four conditions.

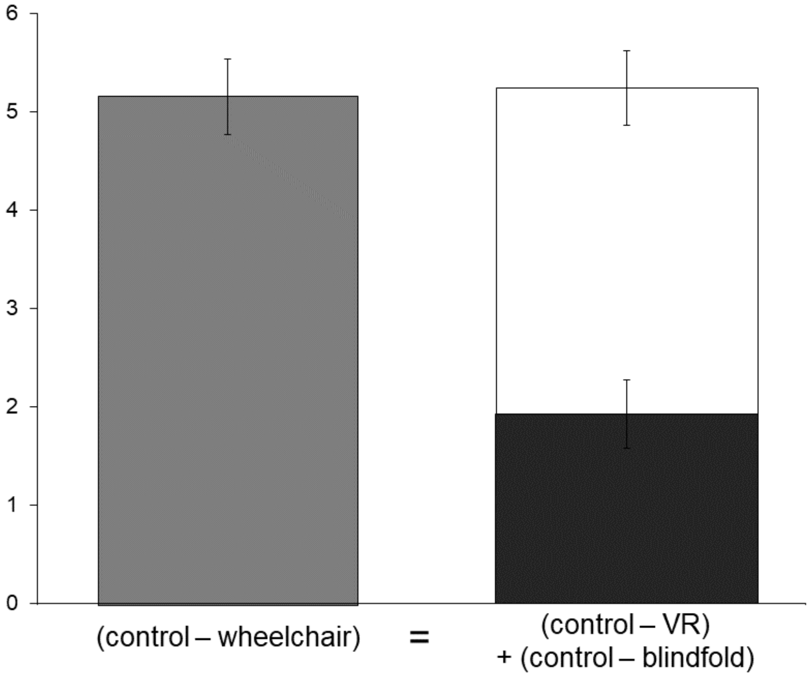

Figure 5.3. Assessment of independent factors contributing to P300 ERP attenuation. A squared factorial design was used to isolate and assess the contribution of visual flow and vestibular input as factors underlying reallocation of attentional resources. The wheelchair condition involves both visual flow and inertial information and led to the greatest P300 attenuation in comparison to a control condition involving neither of these factors (left bar). The respective effects of the factors were computed as a difference of P300 magnitude between the control condition and intermediate conditions isolating one factor. The VR condition involved visual flow without inertial input (white) and the blindfold condition involved inertial input without visual flow (black). The sum of the respective effects of both independent variables on P300 ERP amplitude was then compared to difference between the control condition and the wheelchair condition (involving both factors). To satisfy a linear additive model, the sum of these individual effects must account for their combined effect. The individual effects of visual and inertial information processing on P300 amplitude are additive.

5.3.2. Behavioural data

There was no main effect of motion on task performance [F(1,23) = 1.835, p = .189, η^2 = .074], but there was a main effect of visual information on the task performance [F(1,23) = 30.918, p = .000, η^2 = .573]. Follow up paired-samples t-tests revealed that task performance was significantly higher during the control condition (mean = 98%, SD = 1) than both the wheelchair [mean = 95%, SD = 2; t(23) = 4.833, p < .001, d = 0.987] and VR conditions [mean = 95.34%, SD = 2.55; t(23) = 4.703, p < .001, d = 0.960]. While task performance was not significantly different between control and blindfold [mean = 97%, SD = 3; t(23) = 1.639, p = .115], task performance in the blindfold condition was significantly higher than in the VR [t(23) = 2.769, p < .05, d = 0.565] and the wheelchair conditions [t(23) = 2.225, p < .05, d = 0.454]. There was no significant difference in task performance between wheelchair and VR condition [t(23)= .094, p = .926] (see Figure 5.4).

Significant correlations were found between P300 amplitudes and task performance in the VR (r_{23} = .418, p < .05) and the wheelchair (r_{23} = .406, p < .05) conditions. By contrast, the control (r_{23} = .333, p = .112) and the blindfold (r_{23} = .383, p = .065) only presented weak correlations linking task performance and P300 amplitude that did not reach significance thresholds.

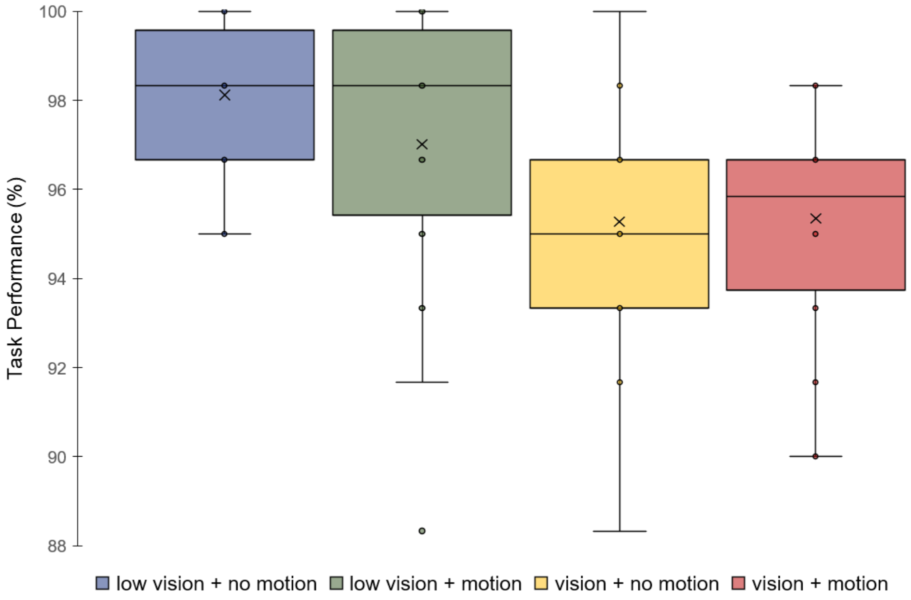

Figure 5.4. Boxplot representing task performance across recording conditions (greywall in blue, blindfold in green, VR in yellow, wheelchair in red). Performance during the greywall and blindfold conditions was significantly higher than in the VR and wheelchair conditions. There was, however, no difference between greywall and blindfold conditions in terms of task performance nor between the VR and wheelchair conditions. These behavioural results suggest that performance is influenced by the demands associated with the presence of visual flow of information.

5.3.3. Analysis of data quality

5.3.3.1. Root Mean Square (RMS)

There was a main effect of visual information on the RMS of the prestimulus period [F(1, 23) = 6.989, p < .05, η^2 = .233]. Moreover, there was a significant interaction between motion and visual factors [F(1, 23) = 8.345, p < .01, η^2 = .266]. Follow up paired-sample t-tests revealed that only the wheelchair condition had significantly lower RMS than all the other conditions. Furthermore, single subject baseline RMS was correlated across all conditions with the exception of greywall and wheelchair, r_{23}=.303, p = .151) suggesting within-subject consistency in terms of residual noise across recording conditions.

5.3.3.2. Baseline standard deviation

There was a significant main effect of visual information on the baseline standard deviation [F(1,23) = 9.499, $p < .01$, $\eta^2 = .292$]. Follow up paired samples t-tests revealed that the wheelchair condition (mean = .07, SD = .02) had significantly lower baseline standard deviation than both the greywall [mean = .08, SD = .02; t(23) = 2.758, $p < .05$], and the blindfold conditions [mean = .08, SD = .02; t(23) = 2.643, $p < .05$]. Moreover, baseline standard deviation was significantly correlated between recording conditions (with the exception of the wheelchair condition) suggesting a high within-subject reliability in terms of residual noise variance.

5.3.3.3. Remaining trials

There was no significant effect of motion on the amount of frequent trials remaining after processing [F(1,23) =.799, p = .381, $\eta^2 = .034$], nor on the amount of target trials remaining [F(1,23) = 2.207, p = .151, $\eta^2 = .088$]. Similarly, there was no significant effect of visual information on the amount of frequent trials remaining after processing [F(1,23) = .085 p = .773, $\eta^2 = .004$], nor on the amount of target trials remaining [F(1,23) = .637, p = .433, $\eta^2 = .027$].

5.3.3.4. Independent Components rejected

The analysis found a significant interaction between motion and visual information on the number of artifactual ICs rejected [F(1,23) = 4.979, $p < .05$, $\eta^2 = .178$]. The number of ICs rejected during the preprocessing of wheelchair condition datasets (mean = 5.79, SD = 2.04) was significantly higher than in both the greywall [mean = 4.541, SD = 2.14; t(23) = 2.186, $p < .05$, d = 0.446] and the VR condition [mean = 4.333, SD = 1.80; t(23) = 3.006, $p < .01$, d = 0.614], but also relatively higher than in the blindfold condition [mean = 4.625, SD = 2.28; t(23) = 2.013, p = .056, d = 0.411]. In comparison to the other conditions where the subject would either fixate a wall or a dynamic recording in front of them, the wheelchair condition offered a 360 degrees visual input to explore, leading to larger head rotations. Therefore, it is highly plausible that the increased number of artifactual ICs found in the wheelchair condition reflects the result of increased neck muscle activity.

5.4. Discussion

The results of the present study show that the reallocation of attentional resources is attributable to two elements of walking: the visual flow associated with displacement, and the inertial sense associated with movement. Both of these elements have been shown to be key determinants of the firing of spatially tuned neurones in rodent electrophysiological studies (Harvey et al., 2009; Chen et al., 2013). Thus, it is likely that visual flow and inertial inputs associated with displacement exert an obligatory capture of attentional resources.

The results show that the processing of visual flow had a significantly larger impact on P300 amplitude than sensory integration of inertial information. This result suggests that visual information is automatically processed, even though it is not directly relevant for the primary task. Moreover, the pattern of data suggests that attentional resources had to be split between the processing of information in these two modalities. Importantly, the respective contributions of visual and motion processing on the attenuation of the P300 ERP amplitude during motion were shown to be additive (i.e., individual effects explain the entirety of the difference when combined). This finding suggest that the attenuation observed during motion in the real-world is entirely explained by the combined effects of these two factors.

Although the results suggest that the effects of visual processing and vestibular processing are additive, it is important to acknowledge that in the present experiment motion speed and acceleration were carefully matched across conditions. However, it can be hypothesized that, in natural settings, increasing motion speed would incidentally increase the amount of visual information that would be encountered. The interaction between different levels of visual feedback and motion speed could therefore be non-linear, as increasing motion speed might not require as much sensory processing resources as an increase of the quantity of visual information to process.

The attentional processing responses (P300) has been shown to be sensitive to the interfering effects of concurrent visual and motion information. This finding suggests that the presence of irrelevant information in the visual and vestibular modality had a specific impact on attentional processing of target stimuli. Moreover, by contrast with the theoretical model of Rees et al. (2001), the present findings suggest that both visual and inertial sensory processes compete with auditory processes for attentional resources, challenging the conception of attentional capacity as being modality specific. These results demonstrate the cross-modality interplay associated with the processing of task-relevant information in the face of a dynamic and embodied experience of the environment.

5.4.1. Task performance

Task performance was significantly reduced in conditions involving visual flow of information. The task performance was however not significantly reduced during movement. These behavioural results partly reflect differences found in the ERP data, with increased visual information as the main factor underlying both ERP amplitude and task performance. Moreover, task performance and P300 amplitude were correlated in conditions with increased visual flow, where the task performance was the most affected. The absence of correlations in the control and blindfold conditions is likely due to ceiling effects. The similarities between P300 amplitude and behavioural performance results, along with the correlations of these results suggest that task performance and P300 amplitude are strongly associated. Overall, the behavioural data imply that the ability to focus attention is significantly diminished during movement.

5.4.2. Limitations

The wheelchair condition presented significantly lower amount of residual noise than other conditions. In addition, a significantly higher number of independent components have been identified as artifacts and discarded in the wheelchair condition than in any other condition. This higher number of artifacts is most likely to be related to muscle neck activity produced by head rotations in that condition specifically. All other conditions did not involve 360 degrees visual exploration of the environment as sight was obstructed or visual information was presented through VR goggles. The reduction of data dimensionality related to the rejection of a higher number of ICs has further reduced the variability of the signal, possibly explaining the significant difference in prestimulus variance from other conditions. Despite the increased prestimulus noise observed in the wheelchair condition, it appears unlikely that the pattern of results can be explained in terms of RMS difference considering the consistency across other conditions in terms of data quality measures.

Moreover, an alternative explanation of the results presented in Chapter 4 was related to the increased danger of moving associated with locomotion in the real-world. Indeed, avoiding hazards during locomotion (e.g., obstacle avoidance, representation of space between the subject and the environment) might have taken substantial amount of attentional resources away from the primary task in the walking condition of the previous study, as shown by previous studies reporting P300 amplitude differences related to the perceived dangerousness of the stimuli. It can therefore be hypothesized that the secondary visual and vestibular information was perceived as particularly relevant in order to preserve the physical integrity of participants during navigation and therefore might have been preferentially processed over target stimuli due to the potential hazard related to the overlooking of such information. However, the present experimental design addresses this issue as the conditions did not involve any behavioural hazard. Indeed, in none of the experimental condition were the participants facing physical hazards nor their physical integrity compromised at any point (i.e., in the case of the wheelchair condition the participants were wheeled down the corridors at a steady pace by the experimenter with no influence on the navigation itself).

In summary, the present data suggests that late attentional processing stages (reflected by the P300) operate as a shared pool of resources that are not modality-specific. Additionally, it is important to note that the wheelchair navigation used within the frame of the second and third ERP studies (see Chapters 4 & 5) was passive (i.e., the experimenter was pushing the participants sitting in the wheelchair), therefore it remains unknown if aspects of physically active wheelchair usage may involve other demands that reduce attention further.

Chapter 6: Brain dynamics reflecting memory during real-world navigation

6.1. Introduction

An extensive body of work in animal neurophysiology has highlighted the prominence of slow oscillation (Theta rhythmicity; 6-12Hz in rodents, 3-8Hz in humans) in relation to active behaviour (orientation, locomotion) and embodied cognitive processes (spatial learning, memory and sensorimotor integration). By contrast, relatively little is known about how natural behaviours (i.e., locomotion, wayfinding) modulate human brain oscillations, or how they affect our cognitive experiences and eventually influence the course of actions taken. As a result, cognitive and neural dynamics related to the experience of, and the interaction with, a complex and ever-changing environment remains to be identified in humans.

In broad terms, the human neurophysiology underlying cognitive phenomena (such as sensorimotor processing, memory and spatial navigation) have yet to be investigated under natural and everyday life circumstances. Previous findings from invasive recording in humans have, however, hinted that the brain switches into a different operating mode during active behaviour. In particular, evidence from intracranial EEG recordings in humans have implicated theta oscillations (originating from the hippocampal and entorhinal regions) in the encoding and retrieval of information in memory, and in supporting cognitive processes involved in spatial representation and navigation. Conceptually, hippocampal theta oscillations have been characterized as “travelling waves”, connecting different regions involved in sensorimotor integration of multimodal information, and therefore playing a crucial role in the correct planning and execution of actions. In short, theta brainwaves have been conceptualized as playing a determinant role in the realization of real-world behaviours.

The present study aims to determine whether neurophysiological dynamics underlying the maintenance of information in working memory during goal-oriented tasks can be captured during natural behaviour in humans, using non-invasive surface EEG recording. For this purpose, brain activity has been recorded while participants were engaged in a navigation task requiring a) spatial information (directions) to be held in mind in order to reach the correct destination, in contrast to b) simply walking.

Before introducing the current study in detail, the following sections will present an overview of the heterogeneous body of evidence highlighting how and which brain oscillations are associated with the processing of spatial information, storage and access of information in memory, and the performance of natural behaviours. The literature reviewed below demonstrates that theta oscillations are an essential rhythmic activity of the brain, serving a wide range of cognitive functions, such as the retrieval of spatial information in humans navigating virtual environments, and multisensory integration of situational and task-dependent information serving action. This has particular relevance for the embodied cognition approach motivating the body of work in this thesis, in this case studying freely behaving individuals navigating real-world environments.

6.1.1. Role of theta rhythm during active behaviours

6.1.1.1. Hippocampal theta oscillations in physically active animals

In contrast to the limited literature that can be found about brain dynamics associated with active behaviour in humans, this field of research has been dominated by electrophysiological recordings in other mammal species. Historically, single-cell recordings in rats have highlighted increases in slow wave power recorded at hippocampal sites in relation to arousal (Coenen, 1975; Vanderwolf, 1969; Whishaw & Vanderwolf, 1973) and movement (Grastyán, Lissák, Madarász, & Donhoffer, 1959; Harper, 1971). Theta activity has also been shown to linearly increase with locomotion speed in rats running along a track (Ledberg & Robbe, 2011; Long et al., 2014; Sławinska & Kasicki, 1998). These findings have initiated a legacy of electrophysiological research investigating modulations of slow oscillatory patterns in the hippocampus (hippocampal Local Field Potentials (LFP) 3-12Hz) in relation to active behaviours.

Due to the wide range of behaviours associated with theta modulations there has been a longstanding debate about the interpretation of hippocampal theta oscillations. Many seemingly distinct functions have been attributed to hippocampal theta rhythm, through studies using various methodologies that were reported using different terminology. Historically, the common consensus was that theta oscillations represent a pervasive “rhythm” of the brain, related to a wide range of behaviours, which theoretically would only be “absent” provided that the animal is immobile and the surrounding environment is not changing (Buzsáki, 2002). This linking of movement to the interpretation of hippocampal theta oscillations is in part the consequence of the nature of the experimental paradigms used to acquire animal brain dynamics. Movement and cognitive processing tend to be confounded in these animal studies due to an overlap between the trained behavioural responses to conditioned stimuli. Maze-based paradigms are dominant in the rodent literature, which does not allow for the disentangling of movement dynamics from the cognitive process elicited when rodents are placed in concrete situations in which previously trained behaviours had to be performed in reaction to conditioned stimuli. The next two sections present seminal work that helped to resolve this historic uncertainty around the interpretation of brain rhythms related to cognitive processing.

6.1.1.2. Attentional processing and executive functions

In a seminal study on conditioned responses to stimuli, Grastyán, Lissák, Madarász, & Donhoffer (1959) reported the occurrence of slow rhythmic potentials in the hippocampus of cats as they learned to associate reflex responses to the presentation of stimuli. Once the conditioned response was stabilized, the prevalence of hippocampal slow waves and hippocampus-neocortex desynchronization would progressively decrease. In case of a behavioural regression after an interval period, or during the conditioning of another response type to the stimuli, theta oscillations would be observed again throughout the associative learning phase between the stimuli and responses until habituation. Following this work, theta rhythmicity was interpreted as an expression of an inhibitory state that is produced as the hippocampus regulates and stabilize temporary connections between sensory input and motor responses.

Subsequent findings revealed that theta activity elicited by the presentation of stimuli persisted throughout training in cats’ hippocampus (Adey, Dunlop, & Hendrix, 1960), suggesting that theta was reflective of attentional processing of novel and relevant stimuli. Brown (1968) recorded hippocampal activity of cats chronically implanted with electrodes, highlighting theta modulations in relation to the arousal state of the autonomous system, but also revealing specific desynchronization of theta rhythm between hippocampus and neocortical sites in relation to behavioural orientation and visual processing. Even though hippocampal theta had been related to different attentional and executive functions, a common conclusion from these initial studies was that theta rhythm reflects some form of cognitive processing of environmental stimuli related to the performance of actions.

6.1.1.3. Memory functions

Following this first theoretical formulation of theta waves as reflecting cognitive function in terms of attentional processing, a number of competing theoretical models have conceptualized theta rhythm as reflecting cognitive processing associated with the comparison of sensory information with previously stored information, giving rise to a memory based interpretation of theta oscillations (Pickenhain & Klingberg, 1967; Vinogradova, 2001). For example, Winson (1978) reported spatial memory deficits in rats following lesions in the medial septal nucleus. These lesions resulted in a disruption of theta oscillations generators which had a significant impact on the navigation of mazes that had been previously learned by the rats. This finding highlighted the role of theta oscillations for the retrieval of spatial information and navigation. Extensive evidence demonstrating the role of the hippocampus in the encoding and retrieval of information in memory has since been reported in various mammal species (Buzsáki, Lai-Wo & Vanderwolf, 1983; Hampton, Hampstead, & Murray, 2004). While studies have documented specific memory impairments in relation to perturbations of hippocampal theta activity in humans (and its extended cortical network, see following sections), the animal literature has primarily examined memory bound to spatial representations and mapping of the environment during active behaviour.

6.1.1.4. Spatial navigation: cognitive map theory and place cells

Evidence for the role of the hippocampus in spatial navigation was already present in early behavioural studies. As observed in rats trained to run through direction-guided linear track (i.e., an alternating series of 180 degrees turns), hippocampal cell assemblies (referred to as place cells, see Moser, Kropff, & Moser, 2008; Muller, 1996) typically discharge sequentially following a contralateral pattern to the direction selected (Christian & Deadwyler, 1986; Muller & Kubie, 1987). Due to the unidirectional nature of the task, it has been argued that travelling through a one-dimensional plane does not involve the construction of a spatial representation of the environment, but rather relates to pure sequential learning, and hippocampal activity has therefore been interpreted as a spatial memory encoding and retrieval mechanism. Further evidence for the role of hippocampal activity in spatial navigation was then found in studies using more complex mazes (e.g., radial maze tasks, see Young, Fox, & Eichenbaum, 1994). The exploration of path crossing mazes gave rise to omnidirectional patterns of hippocampal cell activation related to head direction (Fox & Ranck, 1975; Ranck, 1973). In addition, a distinct range of pyramidal cells in the rat entorhinal cortex (part of the extended hippocampal formation) have been found to be specifically sensitive to allocentric position (i.e., representation of space relative to another person perspective as opposed to an egocentric representation of space which is characterized by a self-centred perspective) in the environment (O'Keefe & Dostrovsky, 1971). The firing rate of enthorinal cells assemblies was found to be specifically triggered when the rats went through certain locations of the environment (place fields). These "place cells" are organized as a grid in the enthorinal cortex, and their pattern of activation reflects an internal mapping of spatial representations (Moser et al., 2008). A distinction was henceforth made between hippocampal theta cells, which are sensitive to movement, and such place cells, which are related to one's position within the environment (O'Keefe, 1979).

Two computational models of spatial navigation have emerged based on the properties of place cells. Based on motion sensitive theta cells, the dead reckoning hypothesis implies an idiothetic exploration of the environment, mainly relying on the coding of self-motion, that can be used as a compass for path integration and to calculate one's position. By contrast, the cognitive map theory postulates that navigation is allocentric and mainly consists of a geometric triangulation of one's self-representation, within an environment spatial representation, relying on the spatial coding of place cells (Burgess & O'Keefe, 1996; O'Keefe & Burgess, 1996). Within the cognitive map theory (O'Keefe & Recce, 1993), hippocampal theta has been suggested to provide a distance metric, by tuning place cell activity pattern accordingly to afferent input related to displacement in space (Buzsáki, 2002, 2005). In line with the dead reckoning navigation proposal, recent evidence has demonstrated the interfering role of theta waves in the enthorinal cortex to selectively phase-lock the firing rate of place cells, enabling a spatiotemporal encoding of distance travelled (speed) and direction (Burgess, 2008; Jeewajee, Barry, O'Keefe, & Burgess, 2008). Initially conceptualized as competing theories, these models may in practice describe complimentary aspects of the spatial representation system.

In addition to coding current self-position in the environment, it has been shown that place cells also map the intended destination (Ainge, Tamosiunaite, Woergoetter, & Dudchenko, 2007). Ambulatory and vestibular self-motion signals (i.e., afferent and efferent sensorimotor information related to locomotion), have been underlined as principal determinants of the firing pattern of place cells (CA1 pyramidal cells) in the rat hippocampus (Czurkó, 1999; Hirase, Czurkó, Csicsvari, & Buzsáki, 1999). In a seminal study, the respective contributions of ambulatory and vestibular signals were revealed by contrasting three conditions (Terrazas, 2005). Rats were walking in a natural environment (both vestibular and ambulatory signals), conducting themselves in a cart (only vestibular signal), and stationary while experiencing pseudomotion in a rotating environment (no ambulatory and no vestibular input). Fewer place cells were activated when there were no ambulatory signals (cart and pseudomotion), and hippocampal theta power was reduced under the pseudomotion condition (suppressing both ambulatory and vestibular input). The optic flow produced by motion is another determinant source of sensory input that substantially contributes to the firing pattern of hippocampal place and theta cells (Jarosiewicz, 2004; Save, Cressant, Thinus-Blanc, & Poucet, 1998). Taken together, these results demonstrate that hippocampal place cells spatial firing pattern is related to the complex interplay of motor commands, proprioceptive feedback, visual input, and vestibular information that constitute an embodied experience of the real-world (Thompson & Varela, 2001).

Firing of local hippocampal fields and, at a neuronal scale, enthorinal “grid” cells, are largely orchestrated by theta frequency during spatial navigation. At a larger scale, theta oscillations are involved in the synchronization of cortical regions involved in memory and spatial cognition networks. The entorhinal cortex interface feeds the hippocampus with cortical information and communicates hippocampal messages to various associative cortical areas of the neocortex (Witter, Groenewegen, Lopes da Silva, & Lohman, 1989). Through multi-electrode recordings on the laminar sites of the rat hippocampus, theta waves travelling along the septotemporal axis of the hippocampus have been highlighted (Lubenov & Siapas, 2009; Patel, Fujisawa, Berényi, Royer, & Buzsáki, 2012). The local spatiotemporal patterns of theta activity suggest that theta rhythm may underlie the encoding of spatial and temporal features. At a larger scale, synchronization of theta activity between cortical and subcortical regions involved in the processing and encoding of information has been observed (Sato & Yamaguchi, 2007; Von Stein & Sarnthein, 2000). Evidence suggests that one of theta oscillations’ primary roles is to facilitate communication between brain structures that are involved in the same course of actions (Buzsáki, 2005). Taken together, these findings clearly demonstrate the need to depart from the obsolete theoretical approach that consisted in attributing the theta rhythm to a specific set of cognitive functions, in favour of functional and connectionist models of cognitive theta rhythm.

6.1.2. Theta rhythm functional network

The discovery of the spatiotemporal propagation patterns of hippocampal theta waves in relation to afferent input has highlighted the role of theta in the binding of multimodal information by facilitating communication between remote brain structures. Unravelling the origin and course of theta travelling waves, studies have shed light on the circuitry involved in the generation of theta oscillations (Pignatelli, Beyeler, & Leinekugel, 2012). Hippocampal regions implicated in theta oscillations (such as Medial Septum and Entorhinal Cortex) are connected with several neocortical regions through theta rhythm synchronization (Colgin, 2016). Two main cortical structures have been linked to the hippocampal-enthorinal system, possibly forming a wider brain network involved in navigation and memory functions. The following subsections will introduce the functional role of theta oscillations linking hippocampal and subcortical structures to cortical areas. The underlying cognitive functions of theta rhythm within the parietal and frontal networks will be discussed at the light of evidence from animal and neurosurgical patients' studies.

6.1.2.1. Theta pathway between hippocampus and parietal cortex

Most of the findings that have been discussed so far have been derived from electrophysiological recordings in mice and rats. Theta rhythm following active behaviour and related to the exploration of the environment has been predominantly observed in rodents' hippocampus. However, other mammal species (e.g., monkeys and rabbits) present patterns of theta activity localized in the parietal cortex. Due to the high projection density of subcortical structures (e.g., thalamic nuclei) involved in the coding of vestibular information to the parietal cortical areas, integration of motion input has been traditionally considered as a primary function of the parietal cortex (Fukushima, 1997). In humans, the Associative Parietal Cortex (APC) interacts with the hippocampal formation through the modulation of neurophysiological dynamics, mainly through de/synchronization of neural populations (as documented by intracranial electrophysiological studies, see Etienne Save & Poucet, 2000). While the APC is specifically involved in the processing of egocentric visuospatial and self-motion information, the hippocampus is involved in computing an allocentric mapping of the environment. According to this account, the dialogue between the hippocampal formation and the APC provides a feedback loop to build and update cognitive maps, depending on the incoming flow of visual, vestibular and motion input (Etienne Save & Poucet, 2009).

Despite this emphasis on the study of parietal cortex in relation to spatial attention and sensorimotor integration within a theta-enabled network, recent evidence from fMRI studies has also highlighted the involvement of parietal regions in episodic memory. BOLD activation signals in the hippocampus and several parietal areas (that were spatially distinct from those that are sensitive to motion) were consistently correlated during successful recollection of items (Vincent et al., 2006). It has been suggested that the parietal cortex is at the interface of perception, attention and spatial representation within a spatial representation network, with a potential role in the storage of spatial representations in episodic memory (although this proposition requires additional evidence, see Andersen, 1997; Kesner, 2009). Regardless of whether this specific account is correct, the broader point remains that the modulation of theta oscillatory dynamics at parietal cortical sites may indicate the processing and retrieval of spatially-bound information during real-world navigation.

6.1.2.2. Synchronization of theta oscillations in the hippocampus and medial prefrontal cortex (mPFC)

In parallel to the cumulative evidence highlighting the role of theta oscillations within the frame of a functional network linking hippocampal and parietal cortical structures, research in rodents have shown that hippocampal theta activity related to spatial working memory was also correlated with theta oscillations recorded in the medial PreFrontal Cortex (mPFC) (Benchenane et al., 2010; Guderian & Düzel, 2005; Siapas, Lubenov, & Wilson, 2005). Moreover, the degree of synchrony between medial prefrontal cortical areas and the hippocampal theta rhythm was found to be linked with behavioural performance during memory tasks. These findings underlined the role of theta oscillations in the communication between subcortical and prefrontal cortical structures during the encoding and recall of spatial information.

Theta oscillations in the mPFC have been associated with memory functions in monkeys (Romo, Brody, Hernández, & Lemus, 1999) and attentional processing in humans (Benchenane, Tiesinga, & Battaglia, 2011). Similar to the findings reported in rodents, O’Neill, Gordon, & Sigurdsson (2013) have provided evidence that theta oscillations associated with spatial working memory recorded in the mPFC synchronize with the hippocampus. An important implication of these findings is that theta dynamics related to spatial memory that are recorded at frontal cortical sites are not just far-field potentials projecting through volume conduction from the hippocampus, but rather reflect frontal cortical activity which is part of a network related to spatial working memory.

Recent studies have reported frontal midline theta oscillations in relation to working memory maintenance and associated with both the encoding and retrieval of information in episodic memory (Hsieh & Ranganath, 2014). Therefore, even though hippocampal theta cannot be captured using surface EEG sensors, its proxy may indeed be captured effectively through non-invasive methods by recording brain dynamics within the extended cortical network involving prefrontal cortex through non-invasive methods (Cavanagh & Frank, 2014). Hippocampal-frontal theta are regarded as crucial oscillating dynamics for memory integration by facilitating memory processes and supporting the constructions of memory representations, through communication between hippocampus and mPFC (Backus, Schoffelen, Szebényi, Hanslmayr, & Doeller, 2016). Consistent with this view, coherence in theta oscillations between hippocampal and frontal recording sites have been interpreted as reflecting the communication between the two brain structures during the alternating dynamic between encoding and retrieval state. Moreover, a context-binding effect has been associated with theta frontal oscillations, suggesting that theta rhythm supports the encoding of contextual information in episodic memory (Staudigl & Hanslmayr, 2013).

6.1.3. Theta rhythm in humans

6.1.3.1. Differences with animal literature

As previously discussed, research examining brain dynamics related to active behaviours has been largely limited in humans, mainly because of previous practical limitations and the invasiveness of research methods used in animals. However, evidence for hippocampal theta and its extended cortical network has been gathered, mainly through recordings acquired during neurosurgery. Neuropsychological studies have also reported a range of spatial and memory impairments related to the perturbation of resting-state theta rhythm. This section provides an overview of current knowledge about theta rhythm in humans and their role in cognitive functions related to memory and spatial navigation.

As hinted by studies in the monkey brain, theta rhythmic activity recorded in rodents' hippocampus may have different properties in humans under comparable behavioural conditions. In a comparative study, Watrous et al. (2013) recorded low-frequency oscillations in rats and humans performing a spatial navigation task in a virtual environment. While both species presented rhythmic fluctuations within the theta range, humans peak frequency was centred around 3Hz, while rats' theta peaked around 8Hz. These results suggest that low-frequency oscillations typically found in rats, although present in human hippocampus, may be less prevalent in humans. This difference may be related to the additional role of human theta rhythm in connecting the hippocampus with cortical networks underlying higher cognitive functions, for example encoding and retrieval of episodic and semantic information in memory (Klimesch, Doppelmayr, Schimke & Ripper, 1997; Klimesch, 1996).

Unlike hippocampal oscillations in rodents displaying different phases across different part of the hippocampus at a specific time, human theta waves present a spatial propagation pattern exhibiting a consistent phase across the hippocampus (H. Zhang & Jacobs, 2015). More than simply highlighting differences in hippocampal theta properties between rodents and humans, this finding suggests that theta travelling waves play a functional role in the propagation of behavioural information within, but also throughout, the hippocampal region. According to this account, disruption of hippocampal theta activity would hinder the communication along the hippocampal-enthorinal-associative cortices network, which would eventually lead to sub-optimal spatial representations and binding of information in memory. This theory has received supporting evidence from neuropsychological studies reporting significant cognitive deficits, such as memory impairments in relation to theta dysrhythmia (Lopez-Pigozzi et al., 2016; Shuman, Amendolara, & Golshani, 2017). Epileptic episodes (interictal epileptiform activity) interfering with theta rhythmicity perturb the encoding and retrieval of information both in rats (Kleen, Scott, Holmes, & Lenck-Santini, 2010) and humans (Kleen et al., 2013). Moreover, epileptic patients with theta disruptions in parietal areas exhibit significant spatial memory impairments (Chauviere et al., 2009).

6.1.3.2. Human theta dynamics during spatial navigation in virtual environments

High amplitude theta episodes have been observed in humans, in different cortical areas, through subdural EEG recording of epilepsy patients navigating computer-generated mazes. Theta oscillation episodes were task dependent, with increasingly more theta bursts when the maze complexity increased, and during recall trials in comparison to learning trials (Kahana, Sekuler, Caplan, Kirschen, & Madsen, 1999). In a maze learning variant of the previous study (Caplan et al., 2001), theta oscillations were more prevalent when the maze length was increased, indicating that cortical theta oscillations might index the encoding demands of spatial information. While most of the task-related rhythmic activity was found in the theta band, higher and lower frequencies appear to covary with decision time while theta did not, suggesting that inter-frequency interactions may reflect distinct aspects of spatial memory encoding and retrieval. Consistent with the rat literature, theta bursts were observed at frontal and parietal electrode sites in humans' surface EEG recorded during a virtual maze navigation task (Bischof & Boulanger, 2003). Interestingly, increases of theta occurred more frequently when reaching corners or following a navigational mistake. These theta episodes appear to be associated with the formation and updating of spatial information in memory. Similarly, in a Magnetoencephalography (MEG) study, an association between theta rhythmic activity and navigational task performance was found in participants navigating through a previously learned virtual environment (Araújo, Baffa, & Wakai, 2002).

Through intracranial electrocorticography recordings (ECOG) of epileptic patients navigating virtual mazes, the sensitivity of hippocampal sites to navigation-related theta modulations has been highlighted and compared to previous findings in rodents. Caplan et al. (2003) have observed that theta oscillations were more prominent when sensorimotor information was dynamic ("in flux" as the authors described it) in comparison to periods of stillness when patients were performing exploratory search and goal-directed behaviours in an artificial environment. These findings suggest that hippocampal theta oscillations are linked with the integration of sensorimotor information and spatial learning. In a follow-up study (Ekstrom et al., 2005), six epileptic patients performed a taxi driving task in virtual reality. During the experiment the participants alternated between searching for passengers (learning phase) and driving them to specific locations (retrieval phase). While the passengers' locations were randomly generated by the computer, landmark destinations remained constant. Theta activity was found to increase similarly in both hippocampal and neocortical recording sites during virtual movement throughout all phases of the game, independently of the experimental condition. The correlation between hippocampal and cortical theta activity seem to be specifically observed in relation to motion, suggesting that both structures are connected to, and play a role in, attentional and sensorimotor integration aspects of spatial navigation.

6.1.3.3. Theta rhythm is associated with the encoding and retrieval of spatial information in humans

Snider, Plank, Lynch, Halgren, & Poizner (2013) probed brain activity of 13 ambulant participants while they were performing a spatial navigation task in an extended virtual environment (i.e., participants were equipped with EEG sensors and a head-mounted display allowing for a wide range of movements and a free exploration of the simulated environment). Theta phase and amplitude over parietal electrode sites were found to be consistent between trials when the participants were walking through a specific portion of the environment that was between the objectives locations and the starting point. Moreover, the strength of spatial theta autocorrelation between the learning and recall session was found to be predictive of objects' location recall a day later. In a recent study, Alekseichuk, Turi, Amador de Lara, Antal, & Paulus (2016) have externally modulated theta and gamma activity in the prefrontal cortex using transcranial Direct Current Stimulation (tDCS). Spatial working memory was improved when high gamma bursts (within 80-100Hz range) were superposed to theta peaks. In contrast increase of gamma power that did not occur during theta peaks did not result in better spatial memory performance. Theta-gamma cross-frequency synchronization and phase coherence seems to play a key role in spatial working memory, but also in episodic memory, as shown in a large-scale intracranial study of neurosurgical patients (Burke et al., 2014).

6.1.4. Relevance of active behaviours for the study of cognition

According to recent accounts of embodied cognition emphasizing the situated nature of cognitive experiences, navigation in the real-world is inherently context-dependent as spatial relationships need to be continuously re-evaluated with respect to the body situation within its environment (Beer, 2000; Clark, 1999). Therefore, successful real-world navigation not only requires online assessment of one's body experiences (location, direction, speed) but also needs to be complimented by a dynamic integration of the incoming flow of environmental input to match one's intentions (Gramann et al., 2011; Robbins & Aydede, 2009).

However, these pervasive aspects of human navigation have not been studied in the context of real-world exploration. In practice, due to the invasive nature of electrocorticography and the immobility of traditional brain imaging methods, human brain activity related to locomotion, spatial navigation and spatial memory has only been studied through proxies. Indeed, in order to circumvent the impracticalities implied by having subjects navigating across the environment while recording their brain activity, and to avoid potential sources of motion-related noise, researchers have typically resorted to immersing their subjects within

Virtual Reality environments (Maguire et al., 1998; O'Keefe & Burgess, 1999). Even though this solution may appear to be an elegant way to investigate spatial cognitive questions, it can be argued that these virtual environments do not provide an accurate representation of the multidimensional nature of our environment.

Evidence from animal studies have provided substantial support for the claim that the brain's modus operandi switches during active behaviour, and that some brain dynamics are suppressed when subjects' mobility is restrained. For example, increased cortical responsiveness to visual stimuli has been observed in mice actively exploring the environment in contrast to being immobilized while watching a virtual representation of a moving environment, highlighting the importance of the sensorimotor cortical network activation state for the processing of sensory input (Harvey, Collman, Dombeck, & Tank, 2009). Moreover, Ferezou et al. (2007) have provided evidence that the spatiotemporal pattern of sensory responses is dynamically modulated by behaviour during sensorimotor integration, spreading from the primary somatosensory barrel to the motor cortex. In mice, locomotion within a simulated environment with the head fixed results in a strong reduction of place cells firing rate and alterations of temporal coding in comparison to unrestrained navigation in the real-world (Chen, King, Burgess, & O'Keefe, 2013; Ravassard et al., 2013). Furthermore, when limb movements are restrained, theta power is significantly reduced and place cells discharges are abolished in rats (Foster, Castro, & McNaughton, 1989). In the absence of whole-body movement, lower discharge rates are observed from neurons responsive to proprioceptive, vestibular and sensorimotor information. Indeed, by restraining head and body movements, an important part of the vestibular, somatosensory and proprioceptive afferent input is eliminated from the cognitive experience of one's environment (Berthoz, 1997; Nitz, 2006). Moreover, as discussed previously, restricting participants' displacement within an environment is likely to result in a suppression of neuronal populations that are specifically sensitive to allocentric position and involved in mapping spatial representations.

6.1.5. Interim conclusion

Theta oscillations are an essential rhythmic activity of the brain, serving a wide range of cognitive functions related to the execution of goal-oriented tasks. By facilitating communication between neural structures, theta activity supports the integration of multimodal sensorial input within the frame of situational and task-dependent construction and updating of representations and execution of actions. Episodes of theta power increase have been particularly observed in relation to the encoding and retrieval of spatial information in humans navigating virtual environments. The animal literature has, however, pinpointed the complex interaction of real-world sensorial experiences in the modulation of theta rhythm within spatial representation systems and subcortical-neocortical navigational networks. The evidence presented here demonstrate the relevance of an embodied approach to the study of spatial cognition in humans. Thus, capitalizing on the opportunity offered by mobile brain imaging techniques to record brain dynamics while participants are freely behaving and navigating in real-world environments is likely to provide novel insight into the neural and cognitive mechanisms of human navigation.

6.1.6. Aims of the study

As outlined above, despite the plethora of evidence highlighting the key role of theta oscillations issued from animal studies, theta driven mechanisms of cognitive processing that underlie real-world behaviour have not been characterized in humans. While the main explanation for this mismatch between animal and human literatures used to be related to the impracticalities of recording brain dynamics in physically active participants, mobile brain imaging now offers a solution to this longstanding issue. This technological development really matters because previous research on animals has demonstrated that embodied aspects related to the construction and updating of one’s body representation (and its spatial relationships within an environment) are not fully captured in subjects that are not actively engaged with their environment, due to the crucial roles of vestibular, visuospatial and motion flow of information.

The present study aims to assess the feasibility of recording brain dynamics associated with memory and sensorimotor processing, typically recorded at frontal (Fz electrode) and parietal (Pz electrode) sites, as reported in animal physiology and invasive human brain recordings, in humans engaged in real-world behaviour using non-invasive mobile EEG. For this purpose, we recorded EEG from participants engaged in walking while holding task-related information in memory. By contrasting conditions involving either task-specific memory workload, or not, during active behaviour, this study aims to: A) capture brain dynamics reflecting memory processing during real-world behaviour, and B) explore whether changes in spectral power recorded at frontal and parietal sites in active humans are analogous to patterns of theta dynamics typically reported in animal physiology studies.

The present study aims to investigate modulations of theta-band activity related to memory workload in individuals engaged in a spatial navigation task. The nature of the information in memory workload is directly related to the execution of the navigational behaviour (following directions), which will allow the investigation of the relationship between theta dynamics and participants' position within the environment. According to previous research on both humans and animals, an increase in overall power within the theta band is expected to arise from memory workload. Moreover, in line with the embodied cognition framework, it is hypothesized that theta dynamics will be context-dependent (situated, see Clark, 2013; Robbins & Aydede, 2009) with higher amplitude oscillations being expressed as the participants move towards the destination in a goal-oriented behaviour (in this case as they get closer to the intersection at the end of the corridor).

6.2. Methods

6.2.1. Participants

A sample of sixteen participants, mainly undergraduate students at the University of Stirling (age range = 18-51, mean = 22, 14 females), took part in this experiment. The participants were clear of any neurological antecedents, presented normal (or corrected-to-normal) vision and audition, and were not affected by any physical and/or cognitive impairments at the time of the experiment (see section 3.2.1 for a detailed list of the inclusion and exclusion criteria). General information regarding the study procedure was given prior to the experiment and written consent was obtained from all participants. Datasets corrupted by technical issues, either in the form of channel disconnections or issues related to experimental event time stamping, were discarded. Data from six participants had to be excluded from the analyses due to such issues. The analyses reported in the results section have therefore been performed on the remaining datasets of 10 participants (N=10).

6.2.2. Experimental design

The present experiment investigated brain dynamics related to memory workload during walking by contrasting two conditions: walking while holding directional instructions in memory, versus simply walking. Participants were asked to navigate through the University of Stirling corridors while following the directions provided by the experimenter, either at the beginning (holding information in mind) or at the end of a corridor (control).

With respect to the specificities of the building in which the experiment took place, only corridors with multiple junctions and of the same length were included in the experimental design of the present study. The instructions regarding the next turn were given either at the beginning (inducing memory workload) or at the end of the corridor (control) preceding an intersection. The EEG trace was timestamped whenever the participants entered one of the corridors included in the experiment, in the middle of the corridor, and at the end of it, therefore providing a means to compute walking speed across corridors of interest. In order to maintain a consistent time window across trials and participants, epoch length was defined with respect to the minimum time taken by all participants to walk through the corridors. Therefore, a trial consisted of a time period of 10 seconds (defined as the 5” preceding and after passing the middle of the corridor). Each of the walking segments included in the analyses were preceded by a 40 seconds long period of walking in adjacent corridors. Both the experimental condition (working memory, control) and the direction (left, right) were pseudo-randomized using predefined routes that were randomly assigned to participants. This procedure provided a means to counterbalance condition order on a trial to trial basis, while ensuring that the instructions would match the specificities of the building used in the experiment (i.e., avoiding the inclusion of corridors that would not meet the requirement of multiple junctions, see Figure 6.1).

Each participant walked through the small corridors 16 times (4 trials per condition). The total number of trials was split in half over two blocks, separated by a resting period during which an impedance check was performed. The instructions were given verbally in a scripted (e.g., “at the end of the corridor, please turn right”) and intelligible manner (as attested by the perfect task performance observed across all participants). The average total distance walked by the participants was 2.4 kilometres and the experimental phase took 60 minutes to complete (including the 5 minutes break halfway through the experiment). Both the mental and physical fatigue related to extended recording periods were factors to consider for the design of the experiment. Moreover, the increased risk of sweat related to the act of walking over a relatively long period may further reduce the signal-to-noise ratio. In this experiment, the length of the corridors was the main limiting factor to the number of trials that could be performed during a recording session.

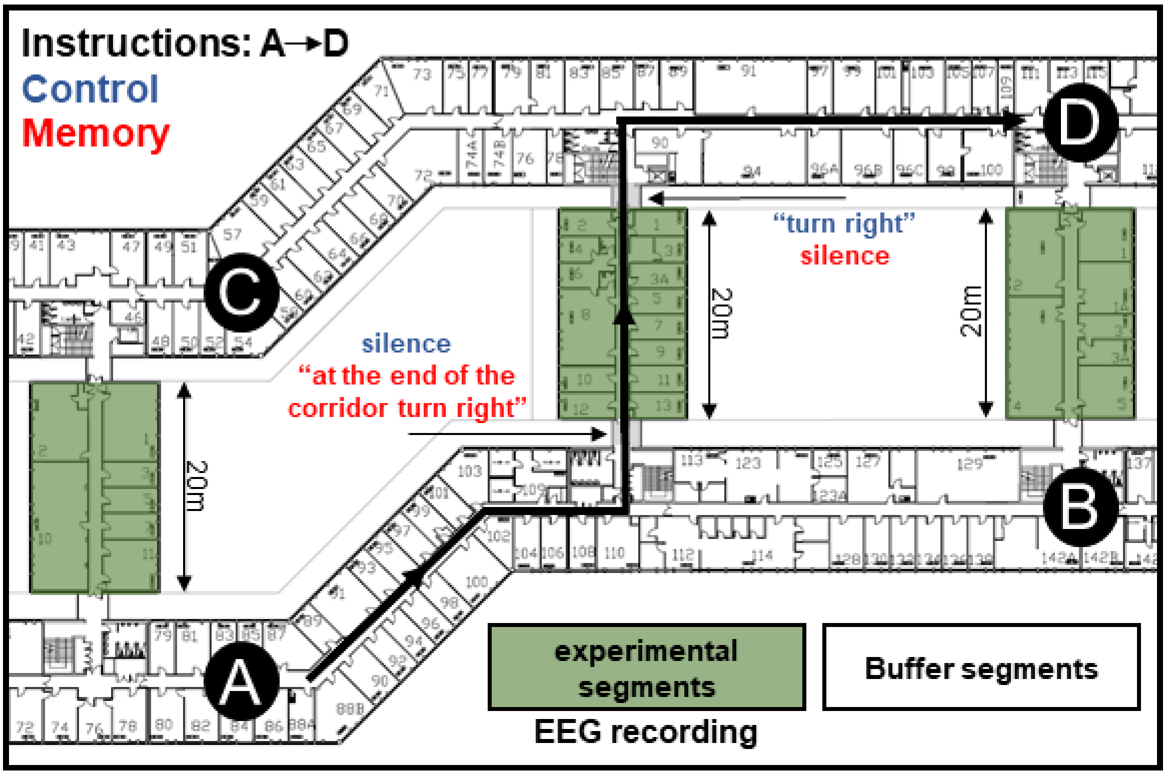

Figure 6.1. Representation of the experimental setup using corridors of the building's layout as pictured. The experimental conditions and example of instructions given across these conditions during a trial going from point A to point D have been colour coded (the control condition in blue and the memory condition in red). The analyses only concern data that was recorded during the experimental segments represented (represented in green).

6.2.3. Material

The specific details of the EEG system used within this study have been detailed in the methodological section of Chapter 3 (see section 3.2.3.1). During this navigation task, experimental event time stamps were sent to the amplifier by the experimenter through the manipulation of a three buttons remote command. In practice, a series of triggers were sent to specifically mark the beginning, middle and end of a corridor with respect to the current experimental condition (normal versus increased memory workload). Pseudo-randomized experimental scripts were generated prior to the recording sessions in order to counter balance conditions, while ensuring that the instructions given were plausible with respect to the design of the building (see Figure 6.1).

6.2.4. Procedure

Two practice trials were performed to familiarize the participant with the task and to ensure that they understood the instructions provided by the experimenter. Participants were asked to walk at a natural pace during the entirety of the experiment. The experimenter was providing instructions to the participants throughout the experiment by following at close distance from them (approximately 3 meters behind). Moreover, it was specifically stated that in the absence of directions given at the beginning of the corridor, the participants would keep going until further notice. The corridors included in the different routes were checked prior to recording, potential obstacles were removed and doors were kept open. The experiment was performed in an ecological setting, purposefully recreating the real-world situation of finding one's way across the building's corridors. The experiment followed a fixed schedule that was mainly designed to avoid major breaks between lectures that could have interrupted the flow of the experiment (i.e., either recording at 9.30 or 13.30). Moreover, the corridors used for this experiment were situated on a floor including mostly researchers' offices and small teaching rooms. Therefore, even though human encounters were consistently part of the participants' experience throughout the experiment, pre-emptive measures were adopted to ensure that their number would not disrupt the experiment.

6.2.5. EEG data processing

EEG data were processed using the EEGLAB (Delorme & Makeig, 2004) open source toolbox for MATLAB (version R2014b, The MathWorks Inc.) and custom-made scripts. In a first preprocessing step the continuous data was visually examined and the portions of the EEG trace displaying extreme levels of noise (e.g., channel disconnections) were manually discarded. The continuous data was then re-referenced offline to the average of all channels.

In a parallel routine aimed at optimizing ICA decomposition, the datasets were band-pass filtered with the successive application of a low-pass filter of 20Hz and a high-pass filter of 1Hz. Then the continuous EEG data was split into consecutive epochs of 1 second (that were not related to experimental events), which were then subjected to statistically-based rejection methods (using a criterion of three standard deviations around the mean). An extended Independent Component Analysis (infomax ICA algorithm, see Bell & Sejnowski, 1995) was performed on these remaining dummy epochs. The ICA features obtained were then back projected to the initial non-filtered dataset. In a second stage of data processing, the initial continuous datasets were band-pass filtered from 0.15 Hz (−6 dB cut-off, filter order 16500) to 120 Hz. Only frequencies within the 1-30Hz range have been included in further analyses, effectively excluding the frequencies at the lower end of the spectrum to avoid distortions introduced by the high-pass filter and motion-related artifacts prominently represented in frequencies above 30Hz (i.e., muscular activity) and line noise. These measures effectively resulted in higher retention rates of trials that were valuable considering the relatively low number of trials that could be recorded using the aforementioned paradigm.

The ICA identified common artefacts such as eye blinks, eye movements and heartbeats, allowing these to be removed. After this ICA-based data pruning, the continuous datasets were then epoched around the onset of events (-7000 to 7000 ms). As the duration of the trials was directly dependent on participants walking speed, some variance was observed. In order to maintain a consistent number of trials for each subject, the minimal duration taken to walk across the corridor was used to define the epoch length applied to all trials. Therefore, the analyses have been performed on 10 second epochs. Time-frequency computations were performed on the extended epochs to compensate for edges distortions, then only time-frequency coefficients within the 10 seconds time window (i.e., centred on the corridors' centre) were used during analyses. The epochs dominated by artifacts were identified using the probability and kurtosis criteria implemented in EEGLAB (using three standard deviations around the mean as a threshold) and such improbable epochs were subsequently rejected from further analysis. This statistical-based epoch rejection procedure resulted in the discarding of one trial per condition on average (with a maximum loss of five out of 16 trials for a single-subject dataset in which a maximum of 3 out of 8 epochs had to be removed for a specific condition). A minimum of 50 percent of trials for each condition survived the epoch rejection procedure for every participant. Trials were then allocated to the control and memory workload conditions, according to the predefined protocol followed during data collection.

6.2.6. Data analyses

In a first frequency-domain analysis of the epoched data, power spectra were computed for the entire epoch duration using Welch's method for computing signal power across frequencies (referred as power spectral density, see Welch, 1967). Single-trial power spectra were computed by averaging the spectral estimates from nine windows of two seconds (with a 50% overlap) for each epoch. Individual channels power spectra values were extracted and subjected to statistical analyses. Power relative to baseline values (in dB) were compared between conditions across *a-priori* frequency bands (Delta 1-3.5Hz; Theta 3.5-8Hz; Alpha 8-12Hz; Beta 12-30Hz; Gamma 30-80Hz) at each electrode site. The statistical analyses reported here focus on data recorded at frontal and parietal recording sites, consistent with the aims of the study (i.e., investigating frontal and parietal spectral modulations during active behaviour). Correlation of power across frequency bands and recording sites were also computed. Power spectral peaks were defined as the frequency at which the averaged maximal power was found within one of the aforementioned frequency bands for each subject, and both their local frequency and amplitude were subject to analyses.

Following up on the trends revealed by the initial exploratory analyses, the spectral dynamics of the data were examined over time. For this purpose, time-frequency dynamics were estimated through the convolution of Morlet wavelets (3 cycles at lowest frequency up to (1-0.5) x Higher frequency, which corresponded to a maximum of 20 cycles at 40Hz in the present study) across epochs duration. Event-Related Spectral (ERS) estimates were computed from 2Hz to 30Hz, with a four to one spectral resolution ratio and a time resolution of 50ms (smoothed through zero-padding ratio of eight to one for plotting purposes only).

Event-Related Spectral Perturbations (ERSP) were computed by normalizing Event-Related Spectra using a divisive baseline on a single-trial basis (gain model, see Grandchamp & Delorme, 2011). The data used as a baseline consisted of a free walking time window of 10 seconds preceding the beginning of a trial. During the baseline, the participants were simply walking across a long corridor without any specific directions or instructions. The timing of the baseline periods was also timestamped manually by the experimenter.

6.3. Results

6.3.1. Walking speed

There was no difference in walking speed between the control (mean = 4.67 km/h, SD = .308) and the memory workload (mean = 4.64 km/h, SD = .305) condition [t(9)= .820, p = .433, d = -.259, BF_{10} = .409]. Walking speed was strongly correlated across the two conditions (r_9 = .940, p < .001, two-tailed), suggesting high within-subject consistency in walking pace.

6.3.2. Task performance

Due to the nature of the experimental conditions contrasted (i.e., direction to memorize against nothing), there was no measure of task performance for the control condition. Nevertheless, it is important to note that task performance was perfect across all participants in the memory workload condition (left and right confusions, if any, were resolved during practice trials).

6.3.3. Power spectra analyses

Mean power spectra were computed across each channel, for both conditions. In order to investigate hypotheses regarding spectral modulations associated with memory demands during the active behaviour, statistical analyses have been performed on channels at frontal and parietal recording sites. Previous research has shown that human frontal theta activity is maximal near the midline during a range of demanding cognitive tasks (Gevins, Smith, McEvoy, & Yu, 1997). Moreover, surface frontal electrodes have shown to be sensitive to activity related to spatial navigation and memory theta networks (see section 3.1.2.2). The following statistical analyses have therefore focused on the frontal electrode "Fz" to investigate hypotheses relative to frontal spectral modulations (see Figure 6.2). Moreover, spectral modulations associated with memory and spatial navigation have also been reported at parietal recording sites (see section 3.1.2.1). In order to maintain a consistent spatial distribution between electrodes included in the analyses, the midline parietal electrode "Pz" was subjected to statistical analyses to investigate parietal spectral modulations. Based on this hypothesis-driven approach to the definition of channels of interest, further statistical tests were carried out on the average power within each frequency band to evaluate power spectral differences between conditions. In addition, analyses based on power peaks were performed to explore power peaks distribution within frequency bands and investigate potential differences in terms of power spectral activity based on the individuals' power peaks.

6.3.3.1. Mean spectral power across frequency bands

Mean frontal spectral power

Frontal spectral activity was significantly higher in the memory condition in comparison to the control condition in both the delta [$t(9) = 3.932$, $p = .003$, $d = 1.243$, $BF_{10} = 14.697$] and the theta bands [$t(9) = 2.875$, $p = . 018$, $d = .909$, $BF_{10} = 3.831$]. There was no significant difference observed between the two conditions within the alpha [$t(9) = .679$, $p = .514$, $d = .215$, $BF_{10} = .375$] and beta bands [$t(9) = 2.028$, $p = .073$, $d = .641$, $BF_{10} = 1.326$].

To investigate the relationships between frequency bands in terms of spectral power modulations, cross-frequency correlations were performed on the mean spectral power recorded at frontal site for each condition. In both the control and memory conditions, delta and theta power were found to be positively correlated (control: $r_9 = .894$, $p < .001$; memory: $r_9 = .775$, $p = .008$) suggesting a strong relationship between lower frequency bands in terms of power spectral modulation. This may be explained by a skewed distribution of power peaks towards the higher and lower ends of the delta and theta bands respectively. This issue will be examined through power peaks-based analyses.

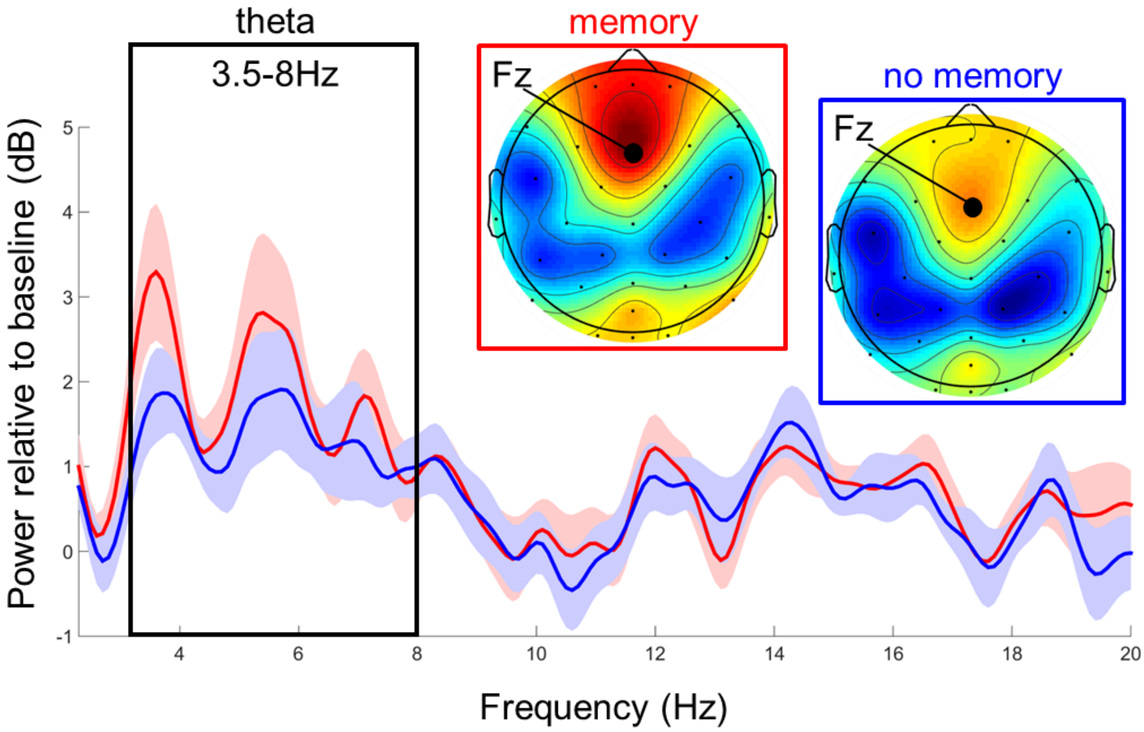

Figure 6.2. Grand averaged power spectra recorded at frontal electrode 'Fz' for both conditions across all participants (N=10) for the whole epoch (10 seconds duration, centred on reaching the middle of the corridor). Similar pattern of activity was observed across recording conditions with an increase of power within the Theta band (most prominently at frontal electrodes) in the memory workload condition compared to the control condition.

Mean parietal spectral power

There was no significant difference between the memory and control conditions in terms of mean spectral power recorded at parietal site in any of the frequency bands investigated [delta: t(9) = 1.169, p = .272, d = .370, BF_{10} = .535; theta: t(9) = .539, p = .603, d = .171, BF_{10} = .349; alpha: t(9) = 1.123, p = .290, d = .355, BF_{10} = .514; beta: t(9) = .197, p = .848, d = .062, BF_{10} = .314].

6.3.3.2. Power peak-based analyses

Performing power peak-based analyses provides additional insights into the most prominent spectral features contributing to spectral power within each frequency band. The characterization of a power peak sheds light on the most responsive frequency to the experimental manipulations, potentially increasing the sensitivity of statistical analyses to band-specific local features. Moreover, the distribution pattern of power peaks within a frequency band may be informative of potential sub-bands or cross-frequency bands effects.

Consistency between results issued from mean spectral power and power peak-based analyses may be interpreted as an indicator of the robustness of the effects reported.

Frontal power peak frequency

The frequencies at which frontal power peaks were observed within *a-priori* frequency bands were not found to be different between recording conditions [delta, t(9) = .167, p = .871, d = -.053, BF_{10} = .313; theta, t(9) = 1.337, p = .214, d = -.423, BF_{10} = .624; alpha, t(9) = .108, p = .917, d = -.034, BF_{10} = .310; beta, t(9) = 1.053, p = .320, d = .333, BF_{10} = .485]. Interestingly, mean power peak frequencies follow a normal distribution around the central frequency for theta (memory: mean = 4.730, SD = .953, Kolmogorov-Smirnov’s test of normality (K-S): p > .05; control condition: mean = 5.090, SD = .916, K-S: p > .05) and alpha (memory: mean = 10.230, SD = 1.956, K-S: p > .05; control condition: mean = 10.300, SD = 1.861, K-S: p > .05) frequency bands. Power peaks within the beta band was mainly found in the lower range of the frequency band (memory: mean = 22.990, SD = 8.925, K-S: p < .05; control condition: mean = 20.040, SD = 6.716, K-S: p > .05), while delta power peaks were majorly found in the upper end of the band (memory: mean = 2.760, SD = 1.039, K-S: p < .05; control condition: mean = 2.780, SD = 0.890, K-S: p < .05).

Frontal power peak amplitude

Peak power recorded at frontal site (‘Fz’ electrode) was significantly higher in the memory condition within delta [t(9) = 4.560, p = .001, d = 1.442, BF_{10} = 31.504] and theta [t(9) = 4.957, p < .001, d = 1.568, BF_{10} = 50.102] bands. There was no significant difference between the two conditions in alpha [t(9) = .116, p = .910, d = -.037, BF_{10} = .311] and beta [t(9) = .729, p = .485, d = .230, BF_{10} = .386] power peaks. Peak power recorded within delta and theta bands was strongly correlated for both conditions (memory: r_9 = .913, p <.001; control condition: r_9 = .773, p = .009, two-tailed), suggesting an association between the two lower frequency bands (delta and theta) in terms of spectral power.

Parietal power peak frequency

The frequencies at which parietal power peaks were observed within *a-priori* frequency bands were not found to be different between recording conditions [delta, t(9) = 1.252, p = .242, d = .396, BF_{10} = .576; theta, t(9) = .139, p = .892, d = .044, BF_{10} = .311; alpha, t(9) = .200, p = .846, d = .063, BF_{10} = .314; beta, t(9) = .873, p = .405, d = .276, BF_{10} = .424]. Interestingly, mean power peak frequencies follow a normal distribution around the central frequency for theta (memory: mean = 4.70, SD = 1.181, K-S: p > .05; control condition: mean = 4.74, SD = 1.148, K-S: p > .05) , alpha (memory: mean = 10.85, SD = 1.555; control condition: mean = 10.72, SD = 1.702) and beta (memory: mean = 20.92, SD = 7.249; control condition: mean = 18.85, SD = 6.169) frequency bands. Power peaks within the delta band was mainly found in the upper range of the frequency band (memory: mean = 2.32, SD = .692, K-S: $p < .05$; control condition: mean = 2.06, SD = 0.779, K-S: $p < .05$).

Parietal power peak amplitude

Similar to the results found for mean spectral power recorded at parietal site, there was no significant difference between conditions in terms of power peak amplitude within the delta [t(9) = 1.920, p = .087, d = .607, BF$_{10}$ = 1.167], theta [t(9) = .829, p = .429, d = .262, BF$_{10}$ = .411], alpha [t(9) = .221, p = .830, d =.070, BF$_{10}$ = .315] and beta [t(9) = 1.813, p = .103, d = .573, BF$_{10}$ = 1.032] bands.

		Delta 1-3.5Hz	Theta 3.5-8Hz	Alpha 8-12Hz	Beta 12-30Hz
Fz	Mean spectral power	🟩 **	🟩 *	🟥	🟥
	Power peak amplitude	🟩 ***	🟩 ***	🟥	🟥
	Power peak frequency	🟥	🟥	🟥	🟥
Pz	Mean spectral power	🟥	🟥	🟥	🟥
	Power peak amplitude	🟥	🟥	🟥	🟥
	Power peak frequency	🟥	🟥	🟥	🟥

* = $p < .05$, ** = $p < .01$, *** = $p < .001$

Table 6.1. Summary of the main results issued from the comparison of mean spectral power and power peak measures between the two conditions (memory and no memory). Paired-samples t-tests were applied to contrast the two conditions measures across both frontal (Fz) and parietal (Pz) electrodes. Comparisons reaching statistical significance thresholds are reported using an annotation system indicative of the significance level.

6.3.4. Spectral power changes over time

Power spectral analysis of the entire duration of the epoch highlighted a significant increase of frontal theta activity associated with memory workload. In contrast, there was no significant effect of the memory demands on the data recorded at the parietal site. As discussed in Chapter 2, however, the discrete quantification of spectral power offers really high frequency resolution at the expense of temporal resolution. Therefore, non-stationary dynamics and modulations of spectral activity associated with the position of the participant in the environment cannot be captured using the average power over a long period of time (10 seconds in the present experiment). In order to explore spectral dynamics associated with memory over the course of the epoch duration, time-resolved spectral analyses need to be applied. To achieve this purpose, difference in power between conditions (ERSP) were averaged within five consecutive bins of two seconds to discretely evaluate spectral power course across the epoch time window (based on the approach used in Onton, Delorme, &

Makeig, 2005). Repeated measure ANOVA were then carried out for each frequency band to investigate the effect of time as a factor (divided into 5 consecutive bins of 2 seconds) on spectral power. Based on the dichotomic pattern of power peaks distribution observed within the theta band (see Frontal power peak frequency results in section 6.3.3.2.), further analyses will investigate the lower (3.5-6Hz) and upper (6-8Hz) theta sub-bands separately.

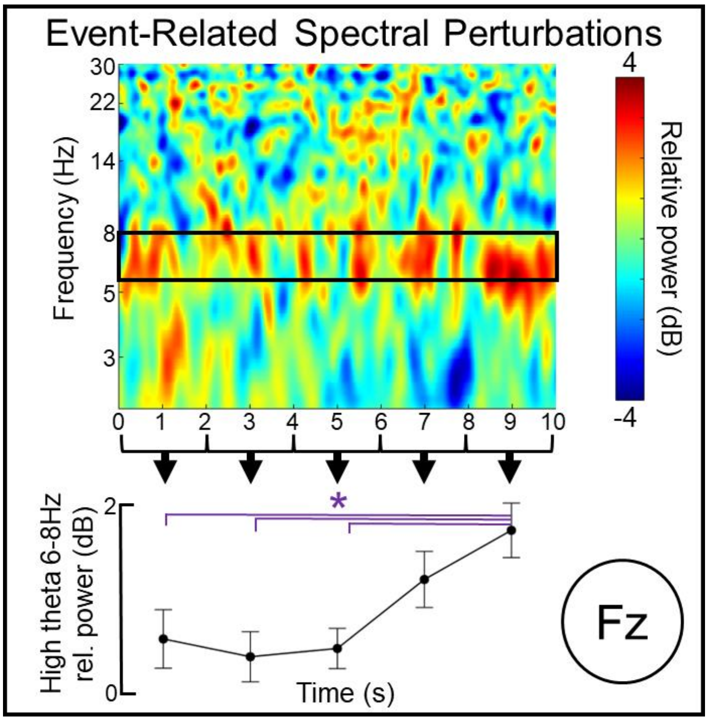

Figure 6.3. Top: Event-Related Spectral Perturbations induced by the memory effect at frontal electrode (Fz). Power values were computed relative to the average spectral activity recorded during the control condition. Bottom: Mean ERSP within the upper-theta sub-band (6-8Hz) was independently computed within five consecutive time bins (of 2 seconds each). Spectral activity related to the memory effect progressively increased within the upper-theta sub-band throughout the trial.

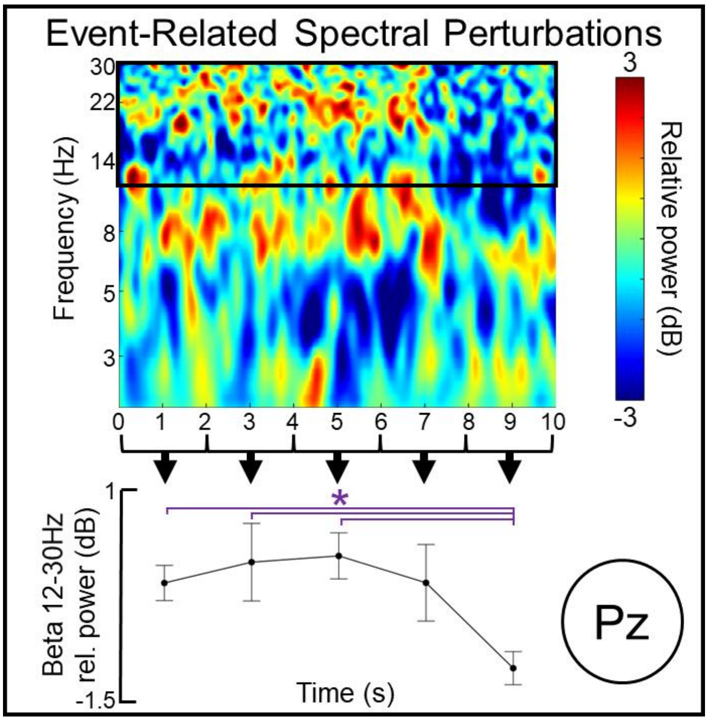

Figure 6.4. Top: Event-Related Spectral Perturbations induced by the memory effect at parietal electrode (Pz). Power values were computed relative to the average spectral activity recorded during the control condition. Bottom: Mean ERSP within the beta band was independently computed within five consecutive time bins (of 2 seconds each). A significant decrease of parietal beta power related to the memory effect is observed towards the end of the trials. A similar pattern (although les prominent) of spectral perturbations was observed within the alpha bandwave.

6.3.4.1. Frontal Event-Related Spectral Perturbations

Relative power spectral activity was not affected over time within the delta band [F(4,36) = 2.426, p = .066, η^2 = .212], the whole theta band [F(4,36) = 1.513, p = .219, η^2 = .144], the lower-theta sub-band [F(4,36) = 1.396, p = .255, η^2 = .134], the alpha band [F(4,36) = 2.654, p = .059, η^2 = .218], nor the beta band [F(4,36) =.289, p = .883, η^2 = .031]. However, there was a main effect of time on relative power within the upper-theta sub-band [F(4,36) =4.304, p = .006, η^2 = .324].

Post-hoc paired samples t-tests revealed that upper-theta power was significantly higher at the end of the trial than in the first [t(9) = 3.227, p = .010, d = 1.020, BF_{10} = 6.020], second [t(9) = 3.187, p = .011, d = 1.008, BF_{10} = 5.723], and third [t(9) = 3.635, p = .005, d = 1.150, BF_{10} = 10.128] time bins (see Figure 6.3). Bayes factors further suggest substantial and strong evidence for the increase of upper-theta power observed in the last time bin. Mean upper-theta power recorded in the two last time bins did not significantly differ [t(9) = 1.114, p = .294, d = .352, BF_{10} = 0.510]. The first three segments did not present any significant difference in terms of upper-theta power either. Upper-theta activity recorded within the fourth segment was significantly higher than in the third segment [t(9) = 2.803, p = .021, d = .886, BF_{10} = 3.494], although the Bayes factor indicates that this difference is rather weak and could be interpreted as anecdotical.

6.3.4.2. Parietal Event-Related Spectral Perturbations

Relative spectral activity recorded at parietal electrode was not significantly affected over time within the delta band [F(4,36) = .800, p = .533, η^2 = .082], nor the lower-theta [F(4,36) = 1.748, p = .161, η^2 = .163] or upper-theta [F(4,36) = .122, p = .974, η^2 = .013] sub-bands. Relative power within the alpha band was only marginally affected over time [F(4,36) = 2.570, p = .054, η^2 = .222]. Power recorded within the beta band was significantly affected over the time course of trials [F(4,36) = 3.041, p = .029, η^2 = .253].

Beta power recorded in the middle of each trial (third time bin) was significantly higher than in the first [t(9) = 2.395, p = .040, d = .757, BF_{10} = 2.079] and fifth [t(9) = 2.803, p = .021, d = .886, BF_{10} = 3.494] time bins. Beta relative power recorded within the second [t(9) = 1.385, p = .199, d = .438, BF_{10} = 0.654] and fourth [t(9) = 1.924, p = .087, d = .608, BF_{10} = 1.172] time bins was not significantly different than beta activity recorded within the third portion of the trials. A significant decrease of beta power was observed in the last portion of the trials in comparison to the second [t(9) = 2.326, p = .045, d = .736, BF_{10} = 1.909] and third [t(9) = 2.369, p = .042, d = .749, BF_{10} = 2.013] time bins (see Figure 6.4).

6.4. Discussion

6.4.1. Main results

The present results highlight an increase of frontal activity across lower frequency bands (delta and theta) when participants were performing a spatial memory task. The high correlation between spectral power within the delta and theta bands suggests a strong relationship of the rhythmic modulations observed across these two bands. Moreover, the skewed distribution of delta power towards the upper end of the band further suggests that the effect observed essentially spans over an extension of the traditional human theta band (ranging from 2-8Hz). These results are in line with intracranial EEG studies showing strong memory effects (episodic-memory encoding, working memory) at hippocampal sites across both theta and sub-theta bands (Based on the hypothesis-driven approach, and for clarity, the memory effect observed in the present experiment will be discussed as a frontal theta modulation.

As outlined in the introduction, theta rhythm has been linked with a wide range of cognitive processes, with a large body of evidence highlighting its role in supporting memory and spatial abilities. This result is in line with previous findings issued from both animal and human intracranial recordings highlighting theta power increase associated with the encoding and retrieval of spatial information as part of a spatial-memory network (i.e., involving frontal and parietal cortices and subcortical structures such as the hippocampus). More specifically, the present findings are analogous to patterns of theta activity recorded at frontal and mediofrontal sites that have been linked with memory (see section 4.1.2.2 on mPFC). Importantly, the present findings demonstrate that brain dynamics reflecting cognitive processing, in the present case memory processes, can be recorded non-invasively under natural navigational circumstances in a real-world environment.

Strikingly, the time course of spectral power within the upper-theta band increased as the participants were moving towards the objective. This finding is consistent with the bursts of theta power that have been previously reported as participants were getting closer to intersections in a virtual maze navigation (Bischof & Boulanger, 2003). Whether the increase of frontal theta observed in the present study reflects spatial cognitive processing during real-world behaviour (i.e., approaching the destination), or reflect goal-oriented dynamics (i.e., relevance of information for the task at a specific position and time) remains however unclear. The specific modulation of the upper-theta sub band over the course of the trials observed in the present study is also in line with recent findings highlighting hippocampal upper-theta power modulations during a real-world navigation task using intracranial recording (Bohbot, Copara, Gotman, & Ekstrom, 2017). In their study, Bohbot et al. (2017) demonstrated that hippocampal dynamics related to real-world navigation were most prominent in the upper-theta frequency range (6-9Hz) in comparison to virtual environments. Interestingly, upper-theta dynamics associated with spatial navigation are similar to the range of oscillations related to maze navigation in rodents. Taken together, these results suggest that human theta rhythmicity associated with spatial navigation may be closer to theta oscillations typically recorded in rodents than previously thought. Furthermore, it can be speculated that these differences of theta rhythmicity may be related to the multimodal and dynamic experience of the real-world, emphasizing the importance of movement and sensorimotor information (vestibular, motion and visual input) for the capture of brain dynamics accurately reflecting natural cognitive experiences and further strengthening the case for a real-world approach applied to the study of human cognition. Indeed, the dynamic changes of theta power observed within trials seem to indicate context-dependent factors influencing brain rhythmicity and potentially yield an impact on spatial-related cognitive processes. It is worth noting that the experimental manipulation did not lead to significant changes in walking pace, which suggests that walking demands did not compete with the performance of the task. This additional finding compliments previous reports suggesting that spatial working memory performance and walking speed were not related in healthy subjects (Kline, Poggensee, & Ferris, 2014).

6.4.2. Not just motion related

The recording, and by extension the interpretation, of brain signals acquired during real-world behaviour such as spatial navigation requires caution. As demonstrated in the animal literature, theta activity is associated with a wide range of active behaviours. Amongst these behaviours, locomotion appears to be strongly associated with theta activity. Moreover, previous research in humans has shown that walking induces spectral perturbations phase locked to gait cycle, with faster walking pace resulting in significant power increase in slow frequency bands. Since the aim of the present study was to capture brain activity related to spatial memory, it is important to address if and how theta dynamics relate to locomotion. In the present study, strong within and inter-subject consistency in terms of walking pace were observed, suggesting that the participants were walking at regular pace throughout the experiment. Moreover, as noted above, there were no statistically significant difference induced by the experimental manipulation on walking speed, which indicates that walking pace was not altered by memory workload. Therefore, it can be argued that it is unlikely that the spectral differences observed between the two experimental conditions are associated with changes of walking dynamics within the frame of this experiment.

Nevertheless, gait dynamics were not formally measured within the frame of this experiment, and therefore the presence of changes in the strides length or in the gait cycle frequency, which could have resulted in the phase-locking of slow brain rhythms such as theta, cannot be assessed. Even though the main difference observed between conditions coincided with the plausible range of the frequencies typically modulated by gait dynamics, the effect was not observed in the following harmonics (12-14, 16-18, 20-22Hz) of these frequencies between recording conditions. Indeed, Gwin, Gramann, Makeig & Ferris (2010) reported that increase in power related to gait dynamics were reliable effects (in comparison to modulations induced by a visual oddball task) with resonances that could be observed across several harmonics. Thus, if the difference in spectral power between conditions was purely a by-product of gait-related activity, it would have been expected to find significant differences across a wider range of frequencies, namely the harmonics of the fundamental stepping frequency (see Chapter 8).

6.4.3. Limitations

This proof-of-concept experiment achieved its main purpose by successfully demonstrating the feasibility of recording spectral dynamics related to spatial navigation. Nonetheless, the present study also highlights potential pitfalls restricting the interpretations that can be drawn from the results. A first limitation lies in data quantity issues, potentially resulting in the loss of statistical power to identify potential differences between conditions, especially at higher frequency, where spectral power modulations are more subtle (Cohen, 2017). This issue is related to a mixture of factors; including the nature of the task and experimental design inherently limiting the number of trials that could be recorded for each participant, the low number of participants included in the study (mostly due to rejection of entire datasets due to channel disconnections and timestamping issues), and finally the low number of trials that survived the processing procedures.

A second limitation of the present study concerns the limited range of frequencies investigated. Spectral activity over 40Hz has not been subject to statistical analyses due to the prominent distortions of the signal around 50Hz (and following harmonics) related to line noise. The classic processing approach to deal with line noise through the application of a notch-filter did not produce satisfactory results here because it drastically attenuates the strength of all of the signals around 50Hz. Therefore, instead of making a hole in the power spectrum, the data considered for analysis did not include power above 40Hz. Even though this has not been formally assessed within this study, it is plausible that a substantial percentage of trials discarded may be due to the variance in high-frequencies related to line noise.

A third limitation is that walking speed was only characterized discretely and walking dynamics were not captured. The characterisation of brain dynamics related to walking has been a growing field over the last decade. Treadmill studies have reported spectral dynamics related to specific stages of the gait cycle (e.g., heel strikes). Theta and delta power have been found to be associated strongly with these gait-related events (Castermans, Duvinage, Cheron, & Dutoit, 2014; Presacco, Goodman, Forrester, & Contreras-Vidal, 2011). It would therefore be interesting to explore how, in human participants, brain dynamics are affected by walking speed, following the current proof-of-concept (see Chapter 8).

The next studies will build upon the current study to address practical issues that resulted in the loss of datasets (i.e., issues related to manual timestamping) and increase signal-to-noise ratio. Moreover, despite the high consistency in walking speed observed within participants, the manual timestamping of trials may not be appropriate to accurately assess walking speed and introduce variance that could overshadow significant differences between conditions. Therefore, future studies require the use of precise timestamping methods that capture walking speed and define epochs boundaries accurately.

Furthermore, contrasting the real-world conditions (i.e., walking and spatial memory) with stationary conditions (e.g., navigation in a Virtual Reality environment with and without navigational instructions) would have shed further light on the nature of the present findings as these comparisons would have indicated whether the effects reported are found in both real and virtual cases and therefore reflect general spatial cognitive processes (i.e., spatial representations of the environment) or if they are only found in real-world conditions which would suggest that they are specifically reflecting the processing of sensorimotor input through the vestibular system (Ferre, 2012, Lopez & Blanke, 2012).

6.4.4. Conclusion and follow-up questions

The present experiment demonstrates the feasibility of recording spectral dynamics reflecting cognitive processes while participants are engaged in a real-world spatial navigation task. Inspired by paradigms commonly used in rodents to investigate cognitive functions, this study involved a combination of spatial navigation, memory processing and active behaviour. Theta brain dynamics have been found to reflect the interfacing of all these aspects of real-world cognitive experiences. Even though the present study specifically assessed memory workload effects on theta rhythmic activity, some confounding factors must be taken into account when interpreting the results.

Firstly, despite the fact that the overall walking pace was found consistent within and across participants, features such as stepping frequency (which may have an important impact on EEG power spectral activity) has not been formally recorded. The contribution of transient changes of gait dynamics within trials to the spectral changes observed in the EEG is therefore unknown. Second, the memory workload condition incidentally involved spatial information which was relevant for the ongoing behaviour to be maintained in participants' memory as they walked through a corridor. Even though the increase of theta activity found in the memory condition suggests that the effect is related to memory workload, the specific nature of this effect (i.e., a pure memory effect versus a spatial memory effect) cannot be distinguished on the basis of this initial experiment. Moreover, the time course of theta power, gradually increasing when reaching the end of the corridor, raises further questions concerning the cognitive processes that may underlie such dynamics. Furthermore, the potential effects of such seemingly context/position-dependent brain rhythmicity may be of particular interest in the understanding of the cognitive underpinnings of spatial navigation in humans. What is perhaps less clear is whether the effect reflects memory processes or the relevance of information for the spatial navigation task. Moreover, the spectral dynamics recorded over the trial course presents both frontal and parietal effects which have been associated with distinct functions (respectively memory and spatial processing). Due to the nature of the task used in the present proof-of-concept study and in the light of the present findings, it is unclear whether the effect observed is purely memory or navigation-related. Therefore, these findings need to be supported by further evidence distinguishing spatial and non-spatial memory workload during active behaviour and theta activity related to a pure spatial navigation task. These issues will be addressed in Chapter 7.

Due to the overlap of theta rhythmicity underlying behavioural activity and cognitive processing documented in the animal literature, characterizing locomotion-related brain dynamics is crucial for the interpretation of modulations associated with cognitive experiences, as in the case of the present experiment. The modulation of brain oscillations related to walking speed, and more specifically the contribution of walking pace to the EEG power spectral activity will be addressed in Chapter 8.

Chapter 7: Specificity of brain dynamics reflecting memory and spatial navigation during real-world navigation

7.1. Introduction

7.1.1. Rationale

The key outcome of Chapter 6 was that frontal theta activity was found to be associated with memory, in the context of a spatial navigation task. The next logical step is to determine whether frontal theta is linked to spatial memory specifically, or if it indexes general working memory. In the traditional EEG literature, frontal theta dynamics have been associated with both memory (Burke et al., 2014; Jensen & Tesche, 2002; Onton et al., 2005) and spatial cognitive processes (Bischof & Boulanger, 2003; Cornwell, Johnson, Holroyd, Carver, & Grillon, 2008; Kahana et al., 1999). Recent theoretical models have moreover proposed that low-frequency oscillations have multifaceted roles during navigation (Ekstrom & Watrous, 2014). Indeed, the relationships between delta and theta dynamics observed during spatial navigation task, has led to the hypothesis that low-frequency oscillations may serve a range of cognitive functions such as memory, sensorimotor integration and spatial navigation. This is particularly relevant here since the effects reported in Chapter 6 within the theta band were also present in the lower frequency band (delta band), and from a functional perspective both memory and spatial processes may have been involved in the performance of the navigation task used in the previous study (see Chapter 6).

In the previous study, frontal theta activity appeared to progressively increase over the time-course of a trial in the memory condition, an effect not found in the delta band. This finding show that frontal theta oscillations can be dynamically modulated over the course of the trial. The robust increase towards the end of the trials, as participants reached the end of the corridors, suggests that theta dynamics may reflect context-dependent cognitive processes. In the present case of navigation, this context-dependency would reflect where and when information required for completion of the task is processed. For example, shortly before reaching an intersection there is a requirement for retrieval of task-related spatial information, in this case related to navigational instructions. However, it is unclear whether the observed dynamics of frontal theta reflects context-dependent and task-related retrieval of information related to spatial memory, or alternatively, if it indexes a context-dependent updating of the body position relative to the destination related to spatial navigation. To clarify the nature of the effect observed, the present study will contrast spatial memory, non-spatial memory and spatial navigation conditions. It is of course possible that no task-related or context-dependent effect may exist in relation to frontal theta dynamics, which would suggest that the time-course effects observed in the previous study was related to general memory retrieval. To investigate this possibility, the present study also includes a condition where participants are instructed to hold information that is not relevant to the spatial or temporal aspects of the navigation in mind.

Consistent with our original hypotheses, the findings in the previous study highlighted frontal theta dynamics associated with a spatial memory task. However, the previous EEG literatures also links both spatial cognitive and memory processes with parietal gamma activation. Unfortunately, the previous chapter did not explore parietal gamma. In the context of the previous study, there was a restriction in the range of the frequency spectrum investigated (1-40Hz), essentially due to line noise and prominent movement-related noise at higher frequencies. In the traditional EEG literature, these issues have been commonly handled through aggressive band-stop filtering that drastically attenuate the contribution of noise, but also affect brain signals comprised within the filtered frequencies (and neighbouring frequencies). The consequence of this double-edge cleaning-process is that the contribution of brain signals within the filtered frequency bands is almost nullified, making the analysis of such filtered frequencies invalid. Fortunately, there have been technical developments between conducting the study reported in Chapter 6 and the current study which allow parietal gamma to be examined. Novel signal processing tools have become available to deal with line-noise and higher-frequency noise (that are typically linked with motion and muscular activity, see section 7.2.4.) using adaptive filtering methods that essentially allow the investigation of higher frequency (gamma band) activity of real-world EEG data, as further discussed in the methods section.

7.1.2. Hypotheses

7.1.2.1. Does frontal theta reflect a spatial memory specifically or a general memory effect?

Chapter 7 investigates whether the frontal theta effect found in Chapter 6 reflects memory processing overall or spatial memory processes specifically. A spatial memory condition during which participants are instructed to hold navigational instructions in memory (directions condition) will be contrasted with a general memory condition during which participants hold non-spatial information in memory (a digit span task). If frontal theta is specific to spatial memory, a difference in theta activity should be observed between the spatial and non-spatial memory conditions. Alternatively, if frontal theta is reflective of a general memory effect, then no difference in frontal theta power will be observed between the spatial and non-spatial memory conditions.

7.1.2.2. Does frontal theta reflect a context-dependent retrieval of information?

In the previous study, spectral activity within the upper-theta sub-band appeared to progressively increase as participants walked through the corridor towards the destination while they were holding navigational instruction in mind. This finding raised further questions regarding the nature of frontal theta dynamics: not only as indexing memory processing but also reflective of context-dependent processes supporting spatial navigation. Additionally, there is ample evidence highlighting links between transient theta dynamics recorded in the hippocampus of rodents, and frontal cortex of monkeys and epileptic patients, with spatial navigation processes occurring at critical moments of the navigation (i.e., when reaching an intersection, prior to turning or reorienting in a three-dimensional environment, see section 6.1.1.4). Notably, frontal theta bursts (transient increase of activation) recorded from surface EEG have been reported in human participants reaching the intersections of a virtual maze (Bischof & Boulanger, 2003). Based on these previous findings, and considering the temporal pattern of theta dynamics observed in the previous study, frontal theta may be reflective of spatial or context-dependent navigational processes. To shed light on this matter, in the current chapter, a pure spatial navigation condition (wayfinding) will be contrasted to the memory conditions. The wayfinding condition should mainly induce spectral dynamic activity associated with spatial processing, as the task involves the retrieval of spatial information stored in memory and the updating of internal representations of the spatial relationships between the body and the environment during navigation.

The time course of theta dynamics within a trial will provide further insight concerning the role of frontal theta. If a similar temporal pattern of frontal theta activation is observed in both the spatial memory condition and the spatial navigation condition, but not in the general memory condition, then frontal theta dynamics can be interpreted as indexing task-related context dependency of cognitive processes. By contrast, if no difference is found between conditions in terms of frontal theta dynamics, this would suggest that the pattern of frontal theta observed in the previous study was merely a general memory effect. If frontal theta dynamics are found to be larger in the spatial memory condition relatively to both the general memory condition and the wayfinding condition, it would indicate that task-related context-dependent effects in frontal theta dynamics found in Chapter 6, was specific to the retrieval of spatial memory information. However, if frontal theta dynamics in the spatial navigation condition is comparatively larger than the spatial navigation and general memory conditions, it would indicate that task-related context-dependent effects in frontal theta dynamics found in Chapter 6 was an effect of the updating of spatial representations associated with spatial navigation. If the latter pattern of results is found, we would need to explore whether the effect is specific to the theta band, because the effect would not be strictly related to memory and therefore modulations in the delta and alpha band would be also expected.

7.1.2.3. Does parietal gamma activity index spatial memory processes?

Investigating the role of high frequency activity within the frame of the present real-world navigation paradigm is especially relevant in the light of recent evidence revealing a relationship between activity in the gamma-band (30-100+ Hz) and working memory load (Griesmayr, Gruber, Klimesch, & Sauseng, 2010; Heusser, Poeppel, Ezzyat, & Davachi, 2016; Howard et al., 2003). Furthermore, high-frequency activity appears to play a crucial role in attention and memory functions by connecting remote brain structures (Harris & Gordon, 2015; Jensen, Kaiser, & Lachaux, 2007). Indeed, gamma oscillations have been conceptualized as a communication gateway between neuronal assemblies that are involved in the process of common information (Colgin et al., 2009; Başar & Güntekin, 2013). According to this view, gamma oscillations reflect the transient tuning of spatially distributed brain structures (i.e., via cells firing in synchrony), allowing the communication between brain structures involved in functional networks such as perception, attention and memory. This neural binding mechanism allows associative brain areas to work together, and also allows multimodal communications to occur (Hanslmayr, Staresina, & Bowman, 2016).

Recent evidence has shown coherence in theta and gamma oscillation patterns during episodic memory tasks (Nyhus & Curran, 2010), and the role of hippocampal gamma in temporally linking the activity of distributed neural structures (Colgin & Moser, 2010).

Moreover, gamma has been shown to be specifically associated with alpha or theta, depending on the type of information held in working memory, and more specifically within the context of spatial information during maze navigation tasks (Alekseichuk, Turi, Amador de Lara, Antal, & Paulus, 2016; Roux & Uhlhaas, 2014). These findings are in line with evidence from both EEG and fMRI studies that have linked parietal gamma dynamics with memory and spatial memory processes within the frame of a spatial memory network linking medial Prefrontal Cortex (mPFC), hippocampus and Associative Parietal Cortex (APC) (see section 6.1.2.1).

What would bring the field forward regarding our understanding the role of Gamma oscillation, in the context of spatial memory in navigation tasks, is a direct comparison between spatial memory, spatial navigation, and general memory. Mirroring the above hypothesis driven approach investigating the spatial memory specificity in frontal theta, the current study explored the same comparisons in parietal Gamma, based on the previous literature. Gamma oscillations may provide further insight regarding the specificity of brain dynamics associated with different types of memory and spatial processes. Consequently, the inclusion of higher frequencies analyses may shed further light on the spatiotemporal patterns of brain activity underlying spatial memory processing during real-world navigation. As was postulated for frontal theta in the above hypotheses, if gamma is associated with general memory processes, no differences in power are expected between the spatial and non-spatial memory conditions. According to that hypothesis, both the general memory and spatial memory conditions should exhibit higher overall gamma activity than the wayfinding condition. A difference in gamma activation between the spatial and non-spatial memory condition may reflect the specificity of gamma activity for task-related memory processes. If the latter is true, the spatial memory is expected to exhibit gamma dynamics reflecting retrieval of information related to the task. Therefore, in the case of a difference between spatial memory and general memory conditions in parietal gamma power, the analysis of the course of gamma activity (i.e., segment-based quantification described above to explore context-dependency frontal theta) would strengthen the case for such specificity if the dynamics appear to be modulated only in the spatial memory condition.

7.2. Methods

7.2.1. Participants

Twenty-four participants (age range = 18-40, mean = 22; 22 females) completed this study. The participants did not report any of the exclusion criteria commonly used within the frame of EEG research on healthy populations (for more details see section 3.2.1). Written consent was obtained from all participants. Datasets from one recording session presented abnormal noise due to substantial variations in electrode impedance throughout the recording. These datasets were discarded because the amount of data surviving the processing procedure was not sufficient to proceed with further analyses. The analyses reported in the results section have therefore been performed on the remaining datasets, recorded from the other 23 participants.

7.2.2. Experimental design

The present study aimed to investigate brain dynamics related to memory during real-world behaviour. More specifically, this experiment aims to address the pending question of the specificity of frontal theta and parietal gamma oscillations as either reflective of spatial memory or spatial navigation processes. For this purpose, brain activity has been recorded under four conditions: 1) a “control” condition where participants were walking from one point to the other without having to hold any specific information in mind, guided between corridors by the experimenter; 2) a “directions” condition where the participants were instructed about the directions to follow at the beginning of each trial, through 2 corners; 3) a “numbers” condition where participants had no directions or wayfinding instructions of any kind, but instead had to recall three digits upon reaching the end of the trial; and 4) a “wayfinding” condition where participants were asked to move to a landmark point previously learned. This condition involves both the retrieval of spatial information relative to the position of the different landmarks that were acquired during previous experiences (i.e., completion of trials in other conditions) and the updating of an egocentric-based representation of the participants’ location, with regards to the destination, in order to select a relevant route. The wayfinding condition was always carried out at the end of the recording session because of the requirement for previous experiences of the environment to integrate landmarks positions. The order of the other conditions was, however, counterbalanced across participants.

In order to investigate whether the temporal dynamics of spectral activity were reflective of task-related and/or context-dependent processing, or simply related to changes in terms of cognitive workload, the initial recording of single corridors used in Chapter 6 was extended to a series of three corridors. A corollary of this change is that the numbers of navigational instructions to hold in mind would be greater, potentially increasing the cognitive workload associated with the induced memory effect. Consequently, the number of items that participants were required to hold in working memory in the directions and the numbers conditions were matched and kept consistent across trials. Due to the architecture of the building and practical considerations regarding the length of the experiment and total walking distance, three turns appeared to be the best compromise between ensuring a memory effect and the aforementioned limiting factors.

Each trial involved walking through three corridors and EEG data was segmented accordingly into three separate segments for each trial. In the conditions that did not require participants to maintain instructions about the route (i.e., the ‘control’ and ‘numbers’ conditions) participants were given directions as they went along in an ‘online’ fashion. In the conditions that did require participants to maintain instructions about the route, they were given directions at the start of the trial either in the form of left/right directions (in the ‘directions’ condition) or high-level wayfinding instructions in the form of a location as an objective (in the ‘wayfinding’ condition). The participants completed four trials for each task condition, leading to a total of 16 trials, each including three segments corresponding to the corridors that were traversed during the trial.

7.2.3. Material

Throughout the study the participants were navigating through an H-shaped maze with a central corridor common to all trials (see Figure 7.1). Within each trial participants walked through three segments, corresponding to the corridors that were traversed during the trial. These segments were 20 meters long and were consistently spaced (i.e., 20 meters from each other), allowing for transition periods during which ‘online’ instructions for the ‘control’ and ‘numbers’ conditions were given to the participants. Similar to the previous study, EEG data was epoched based on a time window around the middle of the corridor. Given the high within and between-subjects consistency in terms of walking speed, minimal trial length was found to be similar to the previous study. The time window used for epoch extraction was 10 seconds long (centred around a trigger timestamping the crossing of the middle of the corridor).

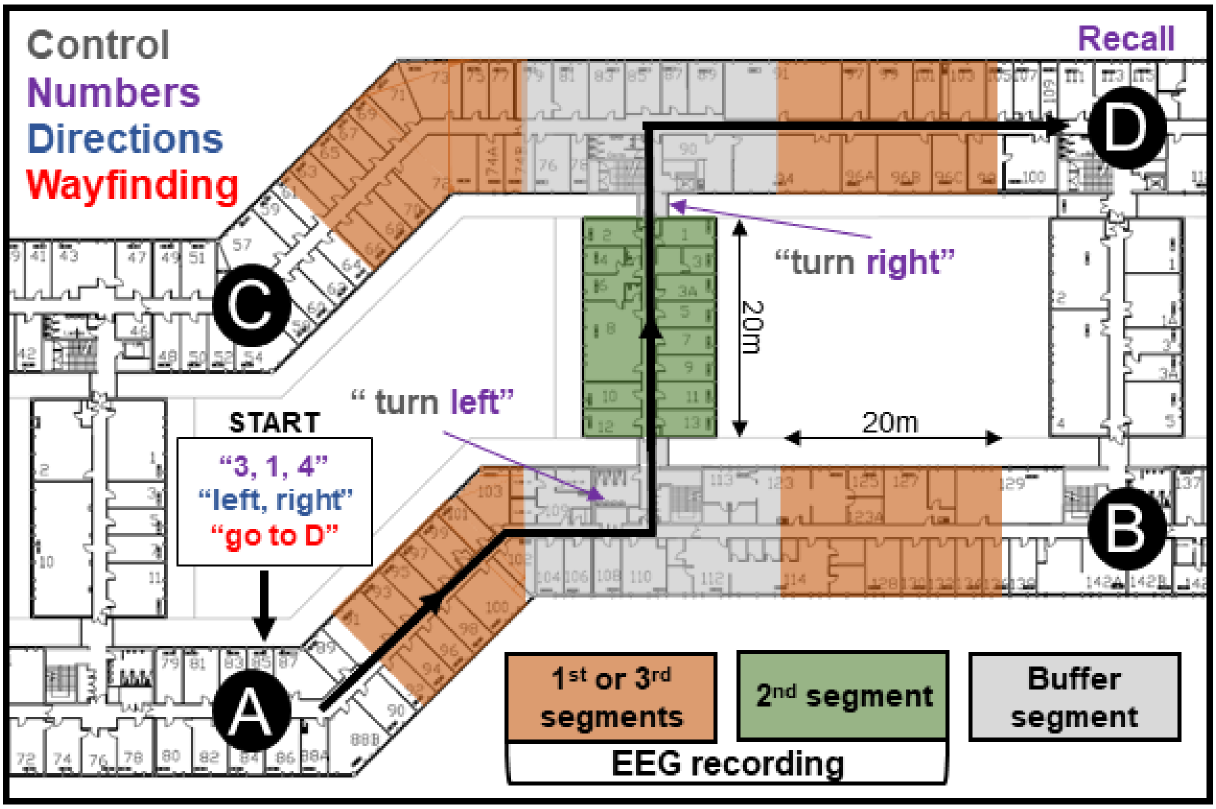

Figure 7.1. Representation of the experimental setup using an H-shaped maze formed by the corridors of the building's layout as pictured. The experimental conditions and example of instructions given across these conditions during a trial going from point A to point D have been colour coded (the "control" condition in black, the 'numbers' condition in purple, the 'directions' condition in blue, and the 'wayfinding' condition in red). Orange sections are alternatively first or last (third segment of a trial). The green segment is common to all trials. The grey segments were used as buffer zone, where participants received information for the next trial, or online instructions in the case of both control and numbers conditions. Landmarks A, B, C and D were identified by wall signs that were not visible from the other side of the corridor. Landmark positions were counterbalanced across participants.

The participants were equipped with a backpack containing the EEG amplifier and data storage and a headcap filled with 32 electrodes (see section 3.2.3.1). During the experiment, participants were followed by the experimenter, who provided them with the instructions, as described in Chapter 6. Infrared-based motion sensors were used to send triggers to the EEG trace and increase recording accuracy of experimental events (see Figure 7.2). The motion sensors were placed at the beginning and at the end of each corridor segment. In comparison to the manual registration through button pressing used in the previous study, the motion sensors increased the event timestamping accuracy. Even though the detection rate was high (82% of triggers were correctly sent to the amplifier), manual registration was simultaneously used to ensure that the timing of trials which both triggers had not been detected could nevertheless be retrieved. The experimenter therefore sent a trigger through button pressing when participants reached the middle of the experimental segments. In the case of a missing trigger from the motion sensors, the timing of the manual trigger was used to extrapolate the missing trigger's timing by mirroring the trigger timing. There was no trial with more than one motion sensor trigger missing, therefore the event timings have been successfully retrieved across all trials for all the participants. The walking speed across each segment was computed by dividing the duration between the two motion sensors from the length of the segment (which was kept consistent).

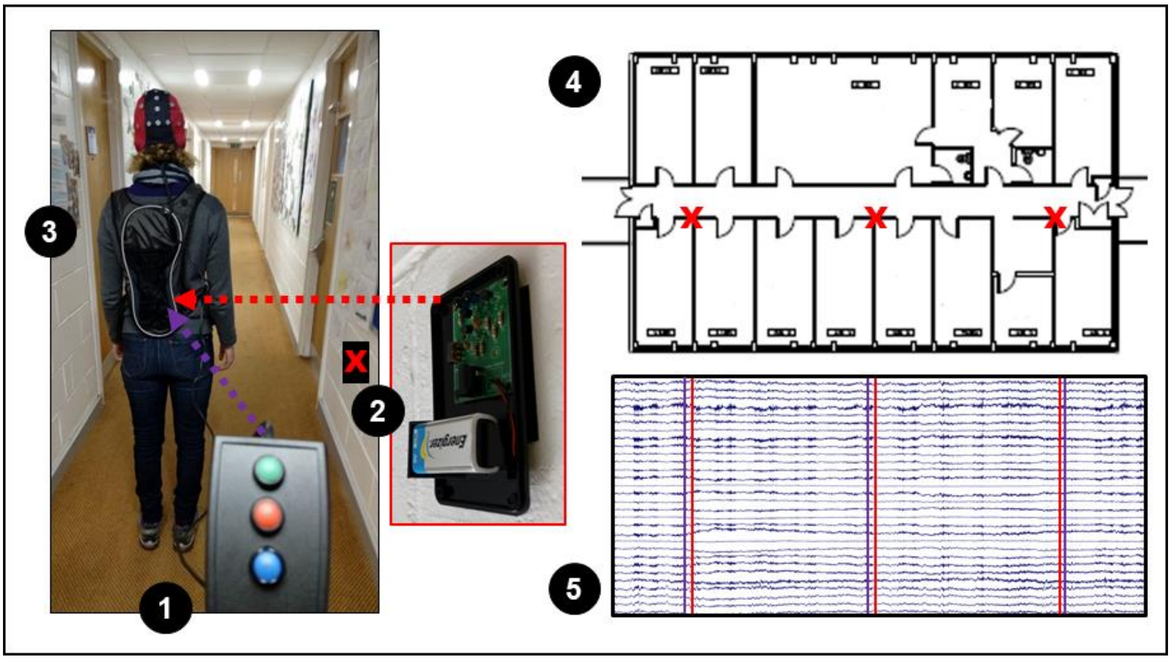

Figure 7.2. Methods used to acquire accurate timing of participants' position within trials. [1] A remote command was controlled by the experimenter to manually encode the crossing of experimental position markers. This approach was already used in Chapter 6. [2] Relatively small devices producing a focused infrared beam were placed on the walls at relevant experimental locations. [3] Participants were equipped with a backpack containing the EEG system (amplifier and data acquisition tablet) and sensors specifically sensitive to the light frequency emitted by the infrared beams placed on the walls. [4] Position of the infrared-emitting devices, marking the beginning, middle and end of experimental segments. [5] Both the manual activation of the remote command and the detection of infrared light send triggers to the amplifier that are used to timestamp the continuous EEG recording.

7.2.4. EEG data processing

EEG data were processed using the EEGLAB (Delorme & Makeig, 2004) open source toolbox for MATLAB (version R2014b, The MathWorks Inc.) and custom-made scripts. In a first preprocessing step the continuous data was visually examined and the portions of the EEG trace displaying extreme levels of noise (e.g., channel disconnections) were manually discarded. The continuous data was then re-referenced offline to the average of all channels.

Data was processed using a two-step parallel routine designed to optimize ICA decomposition. In a first step the datasets were band-pass filtered with the successive application of a low-pass filter of 20Hz and a high-pass filter of 1Hz. Then the continuous EEG data was split into consecutive epochs of 1 second (that were not related to experimental events), and subjected to statistically-based rejection methods (using a threshold of three standard deviations around the mean). An extended Independent Component Analysis (infomax ICA algorithm, see Bell & Sejnowski, 1995) was performed on these remaining dummy epochs. The ICA features obtained were then back projected to the initial non-filtered dataset.

In a second processing step, the initial continuous datasets were band-pass filtered from 0.15 Hz (−6 dB cut-off, filter order 16500) to 120 Hz. As discussed in Chapter 6 (section 6.4.3), the range of the frequency spectrum investigated was limited from 0.1 to 40Hz, mainly due to unsatisfactory results in notch-filtering line noise at 50Hz. Indeed, the application of a notch-filter leaves a considerable ‘hole’ in the frequency spectrum, causing distortions in the neighbouring frequencies which would invalidate the characterization of power across a substantial part of the gamma band. Prior to the processing of the present study data, a novel processing approach has been developed to deal with line noise and high-frequency noise, through the use of targeted filtering applied in both the frequency and the time domain (Mullen, 2016, CleanLine plugin for EEGlab toolbox). An adaptive sliding window filter was therefore applied to selectively attenuate line noise at 50Hz without substantially contaminating neighbouring frequencies. Due to our hypotheses, only frequencies within the 1-80Hz range have been included in further analyses, effectively excluding the frequencies at the ends of the spectrum which may contain distortions introduced by the high and low-pass filters.

The ICA components indicating common artefacts such as eye blinks, eye movements and heartbeats were removed. After this ICA-based data pruning, the continuous datasets were then epoched around the onset of events (-7000 to 7000 ms). Time-frequency computations were performed on the extended epochs to compensate for edges distortions, and the output was subsequently trimmed to a length of 10 seconds (consistent with the epoch duration reported in Chapter 6). The epochs dominated by artifacts were identified using the probability and kurtosis criteria implemented in EEGLAB (using three standard deviations from the mean as thresholds) and improbable epochs were subsequently rejected from further analysis. Epochs were then split based on their corresponding experimental condition. Each trial contained three segments corresponding to the corridors that were traversed during the trial; a distinction was made between the epochs associated with each different segment. During analysis of the data, segments were treated in two ways. In the initial power spectral analysis, the different segments of a trial have been averaged together to extract the mean spectral activity throughout the trial, induced by the cognitive task at hand. By contrast, the second part of the analyses will explore the dynamic changes occurring throughout a trial by contrasting spectral power recorded during the different segment of a trial, effectively characterizing the time-course of spectral activity for each condition.

7.2.5. Data analyses

For the EEG data, mean power spectral activity across the entire trial was quantified separately for each experimental condition, and spectral dynamics over time (Event-Related Spectra, ERS) were computed for each segment of each condition. Normalization of mean power spectra and ERS of the experimental conditions (numbers, directions and wayfinding) was performed by using the average power of the control condition as a subtractive baseline (based on a theoretical additive model, see Grandchamp & Delorme, 2011). This departure from the baseline correction procedure used in the previous study is required because the continuous succession of trials and segments within trials was not suitable for a single-trial based baseline subtraction approach. Indeed, this approach requires that a baseline period systematically precedes each trial/segment, which was not part of the design of this study. The average of single-trial ERSP (Event-Related Spectral Perturbations) was then computed for each of the three segments across the three experimental conditions. Power spectral activity across frequency bands was then discretely quantified by averaging power recorded across frequencies within the *a-priori* Delta (1-3.5Hz), Theta (3.5-8Hz), Alpha (8-12Hz), Beta (12-30Hz) and Gamma (30-80Hz) bands. Following the distinct patterns of theta dynamics reported in the previous study, power within the lower (3.5-6Hz) and upper (6-8Hz) theta sub-bands were computed and contrasted separately.

Following up on the results reported in Chapter 6, and based on previous literature linking frontal theta and parietal gamma dynamics with memory and spatial cognition, the analyses have focused on midline frontal (Fz) and parietal (Pz) electrode sites. Similar to the approach used in the previous study, power spectra were computed within a consistent time window centred on the middle of the corridors. Each trial contained three segments for which power spectra and time-frequency decomposition were computed independently. As noted above, unlike in the previous experiment, baseline normalization was performed using the mean power spectral activity recorded during a control condition, rather than the subtraction of the mean spectral activity recorded during a baseline period preceding the experimental time window. This difference is due to the specific nature of the experimental design used, which aimed to characterise of spectral activity over consecutive segments within trial. Due to the consequent absence of consistent baseline periods (i.e., activity not related to the experimental task) preceding the different segments of a trial, the use of trial-based normalization, as used in Chapter 6, cannot be applied in the current analyses.

The rest of the analyses followed a similar approach to the previous study, primarily focusing on the quantification of overall spectral changes for each condition (see section 6.2.6) as a first stage of analysis, followed by a quantification of spectral power changes over the course of trials. In the first step, for each condition, the mean power spectral activity at frontal and parietal sites was computed across the entire length of the trials. Relative power spectral activity was then averaged across frequency bands, before being subjected to statistical comparisons. To address the pending question regarding whether frontal theta dynamics reflect context-dependent cognitive processes, the second stage of analysis consisted of the comparison of spectral activity recorded over the different segments of the trials (first, middle and last segments). In this segment-based analysis of spectral power, the effects of both cognitive task type and the relative position of the participant within a trial on the average power were investigated across frequency bands. For this purpose, 3x3 repeated measures ANOVAs, with task (numbers, directions, wayfinding) and position (first, second and third segment) as factors, were applied to the measures of power recorded within the different frequency bands across the entire duration of a segment. This approach offers the potential to highlight situational brain dynamics (i.e., context-dependent) that depends on the position of the participants in the environment.

Finally, depending on the hypothesized findings, power spectral modulation analyses may be extended to other frequency bands (i.e., within the range of the unfiltered [1-80Hz]) power spectrum). This exploratory third stage of data analysis provides context to the results highlighted in the initial hypothesis-driven analyses by assessing the spectral and spatial specificity of the effects observed. For example, if spatial navigation is found to modulate frontal theta activity, then follow-up analysis is required to explore such modulation in neighbouring frequencies. Indeed, modulation in neighbouring frequencies would indicate that the effect observed is not specific to the band investigated. Similarly, comparing the pattern of spectral modulations across electrodes will provide information relative to the spatial distribution of the effects.

7.3. Results

7.3.1. Frontal Theta hypotheses

To investigate the effect of the experimental tasks on frontal theta activity, a one-way ANOVA including cognitive task (numbers, directions and wayfinding) as factor was carried out. The type of task yielded a significant impact on frontal theta power [$F(2, 44) = 6.694$, $p = .003$, $\eta^2 = .233$]. Each hypothesis was explored using post-hoc t-test comparisons (with the application of Bonferroni correction for multiple comparisons).

7.3.1.1. Modulation of Frontal Theta is not specific to spatial memory

To address the first hypothesis examining whether frontal theta reflects general working memory or spatial memory processes, the power spectral activity within the theta band (3.5-8Hz) recorded at frontal site for the directions (spatial memory) was contrasted to the numbers (non-spatial memory) condition using a paired-sample t-test. This comparison reveals no significant difference in terms of mean frontal theta power between the two memory conditions [directions-numbers: $t(22) = -.598$, $p = .556$, $d = -.125$, $BF_{10} = .257$].

7.3.1.2. Increase of Frontal Theta activation is related to spatial navigation

Further to the comparison of frontal theta power across the two memory conditions, comparing frontal theta power of the spatial navigation condition was included to disentangle the nature of the frontal theta effect that was observed in the previous experiment, as reflecting either a memory effect of a spatial navigation effect. Post-hoc paired-sample t-tests revealed that frontal theta power was significantly larger in the wayfinding condition than recorded in both the spatial memory condition [directions: $t(22) = 2.896$, $p = .008$, $d = .604$, $BF_{10} = 5.695$] and the general memory condition [numbers: $t(22) = 3.291$, $p = .003$, $d = .686$, $BF_{10} = 12.473$]. The wayfinding condition presented significantly more theta power than both memory conditions (see Figure 7.3). This finding suggests that the modulation of frontal theta reported in Chapter 6 may index spatial navigation processes rather than reflecting a pure memory effect.

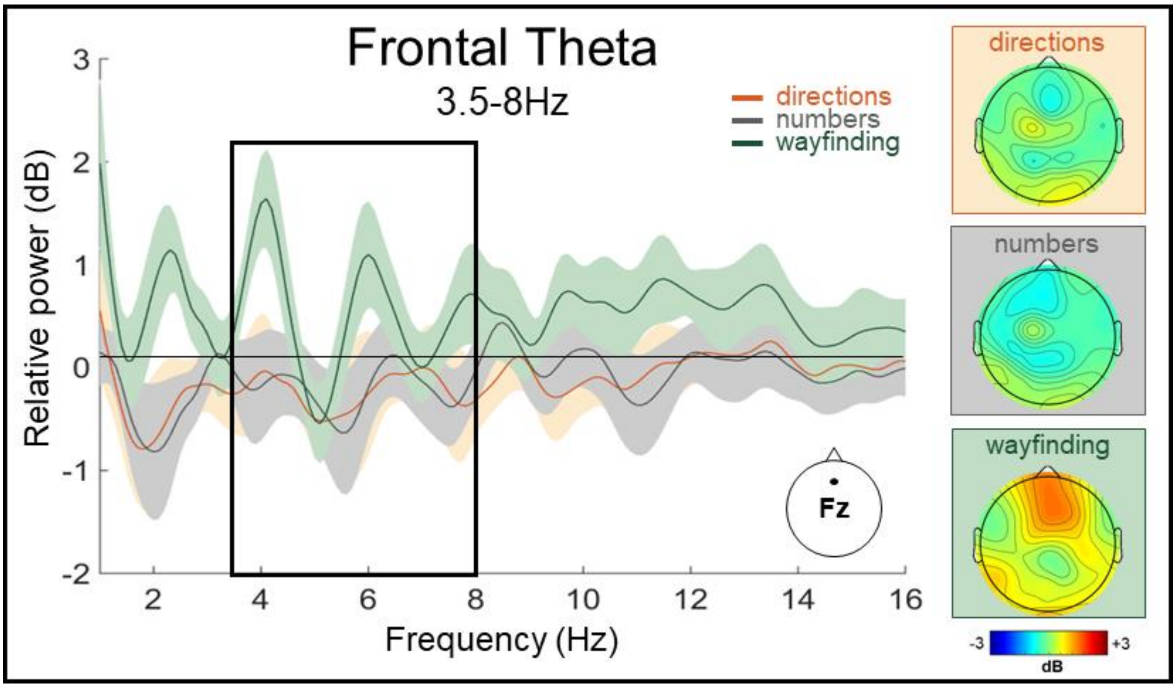

Figure 7.3. Grand average power spectra (N=23) for each experimental condition (directions in orange, numbers in grey, wayfinding in green) recorded at frontal electrode "Fz". The frequencies included within the theta band range from 3.5 to 8Hz as indicated by the frame. Scalp maps representing the spatial distribution of mean theta band power are presented for each experimental condition. The wayfinding condition presents higher theta power at frontal electrode Fz. This finding is supported by the spatial distribution of theta power, which is found maximal at frontal electrode sites for the wayfinding condition, while the other conditions do not show modulations in the theta band.

7.3.1.3. Frontal Theta dynamics over the course of the trial

Further to the outcomes of Chapter 6, in which frontal theta activity was found to be differentially modulated towards the end of the trial, in the current study the presence of a dynamic pattern of frontal theta activity over the time-course of wayfinding trials would strengthen the evidence for spatial navigation related frontal theta modulation. The following analysis contrasts spectral activity of the different segments for the spatial navigation condition, to determine whether a variable time-course temporal dynamic is observed in the spatial navigation condition.

Planned t-tests revealed that the wayfinding condition presented a dynamic pattern of frontal theta modulation throughout trials (see Figure 7.4), with a significant increase of theta power observed during the middle [t(22) = 2.999, p = .007, d = .625, BF_{10} = 6.961] and last [t(22) = 3.891, p < .001, d = .811, BF_{10} = 43.694] segments in comparison to the first segment. There was, however, no significant difference in terms of frontal theta power recorded during the wayfinding condition between the second and third segments [t(22) = .894, p = .381, d = .186, BF_{10} = .313].

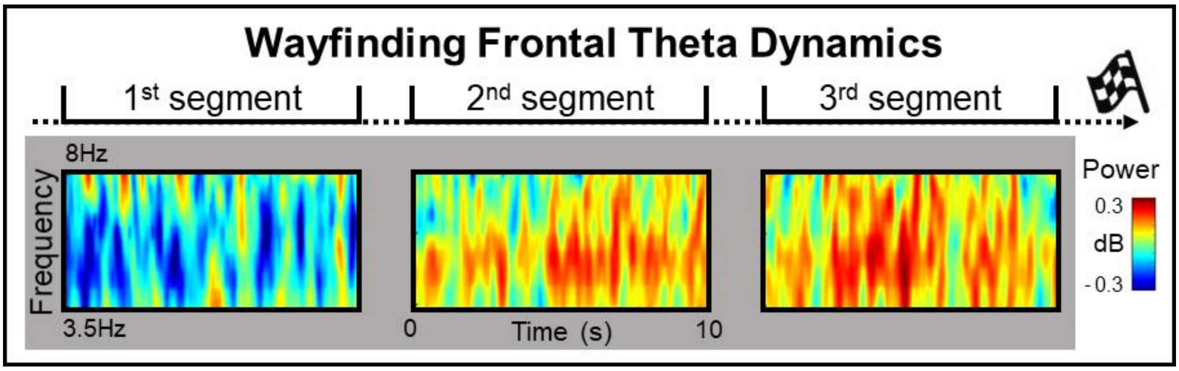

Figure 7.4. Grand average Event-Related Spectral Perturbations (N=23) relative to control condition recorded at frontal electrode "Fz". The time-frequency plots present frontal theta dynamics across the three segments of a spatial navigation (wayfinding condition) trial. A gradual increase of theta is observed throughout the middle and last segments of the trials. The magnitude of mean frontal theta power is significantly higher during the middle and last segments than at the beginning of the trial.

The increase of frontal theta power across the three segments of the wayfinding trials sheds light on the nature of the time-course effect reported in the previous study. The presence of an increase of activity as participants get closer to their destination provides further supporting evidence for the interpretation of frontal theta dynamics as reflecting a spatial navigation effect.

7.3.2. Parietal Gamma hypotheses

In line with the analyses applied to frontal theta, the effect of memory, spatial memory and spatial navigation on parietal activity within the gamma band was investigated through a one-way ANOVA. The experimental task manipulation yielded a significant impact on gamma power recorded at parietal site [F(2, 44) = 5.840, p = .006, η^2 = .210]. This main effect was further investigated by contrasting conditions through paired-sample t-tests.

7.3.2.1. Increase of Parietal Gamma activity associated with spatial memory

Significantly higher parietal gamma power was found in the directions condition than in any other experimental condition [numbers: t(22) = 3.423, p = .002, d = .714, BF_{10} = 16.363; wayfinding: t(22) = 3.284, p = .003, d = .685, BF_{10} = 12.302]. Furthermore, there was no significant difference between the wayfinding and the numbers conditions in terms of parietal gamma power [numbers-wayfinding: t(22) = -.069, p = .945, d = -.014, BF_{10} = .219]. This result suggests that parietal gamma is specifically sensitive to spatial memory processes. The difference in parietal gamma power between the spatial memory and the non-spatial memory conditions (see Figure 7.5) questions the interpretation of parietal gamma modulation as reflecting a pure memory effect.

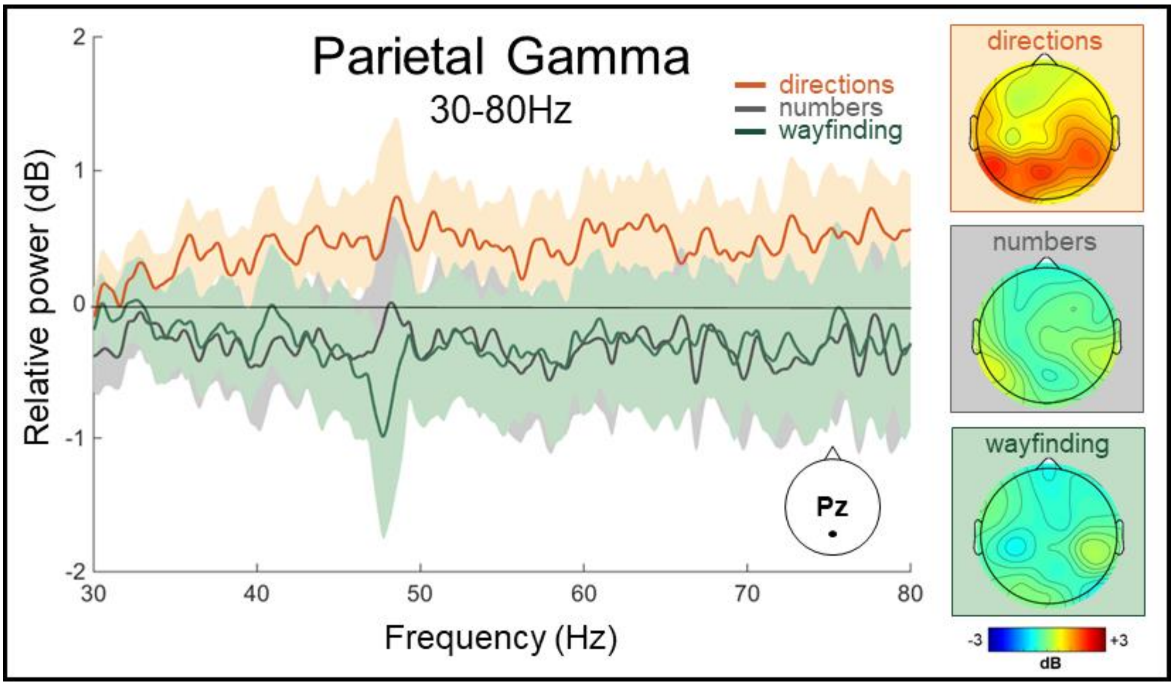

Figure 7.5. Grand average (N=23) power spectra recorded at Parietal electrode "Pz". The power spectra range from 30 to 80Hz consistent with the *a*-priori definition of the gamma frequency band. The coloured lines represent each experimental condition (directions in orange, numbers in grey, wayfinding in green). Scalp maps representing the spatial distribution of mean gamma band power are presented for each condition. The directions condition presents higher gamma power than the numbers and wayfinding condition at the midline parietal electrode investigated. This finding is further supported by the spatial distribution of gamma power related to the spatial memory condition (directions) which is the most prominent over parietal electrode sites.

7.3.2.2. Parietal Gamma dynamics reflect context-dependent processes

It can be hypothesized that parietal gamma dynamics reflect the when and where information relevant for the performance of the task is processed (i.e., reaching destination following instructions). This context-dependent interpretation of parietal gamma modulation is in line with previous research linking increase of parietal high-gamma activation (>50Hz) with encoding, consolidation and retrieval of task-related information in memory, in relation to the participant's position during virtual navigation tasks (Morgan et al., 2011; White, Congedo, Ciorciari, & Silberstein, 2012). According to a context-dependent interpretation, it is expected that parietal gamma activity would be dynamically modulated by the position of the individual in the environment.

Alternatively, if the increase of gamma activity observed in the spatial memory condition is not reflecting context-dependent memory processes, then no substantial difference in terms of parietal gamma activation would be expected between the different segments of the trials. The following analyses investigate parietal gamma activity over the course of the trial, which may shed light on whether parietal gamma activation is reflective of context-dependent spatial memory processes.

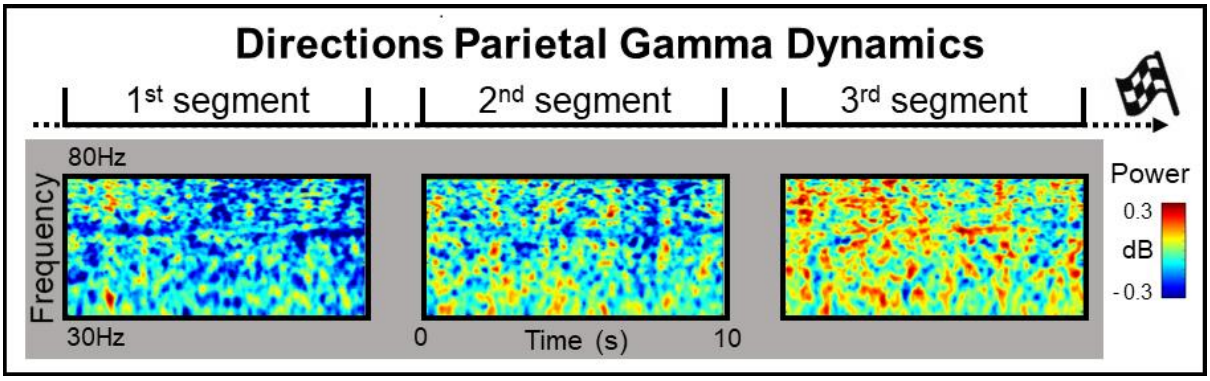

Figure 7.6. Grand average Event-Related Spectral Perturbations (N=23) relative to control condition, recorded at parietal electrode "Pz". The time-frequency plots present parietal gamma dynamics across the three segments of a spatial memory (directions condition) trial. An increase of parietal gamma activity is observed over the course of the trial. The magnitude of mean parietal gamma power is significantly higher during the last segment than at the beginning of the trial.

Paired-sample t-tests were carried out to investigate the modulation of parietal gamma power across the different segments of the trial. When participants performed the spatial memory task, parietal gamma activity was significantly higher in the last segment than both at the beginning [t(22) = 2.162, p = .042, d = .451, BF_{10} = 1.522] and in the middle [t(22) = 2.319, p = .030, d = .484, BF_{10} = 1.983] of the trial. There was no significant difference in parietal gamma power recorded between the first and second segments of the trials within the spatial memory condition [t(22) = .581, p = .567, d = .121, BF_{10} = .255]. Therefore, the spatial memory condition (directions) presents an increase of gamma activity in the last segment of the trials specifically (see Figure 7.6).

This progressive increase of gamma activity may correspond to the framework proposed by Herrmann, Munk & Engel (2004), relating gamma activation to the readout and utilization of task-related information following an initial matching process comparing bottom-up and top-down information. According to this theory, the progressive gamma-band activation observed in the present study may reflect the readout and utilization of spatial information in memory, as it becomes relevant to the ongoing task (i.e., navigating to a certain destination accordingly to the instructions). This result therefore strengthens the interpretation of parietal gamma activation as reflective of context-dependent cognitive processes associated with spatial memory.

7.3.3. Follow-up analyses

The analyses reported so far have focused on the hypotheses regarding the modulation of frontal theta and parietal gamma dynamics based on the previous literature and the findings reported in Chapter 6. The predicted effects found in parietal gamma would be strengthened if follow-up analyses show that the effects are specific to the gamma band and parietal recording site (e.g., Pz electrode) and are not evident in the other frequency bands/recording sites. Furthermore, arising from the finding that suggest frontal theta is associated with spatial navigation rather than spatial memory, it is necessary to explore the modulation in the spatial navigation condition in other bands. This is because the present results are indicating that frontal theta dynamics do not reflect a memory effect. As suggested by previous findings, there is therefore no reason to assume that this frontal effect would be restricted to the theta band (see introduction section of this chapter). Therefore, to investigate whether the effects issued from hypothesis-driven analyses are specific to the bands investigated or extend to neighbouring frequency bands, the range of frequencies investigated was extended to the whole power spectrum (i.e., within the limits of low-pass and high-pass filters applied to the EEG signals). Moreover, performing these analyses across electrodes also assesses the spatial distribution of the effects observed. For this purpose, a series of one-way ANOVAs have been performed to assess the effect of the experimental task manipulation on spectral power within each frequency bands (not included in the hypothesis-driven analyses) for each electrode. In addition, a series of repeated measures ANOVAs were applied to investigate the time-course of spectral dynamics within the different frequency bands for each recording site. A comprehensive report of the statistical analyses of all comparisons are included in the Appendix for completeness. The sections below will concentrate on each of the posited follow-up questions to explore specificity of the findings reported in this chapter so far.

7.3.3.1. Specificity of parietal gamma dynamics related to spatial memory

The hypothesis-driven analyses revealed that the spatial memory condition (directions) was associated with higher gamma band activity than either the spatial navigation (wayfinding) or the non-spatial memory (numbers) conditions. The specificity of the parietal gamma effects related to spatial memory was assessed by investigating modulations across frequency bands and electrode sites. These follow up analyses reveal that elevated levels of activity observed in the gamma band in relation to spatial memory was not observed in any other frequency band (see Figure 7.7 and Appendix section A.1). This result strongly supports the conclusion that the gamma band was specifically sensitive to the spatial memory effects. Moreover, even though a significant difference in gamma activation between the experimental conditions was also found at frontal electrode Fz (see section A.1.4), the size of this effect was however larger over the parietal electrode (as indicated by the effect sizes reported in section 7.3.2). These findings strengthen the hypothesis-driven analyses (discussed in section 7.1.2.3 above) by highlighting the specificity of the gamma band modulation in relation to spatial memory and the prominence of the effect at parietal electrode Pz.

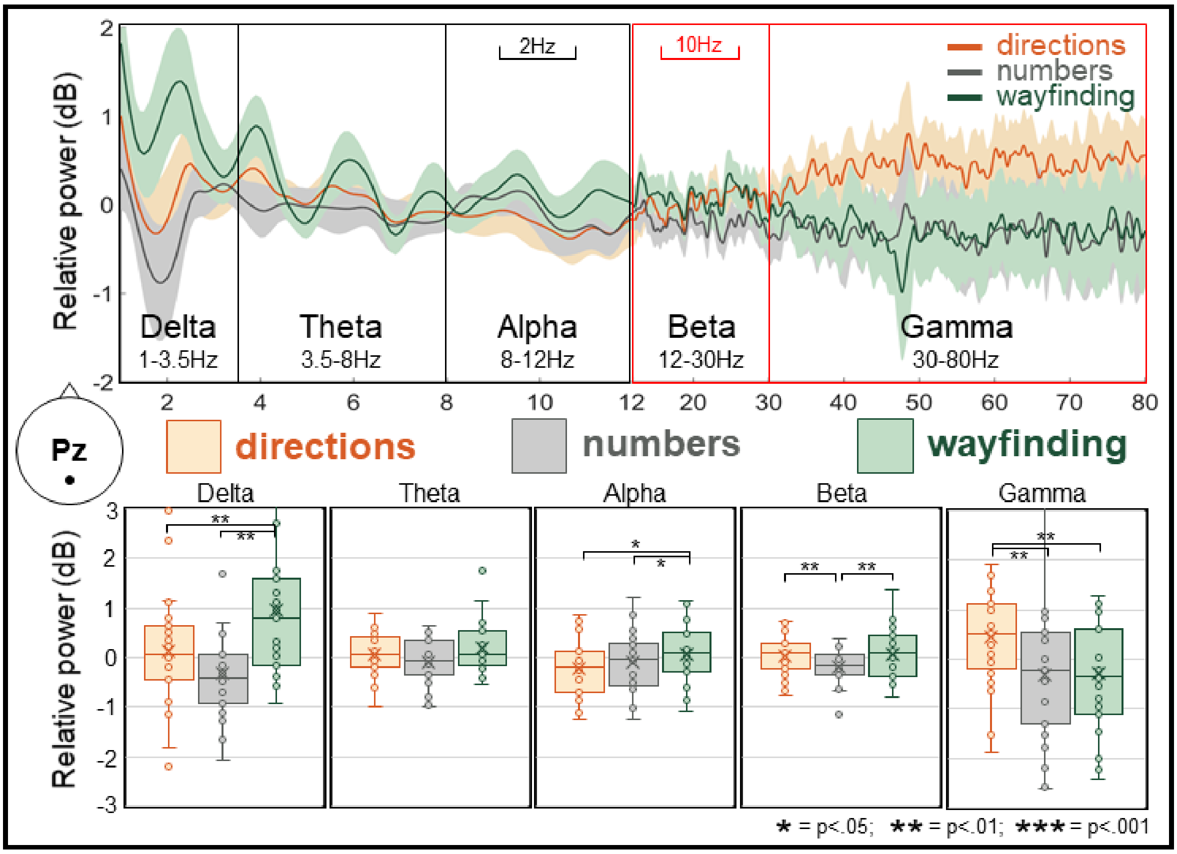

Figure 7.7. Normalized power spectra recorded at parietal electrode Pz for the experimental conditions (directions in orange, numbers in grey, and wayfinding in green). It is important to note that a change of scale (change from the initial 2Hz increment for lower frequencies to a 10 Hz increment for higher frequencies indicated by the red frames) was applied to increase the readability of spectral modulations within lower frequency bands. The wayfinding condition presents more power across the delta and alpha frequency bands than both the directions (spatial) and numbers (non-spatial) memory conditions. By contrast to what was observed at frontal electrode, there was no significant difference in terms of theta power between conditions. Both the directions and wayfinding conditions presented an increase of beta power in comparison to the numbers condition. The directions condition presents a clear increase of gamma power in comparison to both the numbers and wayfinding conditions.

Furthermore, the hypothesis-driven analyses (discussed in section 7.3.4.2 above), revealed an increase of gamma activity towards the end of the trials, possibly reflective of task-related cognitive processing. By contrast, the current analyses revealed that this pattern of gamma dynamics was not found at frontal site Fz (see Appendix A.2.4 & Figure A.1), nor in the neighbouring frequency beta band at parietal site Pz (see Appendix A.2.8 & Figure A.2), further strengthening the interpretation of the parietal gamma dynamics as indexing context-dependent cognitive processes. This pattern of results is consistent with parietal gamma modulations associated with task-related memory functions (Hanslmayr & Staudigl, 2014;

Howard et al., 2003; Ray & Maunsell, 2015). In relation to the higher parietal gamma activation for the spatial memory task reported above, the current follow-up analyses strengthen that finding by highlighting the specificity of parietal gamma band activation in relation to spatial memory. Moreover, previous research has linked parietal gamma activity increase with associative functions, notably sensorimotor integration and binding mechanisms during encoding and retrieval of task-related information in memory (Lisman & Jensen, 2013).

7.3.3.2. Frontal theta dynamics are not specific to spatial navigation

In a similar manner to parietal gamma activity related to spatial memory, the specificity of frontal theta modulations associated with regards to spatial navigation was investigated by exploring the modulation of activity related to spatial navigation in other frequency bands and across electrodes. These follow-up analyses on the overall mean power activity within each band revealed that the frontal activation effect associated with spatial navigation is not specific to the theta band. In fact, a relative increase of frontal spectral activity was found across all the lower frequencies (delta, theta and alpha, see Figure 7.8) during the wayfinding condition (see sections A.1.1 & A.1.2 of the Appendix). The follow-up analyses shed light on the nature of this modulation by highlighting that this frontal effect is in fact not specific to delta and theta bands but also extends to the alpha band.

The extended range of spectral modulations seen here present similarities with the hippocampal low-frequency oscillations recorded during spatial navigation, typically referred to as “low-frequency oscillations” (Araújo et al., 2002; Bohbot et al., 2017; Jeremy B Caplan et al., 2003; Ekstrom et al., 2005; Kober & Neuper, 2011; Watrous et al., 2013; Watrous, Fried, & Ekstrom, 2011; White et al., 2012). These studies involved epileptic patients (with intracranial arrays of electrode implanted) navigating through virtual environments (with the exception of the study conducted by Bohbot et al., 2017, in which subcortical activity of patients was recorded during real-world navigation). These studies were reporting sub-cortical local field modulations, specifically focusing on the hippocampus structure. The present results suggest that the frontal low-frequency modulations recorded at surface level may share some functional similarities with the hippocampal low-frequency oscillations typically reported during navigation in rodents and epileptic patients (see section 6.1.1.4). These results are of particular interest with regards to the interpretation of frontal delta and theta modulation observed in Chapter 6, highlighting that slow oscillations (rather than theta specifically) are reflective of spatial navigation rather than indexing memory processes.

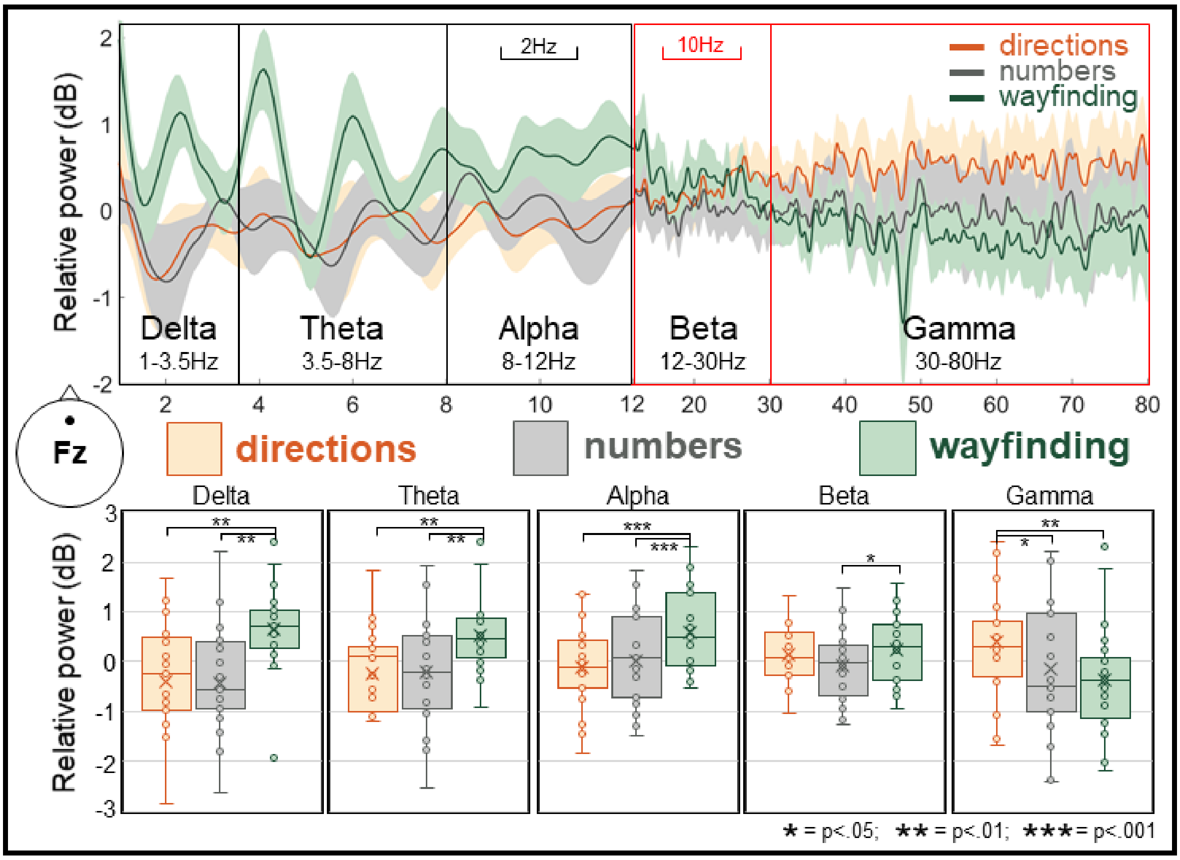

Figure 7.8. Normalized power spectra recorded at frontal electrode Fz for the three experimental conditions (directions in orange, numbers in grey, and wayfinding in green). It is important to note that a change of scale (change from the initial 2Hz increment for lower frequencies to a 10 Hz increment for higher frequencies indicated by the red frames) was applied to increase the readability of spectral modulations within lower frequency bands. The bottom of the figure provides a summary of the spectral power distribution across participants, recorded within *a-priori* frequency bandwaves for each condition. The wayfinding condition presents more power across the lower frequency bands (i.e., delta, theta and alpha) than both the directions and numbers memory conditions. This difference becomes less clear within the beta band. In contrast to lower-frequency bands, the pattern of spectral changes within the gamma band highlights a significant increase of power during the directions condition (spatial memory) in comparison to the other conditions.

Further to the clear pattern of dissociations found for the spatial memory condition in comparison to the other conditions, and for the spatial navigation condition in comparison to the other conditions, no such pattern was found for the non-spatial memory condition (see Appendix for the explorative analyses). No distinctive pattern of spectral activity was found to be associated with the non-spatial memory condition in comparison with the other conditions. Furthermore, the analysis of segment-to-segment spectral dynamics in the non-spatial memory condition did not reveal modulations related to non-spatial memory in any of the bands.

7.3.4. Is walking speed variation a confound?

As discussed in the introduction of the previous chapter (see Section 7.1), the interpretation of low-frequency oscillations found in rodent brains has been a source of controversy due to the memory, spatial navigation and motion-related elements involved in traditional animal research paradigms such as maze-solving tasks. Each of these aspects of task performance have been associated separately with the modulation of low-frequency oscillations, rendering the interpretation of such spectral dynamics as reflective of a specific cognitive process subject to the confounds of the other factors. The present study is therefore relatively unusual in investigating the modulation of these oscillations across conditions that focus either on memory or navigational cognitive aspects.

To assess whether the differences reported between experimental conditions in frontal low-frequency spectral power are related to a confounding effect of walking speed variation, the measures of walking speed were compared between experimental conditions. For this purpose, single-trial measures of walking speed were computed for each of the three segments of the trials (based on the difference between crossing the motion sensors placed at the beginning and end of the corridors). The average walking speed was then computed for each segment of each cognitive task condition (including control condition). Based on the high within and between subjects' consistency in terms of walking speed observed during the previous study, participants' walking pace was not expected to be different between the different experimental conditions. Mean walking speed data are shown in Table 7.1.

Mean walking speed data (km/h)												
Condition	**Control**			**Directions**			**Numbers**			**Wayfinding**		
Segment	*First*	*Middle*	*Last*	*First*	*Middle*	*Last*	*First*	*Middle*	*Last*	*First*	*Middle*	*Last*
Mean	*4.2*	*4.4*	*4.3*	*4.3*	*4.4*	*4.3*	*4.3*	*4.5*	*4.3*	*4.7*	*4.7*	*4.7*
Std.dev	*0.53*	*0.47*	*0.43*	*0.42*	*0.62*	*0.47*	*0.59*	*0.55*	*0.53*	*0.48*	*0.58*	*0.41*
Mean	**4.3**			**4.3**			**4.4**			**4.7**		
Std.dev	**0.48**			**0.50**			**0.55**			**0.49**		

Table 7.1. Mean walking speed across first, middle and last segment of each condition (control, directions, numbers, wayfinding) in km/h. The Grand averages of mean walking speed computed on both a segment and condition basis are presented in bold at the bottom of the table. The segment-specific data indicate a high within and between subject consistency in terms of walking speed across the different segments of a condition. Participants maintained a stable walking speed across all the experimental conditions. However, a significant overall faster speed was observed during the wayfinding condition in comparison to the other conditions.

A 4x3 repeated-measure ANOVA with experimental task manipulation (control, numbers, direction and wayfinding) and participant's position within the trial (first, middle and last segment) included as factors was performed on the average walking speed. This analysis revealed that the type of task yielded a significant impact on the walking speed [$F(3, 66) = 10.108$, $p < .001$, $\eta^2 = .315$]. By contrast, the participant's position within the trial did not have a main effect on walking speed [F(2, 44) = 2.721, $p = .077$, $\eta^2 = .110$]. Moreover, there was no significant interaction between the experimental task manipulation and participant's position within the trial on walking speed [F(6, 132) = 0.749, $p = .611$, $\eta^2 = .033$].

Post-hoc paired-sample t-tests revealed that participants walked significantly faster during the wayfinding condition (mean = 4.7 km/h, SD = .45) than any other condition [control: mean = 4.3 km/h, SD = .45, t(22) = 6.691, $p < .001$, d = 1.395, BF_{10} = 17915.63; directions: mean = 4.3km/h, SD = .45, t(22) = 4.988, $p < .001$, d = 1.040, BF_{10} = 471.95; numbers: mean = 4.3km/h, SD = .53, t(22) = 4.153, $p < .001$, d = .866, BF_{10} = 76.80], while other conditions did not present any significant difference between each other. The walking pace was strongly correlated across cognitive tasks [control and direction: $r_{22} = .731$, $p <.001$; control and numbers: $r_{22} = .653$, $p < .001$; control and wayfinding: $r_{22} = .814$, $p < .001$; direction and numbers: $r_{22} = .492$, $p < .05$; directions and wayfinding: $r_{22} = .688$, $p < .001$; numbers and wayfinding: $r_{22} = .725$, $p < .001$], indicating a high within-subject consistency in terms of walking pace across experimental conditions.

The present results indicate that participants walked significantly faster during the spatial navigation (wayfinding) condition than in any other condition. However, walking speed remained stable over the course of the trial, which contrasts with the pattern of spectral dynamics observed across the different segments. In light of the present results, the impact of walking speed increase as a confounding variable that may affect the spectral modulations associated with the wayfinding condition, cannot be ruled out entirely. To shed light on this issue, the following study (see Chapter 8) focused on characterizing the impact of walking speed changes on spectral activity. Due to differences between the pattern of spectral modulations associated with walking speed increase (overall increase of activity across bands and recording sites, with typical fundamental peaks within the delta band followed by harmonics peaks) and the frontal low-frequency modulations associated with spatial navigation, the present results will be discussed as reflective of spatial navigation effects.

7.4. Discussion

In line with the main hypotheses investigated, this study aimed to address two overarching questions, regarding the nature of the frontal theta effect observed in the previous study and the cognitive function of parietal gamma oscillations. Following a hypothesis-driven approach based on the findings from the previous experiment and evidence from animal and intracranial EEG literature, the analyses focused on the characterization of frontal theta and parietal gamma spectral dynamics in relation to experimental manipulations. However, follow-up analyses extended to the whole range of traditional frequency bands, motivated by the novelty of analysing real-world EEG data that could potentially exhibit different patterns of activation. Moreover, these follow-up analyses were employed to understand whether the effects observed are specific to the hypothesized frequency bands, or if they spread to neighbouring bands. The following sections will discuss the present results in light of relevant literature that provides additional context for the interpretation of the findings.

7.4.1. Summary of the main findings

The first observation that can be drawn from the analyses is that the wayfinding condition elicited low-frequency perturbations (delta, theta and alpha) throughout the different segments of the trials (which involved reaching a destination using a specific route based on previously learned map of the environment) across frontal and parietal electrodes. These results suggest that navigating through a real-world environment leads to widespread changes in low-frequency EEG dynamics recorded across the scalp. Despite the broad spatial distribution of these low-frequency effects, their effect size was found to be largest at frontal electrode Fz, hinting towards an interpretation of this low-frequency oscillations effect as a frontal lobe phenomenon. However, and as discussed in Chapter 2, the estimation of the neural sources of low-dimensional EEG data is problematic for many conceptual and practical reasons (see Section 2.2.2.5). Solving this inverse-problem requires the modelling of post-synaptic potentials propagation (through optical imaging of cortical and sub-cortical brain structures at a subject-level), combined with high-density recording of surface electrodes during spatial navigation, to reach a conceptually valid source estimation of the effects observed. Nonetheless, the frontal distribution of the present findings could inform the design of intracranial EEG studies to investigate the origin of these effects and assess their relation with hippocampal and cortical structures involved in a spatial navigation network. Either way, on the basis of the present data it is only possible to claim a frontally distributed response, but not assessing its origin nor confirming it as a frontal lobe effect.

7.4.1.1. Parietal gamma reflects spatial memory processes

The present results shed light on the specificity of parietal gamma activity for spatial memory; while modulations of parietal gamma were observed in the directions memory workload condition, no significant effect was elicited by the maintenance of digits in memory (numbers condition). This dissociation of spectral activity can however have several interpretations: a) it can be purely explained as a specificity of parietal gamma for spatial information, b) it could be the case that parietal gamma is specifically modulated by the maintenance of information related to the task in memory, or c) the memory workload induced by the digit task in the 'numbers' condition may not be as strong as the memory workload induced by the 'directions' condition.

Although theoretically possible, the last explanation is unlikely. If parietal gamma was purely reflective of memory workload, it should be expected that spectral modulation would have reflected a decreasing effect of memory workload in the directions conditions (Greenberg, Burke, Haque, Kahana, & Zaghloul, 2015). This reduction follows from the study design: while participants progress towards the final destination, the number of items to be maintained in memory is reduced by one after each turn. Therefore, this progressive reduction of information maintained in working memory (phonological loop) would have led to a reduction of parietal gamma power, according to an interpretation of parietal gamma modulations as memory effects (Baddeley, 1986; Burgess & Hitch, 1999; Fisk & Warr, 1996).

In contrast, spectral modulations during the direction workload condition were larger throughout the entirety of the trial, in comparison to the numbers condition, which may reflect the specificity of these modulations to spatial memory processes. Even though the results suggest that spectral dynamics observed frontally are linked with context-dependent processing of task-related information (in this case spatial information), it is nevertheless important to acknowledge that there might be a discrepancy in the workload induced by information of different types (in the present case short series of navigational instructions versus 4 digits spans). It is notable, however, that conditions inducing memory effects mainly elicited spectral changes within the alpha and beta bands throughout the course of a trial. These bands have been highlighted as reflecting working memory processing, and the modulation of alpha and beta prefrontal activity has been associated with memory function (Hanslmayr et al., 2016; Karakaş & Barry, 2017). In the present study, increases in gamma band power were observed at parietal sites for both memory workload conditions, but were more pronounced during the spatial memory condition. This finding is in line with previous studies that have linked gamma power with different memory functions, including memory workload. Finally, it is important to note that previous work has demonstrated the link between frontal low oscillatory modulations and high-frequency parietal dynamics within the frame of encoding and retrieval of information in memory.

7.4.1.2. Parietal gamma dynamics reflect context-dependent processes

Following a similar pattern to that found for frontal theta dynamics recorded throughout the wayfinding condition, parietal gamma dynamics were found to increase as the participants reached the end of the trial during the spatial memory condition. The different spectro-temporal patterns of brain dynamics observed across condition suggests that the cognitive mechanisms underlying navigational abilities are dependent on the position of the body within the environment. The time-frequency decompositions of spectral activity recorded during the different segments of each condition suggests that the wayfinding condition initially presents a frontal alpha-beta synchronization that is typically observed in the latter stages of both memory workload conditions (Hanslmayr et al., 2016), and then switch into a theta-gamma desynchronization, which has been linked with navigational cognitive processes in the wider literature (Benchenane et al., 2011; Sauseng, Griesmayr, Freunberger, & Klimesch, 2010; Staudigl & Hanslmayr, 2013). The relationship between theta and gamma dynamics distributed at frontal and parietal sites suggests that these oscillatory patterns may be involved in a distributed neural network supporting cognitive processes underlying spatial navigation. This extrapolation of the spatio-temporal pattern of results observed is in line with evidence from virtual reality experiments linking the synchronization and desynchronization of theta-gamma dynamics with the communication of task-related and context-dependent spatial information between frontal cortex and associative cortical areas across the parietal region (White et al., 2012). Future work may focus on the contribution of different sources of sensory information to the activation of this network, and its relationship with spatial navigation ability. For example, patterns of theta-gamma synchronicity could be compared between real-world versus virtual navigation to isolate the contribution of vestibular and proprioceptive information.

7.4.1.3. Low frequency frontal activity is related to spatial navigation

In the previous study, the frontal effect observed in the theta band during a spatial memory task raised question about the specificity of frontal theta as a specific marker of spatial memory or as a more general sign of sensitivity to memory processes overall. While contrasting spatial memory and non-spatial memory conditions did not reveal significant difference in frontal theta power, an increase of low frequency activity (comprising theta, but also extending to delta and alpha bands) was observed at frontal electrode during the wayfinding condition. This finding suggests that frontal theta (and lower frequencies) is reflective of spatial navigation, rather than being a pure memory effect.

Based on findings issued from intracranial recordings, hippocampal low frequency oscillations have been hypothesized as indexing goal-oriented spatial information such as the distance from a starting point, or from the destination within the frame of previously learned routes and environments (Bush et al., 2017; Watrous et al., 2011). Previously, frontal low-frequency oscillations have been associated with the processing of task-relevant sensory input and the execution of motor responses (Bland & Oddie, 2001; Jeremy B Caplan et al., 2003; Cruikshank, Singhal, Hueppelsheuser, & Caplan, 2012; Ferezou et al., 2007; Rossignol, 2006). This context-dependent sensorimotor integration is an essential element of spatial navigation because top-down processes are required to dynamically respond to the continuous stream of sensory information. Therefore, the increase of frontal activity observed over the course of the wayfinding trials may reflect the contextual updating of spatial representations, with regards to the navigational task. It is important to recognise that other functions may also play a role. For example, previous studies have reported increases of low-frequency oscillations associated with the presence of landmarks (Sharma et al., 2017; Weidemann, Mollison, & Kahana, 2009). Recent evidence has also demonstrated that theta oscillations episodes are more prevalent, and last longer, as participants get closer to their destination (Vass et al., 2016). The gradual increase of theta activity observed across segments in the present study may therefore reflect the increasing rate of theta episodes as the participants get closer to the landmark they were instructed to navigate to. According to this interpretation, frontal theta dynamics are sensitive to cognitive processes involved in the updating of spatial representations of one’s position relative to goal-oriented objects (i.e., landmarks) in the environment.

7.4.1.4. Nature of low-frequency dynamics during spatial navigation

An important finding in the present data lies in the dynamic changes observed throughout the different segments of a trial. These spectral modulations demonstrate that brain dynamics are dependent on the subject’s situation within the environment. A clear example of this phenomenon can be found in the progressive increase of theta power observed across the different segments composing the wayfinding trials. A similar pattern of theta activity was observed in Chapter 6, where frontal theta was slowly increasing as participants reached the end of the corridor. Due to the experimental design, it was not quite clear in the previous study whether this effect was a result of a build-up of memory workload, indexing task-related cognitive processing (retrieval of the navigational instruction as participants are about to reach an intersection due to the relevance of this information to the task) or related to context-dependent processes reflecting spatial context-updating as participants' position within the environment, and more specifically relative to the destination changes. The present results hint towards a navigational interpretation of this effect, possibly as reflective of processes indexing displacement through space in relation to other objects' spatial representations. One plausible interpretation is that frontal theta indexes context-updating of the body's position within the environment, with respect to one's goals. Taken together these results demonstrate that brain activity recorded during natural navigation reflects cognitive experiences of the environment dynamically, with respect to one's place within the environment amongst meaningful landmarks and destinations. These findings provide further evidence in support of the embodiment framework by demonstrating the situated nature of brain dynamics during wayfinding in a real-world environment (i.e., embedded/interacting with the environment, see Clark, 2013).

Alternatively, low-frequency dynamics could be associated with motion-related cognitive processes or even motion-related noise. Behavioural differences across conditions, such as changes in walking speed, are potential confounds that could undermine the interpretation of the effects observed as reflecting cognitive processes. Despite a high within-subject consistency in terms of walking pace throughout the study, statistically significant differences have nevertheless been observed across cognitive tasks. More specifically, the participants were walking significantly faster throughout the course of the wayfinding trials in comparison to other conditions.

The reason for the faster walking speed observed in the wayfinding condition remains unclear. It can, however, be hypothesized that this difference is at least partially related to the fact that the wayfinding was systematically the last condition of the experiment. Indeed, since this condition was based on the integration of a cognitive map of the environment by the participants through previous experiences (i.e., during the completion of the control, directions and numbers conditions), it was necessary that the participants had been exposed several times to the position of the different landmarks. Therefore, participants may have walked faster at the end of the session due to their familiarity with the environment; equally it may be that given the length of the whole experiment participants may have started experiencing tiredness and wanted to complete the experiment as fast as possible.

In a recent study, Liang, Starrett, & Ekstrom (2018) reported frontal midline delta/theta activity increase when participants were "physically" navigating (using an omnidirectional treadmill) through a virtual environment, in comparison to remaining still (both physically and in the virtual environment). The interpretation of this increase of frontal low-frequency activity as either indexing motion-related dynamics or reflective of cognitive processes supporting spatial navigation was limited due to the lack of walking speed measures. In contrast to the aforementioned study, the measures of walking speed collected in the present study provides further information about the potential impact of walking speed on the effects observed.

Frontal theta activity during the wayfinding condition was found to progressively increase across the segments of the trials. Importantly, however, This pattern of progressive increase of spectral power across segments of the trials was not found in terms of walking speed. Indeed, walking speed was stable across the different segments of the wayfinding trials. Even though this first observation does not rule out walking speed as a confounding factor of the results observed in the wayfinding condition, the dynamic modulation of low-frequency activity across segment cannot be explained by changes in walking speed. Moreover, although the increase of walking speed during the wayfinding was statistically robust (as indexed by the Bayes Factor), the magnitude of this difference corresponds to a 0.3 to 0.4km/h increment in comparison to the other experimental conditions. Whether this relatively small change in walking pace should result in an increase of low-frequency activity as observed in the wayfinding condition remains, however, an unresolved question. To directly investigate this issue, power spectral modulations as a function of walking speed are examined in the next study (see Chapter 8).

In brief, the next chapter reports spectral changes related to walking speed that make it unlikely that the difference in walking speed in the present study was a main factor in the spectral modulations observed in the spatial navigation condition. Put simply, the typical pattern of low-frequency activity (delta and theta harmonics) associated with increasing walking speed were not observed in the present experiment. The absence of such prominent low-frequency activity suggests that participants, even though walking significantly faster during the wayfinding condition, were nonetheless walking at a natural pace that did not lead to the tuning of sensorimotor neuronal activation to the stepping frequency. This finding fits with wider evidence, for example Kline et al. (2014) found that neither walking speed (ranging from slow to slightly above natural pace) nor event-related EEG activity were associated with spatial working memory performance in healthy subjects. The present findings further highlight that in healthy subjects, small variations of gait dynamics (such as walking speed) are unlikely to disrupt cognitive functions or drastically impact neural dynamics associated with cognitive-motor events that are performed or attended concurrently.

7.4.2. Limitations

This study follows-up on the findings reported from the previous study (see Chapter 6). However, the design of the present study does restrict direct comparison of the findings between the two studies. The analyses reported in the previous chapter contrasted a control condition to the spatial memory condition. While a control condition was also part of the present study design, this condition did not have the same role in the statistical analyses because it was used as a baseline. This departure from the design of the previous study is as a consequence of one of the key aims of the present study to characterize brain dynamics at the start, middle and end of the trial. This refinement was done to further investigate the nature of the ‘end of corridor effect’ found in the previous study. In the present study the trials consisted of three segments, with each segment corresponding to a corridor. The naturalistic behaviour in this experiment meant that participants walked from one corridor to the next following experimental instructions. As a result, once a participant was engaged on the path of a trial, there was no time window in between segments to serve as individual baselines between the different segments to which the data could be normalized in the same way as in the previous study. Similarly, at a trial by trial basis the current design meant that consecutive trials were immediately following each other, and there was no baseline period between trials. Instead the control condition served as shared baseline in the current experimental design.

Given the change in design outlined above, in the present experiment statistical analyses therefore compared the non-spatial memory, spatial memory and spatial navigation conditions to each other, only allowing for interpretations about the relative changes observed between these conditions. While the present data allow for the interpretation of spectral dynamics associated with distinct cognitive processes related to spatial navigation and spatial memory, they do not allow use of the same analyses that led to the findings observed in the previous study. The inclusion of such individual baseline periods would have been required for the statistical analyses to allow the characterization of non-spatial memory, spatial memory and spatial navigation effects individually (as opposed to relative to each other). As a consequence, the frontal delta and theta effects observed in the previous study cannot be directly compared to the corresponding condition of the present study (directions), because not only the baseline normalization but also the epochs differ between the two studies. This issue of defining coherent baseline periods is especially challenging within the frame of continuous behaviours such as navigating a real-world environment. It is therefore important for future research to carefully consider how to integrate such baseline periods within the frame of experimental manipulations that are taking place in real-world contexts.

It is to be noted that in both studies (Chapter 6 & 7), the sample of participants was predominantly composed of female psychology students. This skewed distribution raises issues with regards to the research question investigated. Indeed, sex differences have been highlighted in terms of spatial cognitive abilities but also in terms of structural connectome of the human brain (Ingalhalikar, 2014). Therefore, future studies should aim for a balanced gender distribution as this issue may lead to results that are not representative of the whole population and skewed towards a specific gender.

7.4.3. Conclusion

The present results indicate that cognitive processes associated with memory and spatial navigation present different oscillatory dynamics that can be distinguished through non-invasive recordings during real-world behaviour. While frontal activity at lower frequencies was associated with spatial navigation, faster oscillations recorded over parietal scalp electrodes appeared to be sensitive to spatial memory processes. The dissociations observed between spatio-temporal patterns of brain dynamics associated with spatial memory (parietal gamma) and spatial navigation (slow frontal activity) from surface electrode recordings in the real-world is an important step towards building a better understanding of the role and functions of these oscillatory patterns during real-world navigation. Moreover, the present findings highlight the context-dependent nature of brain dynamics associated with such cognitive functions. This novel evidence supports the accounts of embedded and grounded cognitive experiences proposed by the embodiment theoretical framework. Adopting an embodied approach therefore appears to be critical in efforts to capture the context-dependent expressions of cognitive processes underlying complex behaviours such as spatial navigation.

Chapter 8: Effects of walking speed on brain oscillatory patterns

8.1. Introduction

8.1.1. Rationale

In Chapter 6, no significant difference was found between the control and the memory workload conditions in terms of walking speed, ruling out walking speed variations as a driving factor of the theta effect observed. In Chapter 7, however, the participants walked significantly faster during the wayfinding condition and this condition exhibited higher low-frequency power than the other conditions. In light of the previous literature, this difference in walking speed is a potential confound that needs to be considered for the interpretation of the findings. More generally, due to the pervasiveness of walking within the context of real-world behaviours, characterizing the impact of walking speed variations on surface EEG recordings is a crucial issue to address to warrant the validity of a real-world cognition approach.

It has been previously suggested in the animal literature that locomotion is essentially a confound to the brain dynamics (slow oscillatory bands specifically) collected in rodents as they learn to find their way through mazes (see previous discussion of this in section 6.1). The interpretation of theta dynamics as either reflecting cognitive processes or purely indexing active behaviour (such as locomotion) has been a controversial topic in the field of animal electrophysiology for many decades. The persistence of this uncertainty largely reflects the nature of experimental paradigms used to investigate cognitive functions in animals. Indeed, these paradigms always inherently require the animal to engage in some sort of active behaviour (e.g., maze navigation and conditioned responses paradigms) and meaningful brain dynamics are therefore only recorded as the animals are being physically active while completing the task. In order to avoid similar tribulations during the acquisition of real-world brain imaging data, it appears relevant to tackle this issue now that human brain activity is recorded during locomotion, by identifying brain dynamics purely reflecting physical activity related to the performance of real-world behaviours.

Previous research using surface EEG has reported power spectral synchronization to the rhythm of cyclic behaviour using a gait-related approach (Bulea, Kim, Damiano, Stanley &

Park, 2015; Seeber, Scherer, Wagner, Solis-Escalante & Muller-Putz, 2014; Wagner et al., 2016). These findings highlight that the dynamics of human locomotion have an important impact on EEG signals, which is of particular relevance for the interpretation of data recorded during locomotion. The quantification of such effects is crucial for the interpretation of data collected during natural behaviours, especially considering the overlap between cognitive and behavioural effects within the lower frequency range of EEG.

While technically oriented studies have focused on the detection and correction of non-brain signals during treadmill walking, the present study aims to investigate the effects of walking speed modulations on spectral dynamics related to cognitive functions supporting locomotion. For this purpose, brain dynamics will be recorded while participants walked on a treadmill. The use of a treadmill allows experimental control of walking pace. Spectral features across frequency bands can, as a result, be compared across incrementally faster walking speed, ranging from slow to fast walking.

8.1.2 Relationships between cognition and locomotion

In fact, in broader terms, walking as a natural behaviour warrants study in its own right. Despite being automaticity acquired through expertise developed since the early childhood, walking is not a trivial activity from a cognitive perspective. Human walking is actually a very complex task, requiring the simultaneous integration of afferent information from different sources and the coordination of muscles groups to successfully adapt the gait to the changing demands of the environment (Woollacott & Shumway-Cook, 2002; Yogev-Seligmann et al., 2008). For example, within the frame of chronic stroke, walking at faster pace has been shown to exacerbate behavioural symptoms (Dennis et al., 2009), revealing that even slight acceleration places the individuals in a challenging dual-task scenario that has a significant impact on cognitive and behavioural functions. Likewise, in elderly and clinical populations (e.g., Alzheimer's and Parkinson's diseases), the increased cognitive workload associated with locomotion has been shown to severely interfere with the execution of simultaneous motor and cognitive tasks (Yogev et al., 2005; Hausdorff, Schweiger, Herman, Yogev-Seligmann, & Giladi, 2008).

In the light of previous research on cognitive-motor interference, which widely resorts to treadmill walking to manipulate the motor demands within the frame of dual-task paradigms, it appears clear that the execution of even such a pervasive behaviour such as locomotion may alter cognitive functions. This issue is particularly relevant within the frame of a real-world approach to human cognition, because walking is an integral part of the embodied experience of the environment. The opportunity to record brain dynamics during real-world navigation of individuals actively exploring their environment is, however, facing similar confusion as is present in the rodent literature.

While the links between locomotion abilities and cognitive functions have been investigated widely in both healthy and clinical populations (Allali et al., 2008; Scherder et al., 2007; Sheridan, Solomont, Kowall, & Hausdorff, 2003), very few studies have investigated the neural dynamics underlying these interactions.

8.1.3. Motion-related noise in surface-EEG during walking

A series of technically oriented studies, aiming to advance the field of mobile EEG in terms of signal processing, have focused on the characterization of movement-related noise in the EEG during physical activity, and the development of solutions to parse non-brain from brain signals. These studies have assessed the impact of movement intensity by manipulating the speed at which participants were walking on a treadmill (Gwin et al., 2010; Kline, Huang, Snyder, & Ferris, 2015; Oliveira, Schlink, David Hairston, König, & Ferris, 2017; Reis et al., 2014; Snyder, Kline, Huang, & Ferris, 2015). Most of the solutions proposed in these papers have been integrated in the mobile EEG processing pipeline presented in Chapter 2. In principle, the (imperfect) parsing of motion-related noise from brain signals, should however not attenuate the EEG dynamics associated with the cognitive processes supporting walking. The present study will, therefore, focus on the investigation of EEG dynamics associated with cognitive aspects of walking by varying walking speed.

8.1.4. Cognitive markers of human locomotion

While the interdependence between locomotion and cognitive performance has been extensively studied through behavioural and task performance measures during cognitive-motor dual-tasks, the characterization of neural markers reflecting cognitive processes involved in human locomotion has only been recently investigated. One of the first published study by Arnolds, Lopes Da Silva, Aitink, Kamp, & Boeijinga (1980) reported increases of hippocampal activity in the theta band in relation to active behaviour in an epileptic patient. The patient was asked to perform an object naming task twice, and write the name of the presented objects on a blackboard placed 4 meters in front of her. In one condition, the patient was performing this task at her own pace, while in the second part the participant was instructed to walk ‘briskly’. Power spectral activity was significantly higher in the theta-band in association with higher physical activities (walking > writing > sitting). This early single-case intracranial EEG study highlighted a robust relation between natural behaviours in a three-dimensional space and spectral EEG dynamics in the theta band at hippocampal sites, consistent with a large body of observations reported in other mammal species (Buzsáki, 2002).

The neural network underlying walking encompasses several roles, such as the reception and integration of multisensory feedback, as well as the emission of descending motor commands through communications between cortical and subcortical networks and spinal neuronal circuitries (Niell & Stryker, 2010). For example, Bruijn, Van Dieën & Daffertshofer (2015) have reported increased activity in the premotor cortex in relation to balance control during walking. Participants were walking on a treadmill either normally or while being laterally stabilized by elastic chord. Bilateral sources (independent component clusters) of beta activity increase were found at surface electrodes located over the premotor cortical areas (Cz, C3, C4) as balance control demands were reduced in the stabilized condition. This finding suggests that postural and balance control dynamics during locomotion may be indexed by spectral modulations in the beta range (12-30Hz). By contrast, Hülsdünker, Mierau, Neeb, Kleinöder & Strüder (2015) have interpreted changes in theta in relation to transient balance instability as indexing continuous balance control during a range of balance tasks. Upright walking involves constant balance control throughout the gait cycle, as every step perturbs whole body posture and effectively challenges one’s stability.

The adaptability and flexibility of gait is however crucial to maintain and recover balance while putting the whole body in motion (IJmker & Lamoth, 2012). Evidence for this view comes from Wagner et al. (2016), who applied a source-estimation based analysis (see sections 2.2.2.4 & 2.2.2.5) to high-density EEG data (108 electrodes) recorded while participants adapted their gait to auditory cues. This study highlighted distinct oscillatory networks underlying gait adaptation in the beta range. An increase of prefrontal beta power was found in relation to adaptation difficulties, potentially reflecting a higher load of resources required to meet the motor control demands of the adaptation. A suppression of beta power was observed in central and parietal regions following the presentation of a tempo shift cue. This effect has been interpreted as reflecting cognitive control aspects of motor planning and execution (Seeber, Scherer, Wagner, Solis-Escalante, & Müller-Putz, 2015, 2014).

Further evidence for speed related neural correlates of gait comes from Bulea et al. (2015), who reported spectral modulations of prefrontal and sensorimotor areas (using a source localization approach) when participants were adapting their walking speed to either a slow or fast pace on the treadmill. More specifically, prefrontal theta and beta synchronization were prominent throughout gait cycles when participants had to adjust to a faster pace, while sensorimotor alpha desynchronization was observed when participants had to decrease their walking speed. This study used a high-density EEG system and periods of stillness as a baseline to compute gait-related spectral perturbations, which may prove to be impractical within the frame of real-world brain imaging data, as periods of stillness may not conveniently precede data segments of interest.

In a recent study, Cevallos et al. (2015) investigated oscillatory signals associated with the execution, imagination and observation of walking behaviour, highlighting modulations in theta, alpha and beta frequency bands associated with gait dynamics at surface recording sites anatomically placed over sensorimotor areas (C3 and C4 electrodes). Similarly, in parallel to the EEG studies mentioned, evidence from fNIRS studies has also highlighted patterns of prefrontal brain hemodynamics reflecting cognitive-walking interference in healthy aging individuals performing basic arithmetic operations and verbal tasks while walking (Mirelman et al., 2014, 2017). These findings demonstrate that brain dynamics related to walking are observed at different locations at a surface level, suggesting that distributed network underlies functional aspects such as motor planning and control of gait.

Taken together these results underline two main types of spectral dynamics associated with walking activity: 1) sensorimotor spectral dynamics (seen at the Cz electrode) reflecting motor aspects (preparation and adjustment) of walking whose frequency is tuned to gait cycle, and 2) frontal and parietal dynamics (seen at Fz and Pz electrodes) indexing the cognitive load related to the demands of motor performance (changing speed, concurrent cognitive task) (Miller, 2007).

8.1.5. Aims

In the previous studies presented in this thesis walking speed was not the primary focus of investigation and, as such, was either carefully controlled or systematically recorded to ensure that it remained consistent across the different experimental conditions. However, the contribution of variations of walking pace to the EEG signals remains largely unknown. This study therefore aims to quantify the effect of walking speed on brain dynamics recorded at frontal (Fz), central (Cz) and parietal (Pz) sites in order to build an understanding of how walking speed variations might affect EEG recordings.

8.2. Methods

8.2.1. Participants

Twenty-five participants (age range = 18-40, mean = 22; 23 females) completed this study. The participants were clear of any neurological antecedents and did not indicate any of the exclusion criteria (section 3.2.1). Detailed information concerning the study and EEG recording procedures was given to, and written consent obtained from, all participants prior to the experiment.

8.2.2. Experimental design

The present study investigated the effect of walking speed on EEG spectral dynamics. More specifically, guided by previous evidence, this experiment aimed to explore frontal theta power in relation to locomotion speed. For this purpose, background EEG was recorded while participants were walking at 5 different paces. The experiment followed a pyramidal design which consisted in a gradual progression from the slowest (3km/h) to the fastest (5km/h) walking pace, followed by a progressive return to the slowest pace, with a consistent increment of 0.5km/h between trials. Therefore, data was collected across 5 walking speeds: 3km/h (0.83m/s); 3.5km/h (0.97m/s); 4km/h (1.11m/s); 4.5km/h (1.25m/s); and 5km/h (1.39m/s). Following this design, participants walked twice at each pace. Each trial was 30 seconds long, followed by a transition period for the experimenter to ensure that the participant was feeling comfortable and to adjust the treadmill speed.

8.2.3. Material

The participants were walking indoor (in a laboratory environment) on a treadmill (see Figure 8.1). Walking speed was regulated by the treadmill monitoring system. Participants were equipped with a mobile EEG system (see section 3.2.3.1). Prior to recording, participants completed a treadmill-walking habituation procedure to ensure participants' safety and comfort while reducing the self-consciousness related to the act of walking on the treadmill. To ensure participants' comfort and safety, the experimenter asked for feedback about their experience throughout the experiment. There was however no case of interruption across the 25 participants that took part in the study.

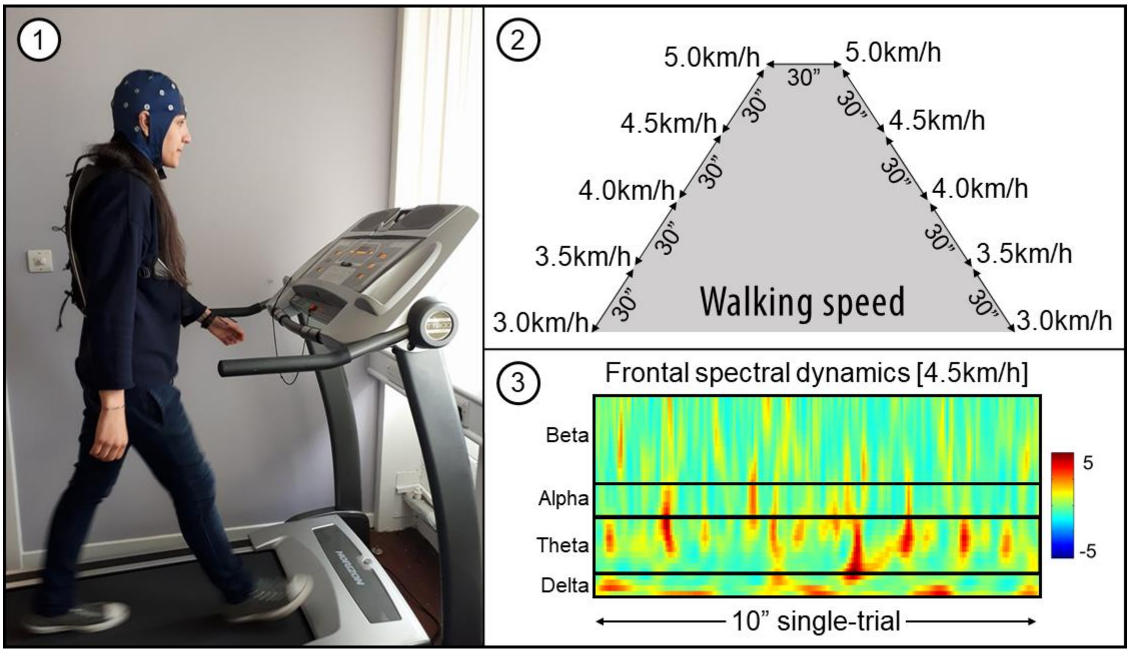

Figure 8.1. Illustration of the experimental setup, experimental design and EEG dynamics recorded in Chapter 8. [1] Participants' walking speed was manipulated through the use of a treadmill paradigm. [2] A pyramidal design was used to incrementally increase or decrease walking speed. Each trial lasted 30 seconds and was followed by a buffer period of approximatively 20 seconds during which the experimenter checked participant's safety and comfort before transitioning towards the following pace. [3] Time-frequency decomposition of single-trial data recorded at frontal site (Fz electrode) during the 4.5km/h (1.25m/s) walking speed. Periodic "bursts" of spectral activity can be observed in the delta and theta bands. These non-stationary episodes of increased activity at lower frequencies cause temporary spectral leakages across alpha and lower-beta bands.

8.2.4. EEG data processing

The processing procedure applied to the data collected in the present study was consistent with those applied in Chapters 6 & 7 (see sections 6.2.6 and 7.2.4).

8.2.5. Data analyses

For the EEG data, mean power spectral activity across the entire trial was quantified discretely for each walking pace. Normalization of mean power spectra was performed by subtracting the average power of the slowest walking pace (based on a theoretical additive model, see Grandchamp & Delorme, 2011). Therefore, the four normalized walking paces have been included in further analyses. Power spectra were computed on a single-trial basis using Welch's method (1967) (which is a variant of Fourier Transform, for further details see section 2.3.3.2), by segmenting the 30 seconds trials into 30 consecutive segments of one second and then averaging the 30 resulting power spectra together. The two trials of each walking speed were then averaged together, giving the participants' power spectra for the corresponding walking pace. Mean power within *a-priori* frequency bands (Delta: 1-3.5Hz, Theta: 3.5-8Hz, Alpha: 8-12Hz, and Beta: 12-30Hz) were then discretely quantified and subject to statistical comparisons across walking speed. Furthermore, single-trial power peak amplitude and frequency were extracted within each *a-priori* frequency band. Pearson's correlation coefficients were computed between spectral features (mean power, peak amplitude and peak frequency) and walking pace for each frequency band (delta, theta, alpha and beta) and recording sites.

8.3. Results

To address questions regarding the contribution of walking speed variations to the results reported in Chapter 7, and based on previous literature reporting a range of spectral dynamics associated with the performance of active behaviours at (pre)frontal, central (sensorimotor) and parietal regions (see Section 6.1.1), the analyses are focused on brain dynamics recorded over frontal, central and parietal midline recording sites (Fz, Cz and Pz electrodes). The inclusion of such evenly distributed midline electrodes (see Figure 3.2) allowed investigation of the spatial distribution of spectral modulations associated with walking speed.

In combination with the traditional mean power spectral analysis of individual frequency bands, power-peak analyses provide additional information regarding local spectral features that may be sensitive to experimental manipulations within *a-priori* frequency bands. Moreover, as a measure of power spectral magnitude, the use of power-peak amplitude may be less sensitive to inter-individual differences (in terms of frequency bands range) than the averaging of spectral activity across bands (that are strictly delimited based on a traditional *a-priori* approach).

The present results highlight three distinct patterns of results (summarized in Table 8.1). Walking speed was found to be significantly correlated with spectral power amplitude (peak amplitude is a more sensitive measure to this relationship than mean spectral power) in the lower frequency range (delta and theta) across all recording sites (see Figure 8.2). This spatial pattern suggests that the effects of walking speed on low-frequency power are widespread. It can be noted that delta features were strongly associated with walking speed at central electrode. Frontal theta was not only correlated with walking speed in terms of the magnitude of spectral power (both in terms of peak amplitude but also overall band power) but there was also a positive relationship between the peak frequency and walking speed. The amplitude of frontal beta peaks was strongly correlated with walking speed.

		Delta [1-3.5Hz]	Theta [3.5-8Hz]	Alpha [8-12Hz]	Beta [12-30Hz]
Fz	Mean spectral power	r = .189, p = .06	**r = .399, p < .001**	r = .276, p = .005	r = .168, p = .094
	Power peak amplitude	**r = .384, p < .001**	**r = .357, p < .001**	**r = .348, p < .001**	**r = .718, p < .001**
	Power peak frequency	r = -.173, p = .086	**r = .335, p < .001**	r = -.115, p = .254	r =-.071, p = .483
Cz	Mean spectral power	**r = .443, p < .001**	**r = .349, p < .001**	r = .085, p = .401	r = .134, p = .184
	Power peak amplitude	**r = .582, p < .001**	**r = .314, p = .001**	r = .163, p = .105	r = .208, p = .038
	Power peak frequency	r = -.085, p = .398	r = .080, p =431	r = .023, p = .818	r = -.151, p = .134
Pz	Mean spectral power	r = .231, p = .021	r = .214, p = .032	r = -.054, p = .591	r = -.019, p = 849
	Power peak amplitude	**r = .375, p < .001**	r = .298, p = .003	r = .007, p = .946	r = .024, p = .810
	Power peak frequency	r = -.052, p = .604	r = -.017, p = .867	r = -.100, p = .322	r = .152, p = .131

Table 8.1. Summary of the correlation coefficients between walking speed and the different spectral features investigated (mean activity within the whole band, peak amplitude and peak frequency) across recording site. Moderate relationships (Pearson's correlation coefficients > .30) are highlighted in different colours potentially reflecting distinct patterns of correlation.

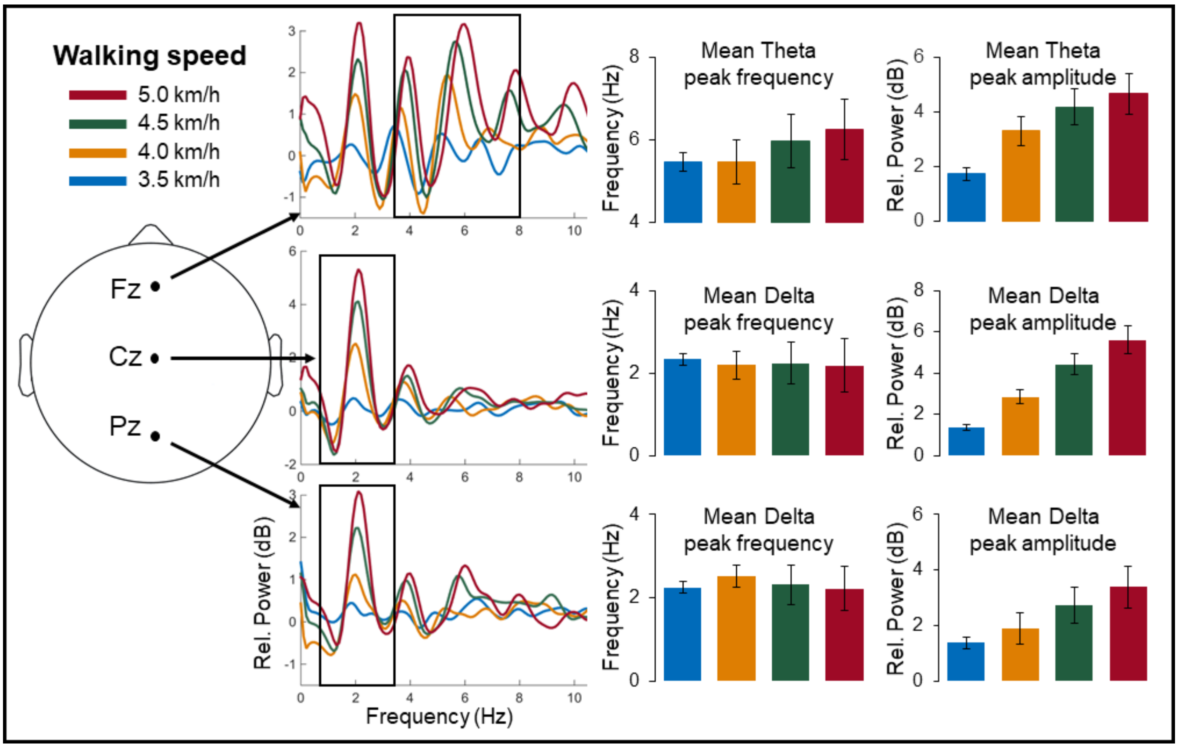

Figure 8.2. Grand-average power spectral activity across lower frequencies (delta and theta bands) associated with walking speed across midline recording sites (dB change relative to baseline). The coloured lines represent power spectral activity for the different walking speed (3.5km/h in blue, 4.0km/h in orange, 4.5km/h in green, 5.0km/h in red). Power spectra plots are presented following a classic scalp map representation (frontal site at the top, central site in the middle and parietal site at the bottom). It should be noted that the scale used to plot power spectra amplitude at electrode Cz is larger than the other recording sites. [1] A strong increase in low-frequency activity (around 2Hz) as a function of walking speed is observed across recording sites, with the largest amplitude found at central electrode Cz. The fact that the same peak amplitude modulation is repeated at regular intervals while decreasing in magnitude suggests that the initial modulation of power spectral activity at the fundamental peak (around 2Hz) has repercussions across its directly following peak harmonics. [2] In addition to the previous pattern characterized by harmonics peaks decreasing in amplitude across the theta band, frontal electrode Fz presents a second peak in the theta band (around 6Hz). This second peak appears to not only be modulated by walking speed increase in terms of its amplitude, but appears to be also sensitive in terms of the frequency at which the effect was observed. This result suggests that frontal theta peaks may index the variations of the stepping frequency (e.g., slower walking pace implies longer gait cycles, and faster walking speeds imply more gait cycles per seconds (Grieve & Gear, 1966; Seitz & Köster, 2012; Seyfried, Steffen, Klingsch, & Boltes, 2005).

8.4. Discussion

The present results highlight the effects of walking speed increase on EEG power spectrum. From these results, three main spectral modulations induced by walking speed increase can be distinguished. The first pattern is a distributed effect (i.e., across all electrodes) of walking speed on the amplitude of spectral power observed within the lower frequencies (delta fundamental peaks around 2Hz and following harmonics at 4, 6 and 8Hz). Secondly, the amplitude and frequency of theta peaks followed a similar increase as a function of walking speed at frontal electrode specifically. Finally, a third effect of walking speed on spectral power was found in frontal beta. The relationship between walking speed increments and frontal beta power was strongly significant (i.e., large effect size) at frontal electrode specifically. The spatial and spectral distinctions made between the effects of walking speed observed across the EEG power spectrum suggest that these effects are of different nature. The following sections will discuss the interpretation of these pattern of spectral activity as either reflecting motion-related noise contaminating the EEG power spectrum, or as indexing cognitive processes associated with locomotion speed. The present findings highlight a dissociation between motion-related noise and cognitive effects related to walking speed. Importantly, the pattern of spectral effects associated with spatial memory reported in the previous study (Chapter 7) does not present a spectral pattern associated with motion-related noise. The present findings therefore provide further support for a cognitive interpretation of the results reported in the previous studies, while underlining the incidence of walking speed variations on EEG power spectrum.

8.4.1. Distributed effect of walking speed on low-frequency activity

The spectral activity across slower frequency bands (delta and theta) was found to significantly increase as a function of walking speed across recording sites. The correlation coefficients were higher for the power peak amplitude than the mean power within a band, suggesting that the relationship between walking speed and power was specific to peaks at certain frequencies, rather than reflecting a whole band modulation. Despite its global distribution across the scalp, it should be noted that the magnitude of this widespread effect of walking speed on delta band power was the most prominent at central recording site Cz. This spatial distribution is in line with previous research highlighting power spectral increase during gait at recording sites in the vicinity of the sensorimotor cortical area (Ferezou et al., 2007; Hamacher et al., 2015; Petersen, Willerslev-Olsen, Conway, & Nielsen, 2012).

The power peak analyses revealed that faster walking speeds (4.5 and 5km/h) presented fundamental peaks within the delta band whose harmonics peaks spread across theta. This finding is consistent with findings from Castermans et al. (2014), reporting increasing peak amplitude at low-delta frequencies in relation to walking speed increase. Moreover, as can be seen in Figure 8.2, the delta fundamental peaks exhibit harmonics peaks that gradually tapper off over the next frequency bands. Even though gait dynamics and body kinematics were not object of the present investigation, it appears plausible that these delta peaks may be associated with the rhythm of the gait cycle (i.e., stepping frequency) and/or physical aspects of walking that present oscillatory pattern (i.e., arms swing, head movements, trunk inclination). This first pattern of low-frequency modulation is potentially reflective of the involvement of cognitive processes supporting motor execution, but could also reflect the contamination of the signal by motion-related artifacts.

Even though the increase of delta peaks magnitude as a function of walking speed and following harmonics was most prominent at the central electrode site, this effect was also observed at frontal and parietal midline electrodes. The widespread spatial distribution of the observed effects on low-frequencies questions the interpretation of delta harmonics as reflecting movement-related artifacts, rather than motor and cognitive processes associated with walking. Indeed, the increase of overall spectral power appeared to be strongly associated with delta power peaks, which is in line with previous findings reporting global increase of EEG activity in relation to walking speed (Castermans et al., 2014; Gwin et al., 2010; Lau, Gwin, & Ferris, 2014). As mentioned in the introduction, these technically oriented studies have focused on the characterization of movement-related noise in the EEG to develop novel signal processing methods to address the specificities of real-world EEG recordings. Based on this body of work, a unique signal processing procedure was applied to the EEG data collected within the frame of this study. This processing pipeline included the pruning of independent sources contributing to the EEG signal that were deemed artifactual (see section 2.2.2.2). A higher proportion of independent components were selected for rejection when participants were walking at faster speeds. This difference suggests that walking speed accelerations induced a greater proportion of noise in the original EEG signals prior to processing. The rejection of artifactual components does not however guarantee that the pruned data is completely free of motion-related noise. Therefore, the explanation of differences in low-frequency spectral power observed between conditions in terms of non-brain artifactual signals cannot be ruled out entirely.

The increase of delta and theta power as a function of walking speed reported here is in line with previous findings linking low-frequency activity with the execution of motor tasks. Nonetheless, it is important to consider the pattern of delta power peaks and its consequences over following frequencies; the distributed increase of delta peak amplitude and following harmonics peaks question the classification of this effect as reflective of a cognitive process. Indeed The present analyses cannot completely rule out the contribution of potential artifactual sources to the changes in delta power peaks observed (Gwin et al., 2010). Future studies may benefit from novel signal processing appraoches based on the subtraction of motion-related artifacts from EEG signals (acquired by template matching regular EEG channels to counterparts “phantom channels” that are isolated from scalp electrical signals to specifically record motion-related noise) to further help disentangling brain signals from noise in data recorded during motion (Oliveira et al., 2017; Oliveira, Schlink, Hairston, König, & Ferris, 2016a).

Interestingly, while the increase of delta power peaks was observed across all electrodes, modulations of spectral power within the theta, alpha and beta bands was only observed at frontal electrode Fz. This specific modulation of theta, alpha and beta power recorded at the frontal electrode potentially reflects distinct processes, for example the cognitive processes of motor control, the argument for which will be unpacked below.

8.4.2. Increase of frontal theta peak amplitude and frequency

A distinct effect was observed as a second fundamental frequency peak found at the frontal recording site, whose harmonics were distributed across the theta to beta range, leading to significant modulations across these bands (which was not reflected over central and parietal electrodes). The modulation of frontal theta peaks amplitude as a function of walking speed followed the same pattern as the delta power peaks recorded at central and parietal electrodes. Based on previous findings, a plausible interpretation of this increase of theta power peak in relation to walking speed is that frontal theta amplitude reflects the cognitive and motor processes involved in faster walking. This interpretation is consistent with recent evidence from fNIRS recordings, showing that frontal haemodynamics are associated with adaptation of walking and running speed on a treadmill (Harada, Miyai, Suzuki, & Kubota, 2009; Suzuki et al., 2004). In addition, the frequency of the frontal theta peaks appeared to be modulated by the walking speed. Indeed, the magnitude of theta power peaks not only increased as a function of walking speed, but the frequency at which these peaks were observed increased incrementally as well. Theta power peaks were found at faster oscillatory rates when participants walked at a faster pace, suggesting a tuning of frontal spectral dynamics to the walking pace. According to this interpretation, frontal theta power peaks may reflect the cognitive demands associated with motor skill execution (Wong, Chan, & Mak, 2014). Moreover, it can be noted that this pattern was not characteristic of delta power peaks, further distinguishing the frontal theta peak increase as a separate effect. This more local frontal effect could reflect the cognitive cost associated with the increased demands in terms of motor and balance control that arise during faster walking pace. This elevation of slow rhythmic activity at frontal recording site is in line with previous animal literature that reported increase of frontal slow spectral power as a function of locomotion speed in rodents.

These present results show similarities with the recent findings of movement-related theta dynamics in the medial temporal lobe during locomotion using intracranial EEG (Aghajan et al., 2016), but also reveal that this effect is observable at frontal and central surface electrodes as well. Taken together, these results highlight a major effect of walking speed on power recorded within the delta band, while suggesting that gait cycle plays an important role in that phenomenon, with the frequency at which delta power peaks were observed also increasing as a function of walking speed.

8.4.3. Increase of beta peak amplitude as a function of walking speed

A strong correlation between walking speed and the amplitude of peaks within 17-20Hz range was observed frontally. This finding is consistent with the previous empirical evidence linking activity within 12-30Hz range with motor control of ongoing actions (Engel & Fries, 2010). By contrast, the motor planning and execution of new voluntary actions have been linked with the suppression of beta oscillations at the expense of faster gamma oscillations (30+Hz) (Gilbertson, 2005). In the specific case of walking, previous studies have shown that a transient desynchronization of beta activity usually occurs prior to gait initiation and during gait adaptation (i.e., changing stride length to avoid an obstacle), indicating a reallocation of motor processes previously dedicated to the continuation of steady-state motor outputs towards the planning and execution of adaptative motor schemes. The sudden increase of beta power following desynchronization (beta rebound) has been interpreted as reflecting an inhibition of adaptive motor processes to regulate motor related activity back to the initial *status quo* (Kristeva, Patino, & Omlor, 2007). Based on the theoretical framework of beta activation reflecting steady-state motor processes, Pogosyan, Gaynor, Eusebio, & Brown (2009) have shown that the specific stimulation of cortical structures at

20Hz (using transcranial Alternating-Current Stimulation) slowed down the execution of novel voluntary actions. Therefore, the increase of beta activity observed in the present study may reflect the inhibition of motor processes that were not directly relevant to the task. In the context of a limited cognitive resources framework (Kahneman, 1973), this would mean that increasing the complexity/difficulty of the walking task increased the cognitive load of walking at the detriment of concurrent processes. It is therefore expected that walking faster may reduce the amount of cognitive resources that can be dedicated to the execution of concurrent actions.

Previous studies have reported beta power increase in relation to physical activity and walking demands at parietal sites (Aghajan et al., 2017; Arnolds et al., 1980). While in the present study such effects were not observed at parietal electrode, it should be noted that these findings come from intracranial recordings that provide a much higher signal-to-noise ratio than surface recordings, which may be essential to the capture of this effect. Following this assumption, the present findings may therefore indicate that this effect, even though observed parietally in intracranial recordings (that were limited to parietal cortical regions), is observed frontally in surface EEG recordings. Another explanation is that parietal beta modulations are phasic gait-related spectral perturbations (Seeber, Scherer, Wagner, Solis-Escalante, & Muller-Putz, 2014; Wagner et al., 2016) reflecting transient desynchronization of the steady-state motor control dynamics to adapt the gait to various circumstances (i.e., speed variation, obstacle avoidance). These transitory spectral dynamics are usually followed by a rebound effect, that normalizes beta dynamics back to an equilibrium of the motor steady-state activity (Y. Zhang, Chen, Bressler, & Ding, 2008). According to this view, therefore, the quantification of beta activity over long time series (like those used in this study) is inherently not sensitive to transient spectral dynamics (see section 2.3.4.1).

8.4.4. Conclusion

In the present study, the effect of variations in locomotion on spectral EEG dynamics was investigated systematically to look at the effect of walking speed. It is useful to shed light on the brain dynamics related to locomotion that experimentally are often a confound during the execution of natural behaviours, as demonstrated by research on physically active animals solving cognitively challenging tasks. This approach is particularly relevant to ensure the validity of the interpretations drawn from EEG dynamics recorded during natural behaviour. Indeed, it is important to consider the impact of natural behaviours (and their variations) on EEG measurements to accurately interpret the modulations observed in real-world EEG data as reflective of cognitive processes. Our results are consistent with the animal and intracranial EEG literature that reveal theta activity recorded at frontal recording sites is sensitive to locomotion speed. Put simply, the tuning of frontal theta features to walking speed suggests that frontal theta may index cognitive processes supporting motor control of walking. It remains however unknown whether these frontal theta features specifically reflect processes underlying motor functions or part of higher order cognitive functions. Due to the interdependence of such cognitive of motor processes, it is therefore difficult to disentangle the individual contribution of these aspects on the effects observed.

With regards to delta activity, such selectivity was not clearly evident. The increases in delta activity related to walking speed were evident across electrodes. Such generalised distribution may reflect motion-related noise in the EEG, which is in line with previous reports of overall EEG delta power increase as a function of physical activity (Castermans et al., 2011, 2014; Cevallos et al., 2015; Gwin et al., 2010, 2011). This interpretation in terms of noise is challenged however by the prominence of the effect over the central electrode, potentially reflecting selectivity related to sensorimotor processes. Further research is required to clarify why the effect is selective to the delta band. The current work did not include gait related analysis, which may clarify the issue of selectivity in future work, especially considering the fact that stepping frequency may be implicated in the modulation. Co-registration of gait dynamics may provide useful information to segment the continuous active-state EEG data and, providing further insight into the brain dynamics associated with the execution of walking behaviour (Knaepen, Mierau, Fernandez Tellez, Lefeber, & Meeusen, 2015). For example, time-locking of the different phases of the gait cycle may reveal distinct patterns of oscillatory dynamics reflecting cognitive and motor processes serving gait adaptability. Similarly, the study of low-frequency spectral dynamics in relation to gait events (heel strikes, phase-related activity within the gait cycle) at various speeds and under different difficulties (i.e., uneven ground, presence of obstacles) may further shed light on the role of frontal and sensorimotor spectral dynamics during walking. If delta activity reflects a cognitive process, then brain oscillations in intact function would tune to the rhythm of behaviours (such as the gait cycle). In compromised function (e.g. falls in the elderly or neurological patients), poor sensorimotor integration would be reflected in a lack of such tuning. The practical implications of such discrepancies between behaviour cycles and brain oscillatory patterns linked to poorer task performance would allow for prediction of behavioural failures (e.g., missing a ball in the context of juggling, falling or stumbling in the context of walking). More speculatively, in the future, the mismatch between brain and behavioural dynamics synchrony could inform neurofeedback interventions (e.g., falls prevention, rehabilitation of gait).

Future studies will likely involve brain imaging of walking under different experimental situations involving the manipulation of task difficulty (e.g., presence of obstacles, changes in walking pace, terrain types and inclination) and on different populations (patients with motor impairments following neurological aetiologies, neurodegenerative diseases with important impact on sensorimotor abilities such as Parkinson’s disease) to shed light on the specificities of adaptive brain mechanisms during locomotion. In this context, frontal theta dynamics may provide a measure of the cognitive load associated with the adaptation of behaviour according to situational circumstances. Further down the line, these brain dynamics could be used within the frame of neurofeedback tools for the assessment and rehabilitation of a range of behaviours that require flexibility in order to adapt to the specificities of the environment.

Considering the magnitude of the changes in overall spectral power introduced by systematic increases in walking speed, the present findings suggest that it is advisable to control for walking speed during real-world EEG investigation, especially if high fluctuations of walking speed are expected. In terms of signal processing of real-world brain imaging data, accounting for dynamic changes of walking pace advocates for the use of single-trial based normalization approaches (Grandchamp & Delorme, 2011) rather than computing baseline corrections based on the average of the prestimulus activity across many trials that may display a wide range of associated walking speeds.

The present findings pose questions regarding the oscillatory dynamics during gait and balance control, and more generally about the role of slow-oscillations in the context of motor control of a wider range of active behaviours. Indeed, the tuning of spectral brain activity to the step frequency indicates the sensitivity of active-state (i.e., activity over extended periods of time during active behaviour as opposed to resting-state dynamics typically recorded during periods of mental stillness) brain dynamics to cyclic behaviours. An extension of the present work could look at the execution of different cyclic behaviours to corroborate the present findings. Moreover, it would be interesting to explore how, and at which stage, active-state tuning occurs within the frame of skill acquisition. Active-state dynamics could be recorded throughout the different stages of learning a novel motor skill that presents an element of rhythmicity. A practical example would be to investigate the progression of active-state dynamics as participants learn to juggle. Exploring the relationships between behaviour and brain active states as participants improve and integrate the motor schemes involved in the execution of complex behaviours would shed light on the links between active-state rhythmicity and skill acquisition.

Chapter 9: General Discussion

9.1. Summary of findings

Throughout this thesis it has been demonstrated that human cognition can be successfully captured through mobile brain imaging. In a first series of studies (Chapters 3, 4 & 5), attentional processing of task-relevant information under real-world circumstances was explored. Across a series of three P300 ERP experiments, aspects of real-world experience underlying reallocation of attentional resources have been investigated. This series of studies has incrementally narrowed down the factors driving a recapture of attentional resources during natural behaviour. These findings have highlighted the prominent interference of the visual flow of information but also the role of the integration of input related to displacement through the environment in the distribution of attentional resources. These findings have also demonstrated that walking activity is not a significantly taxing behaviour in terms of attentional resources for healthy subjects. From a theoretical standpoint, the results support an interactive model of attentional capacity between different modalities, as opposed to a segregation of attentional resources across different modalities. Furthermore, these results suggest that attentional processing is inherently bound with our experience of the environment, providing additional support for an embodied theoretical framework of human cognition.

In a second series of studies (Chapters 6 & 7), brains oscillations associated with spatial memory were investigated during real-world navigation tasks. A first critical finding is that theta oscillations indexing spatial cognitive processes, usually recorded at hippocampal sites invasively, were recorded in physically active human participants using scalp EEG. The results are consistent with previous findings issued from both invasive animal and human brain imaging studies that have documented theta waves associated with memory mechanisms originating from the hippocampus and projecting to frontal and prefrontal cortical areas. Following this initial result, a second study explored the specificity of frontal theta dynamics as reflecting either memory, spatial memory or navigational processes. The spatial navigation condition was associated with frontal theta increase while the memory conditions did not exhibit increase of frontal theta activity. Moreover, this frontal power increase was also observed across the delta and alpha frequency bands, indicating that this navigational effect is associated with modulation across low-frequencies. It also appeared that holding spatial information in mind elicited an increase of parietal gamma power, as commonly found in the working memory literature.

In Chapter 6, theta activity associated with the performance of the navigational task became more prominent as the participants got closer to their destination. This finding was further explored in Chapter 7 by splitting the trials into three segments corresponding to the position of the participants relative to the destination. Interestingly, when participants had to find their way based on previous learning of the environment, a progressive increase of frontal theta activity was observed across the different segments of a trial as participants get closer to their destination. This pattern of frontal theta dynamics was not observed in the memory conditions. However, the spatial memory condition also presented a progressive increase of parietal gamma activation. These findings not only demonstrate that brain dynamics associated with spatial navigation can be recorded in the real-world using surface electrodes but also highlight the context-dependent nature of cognitive processes involved in spatial navigation. Moreover, a double dissociation was observed in spectral dynamics associated with wayfinding and spatial memory: frontal low-frequency oscillations were associated with wayfinding, while parietal high-frequency oscillations were associated with spatial memory. The implication of this finding is that distinct cognitive processes underlying real-world navigation can be recorded using surface EEG recordings in actively behaving subjects.

The present thesis also reported clear patterns of rhythmic brain activity associated with walking speed at different paces on a treadmill (see Chapter 8). The findings reveal an overall increase of spectral power across lower frequencies (ranging from delta to alpha) as a function of walking speed across midline electrodes. It appeared that this gradual overall increase was mainly driven by the amplitude of delta peaks that were most prominent at central midline recording site but spread over frontal and parietal electrodes as well. Importantly, frequencies at which amplitude peaks were observed gradually increased as a function of walking speed highlighting the link between EEG and behavioural dynamics. Moreover, power peaks across frequency bands were all highly correlated with delta peak amplitude. This high correlation, in addition to the fact that peaks' frequency occurred at fixed intervals across the frequency spectrum, progressively tapering off, suggest that the peaks observed at higher frequencies were harmonics of the initial delta fundamental spectral activity. Even though gait dynamics were not recorded in the present experiment, nor participants stride length, it is plausible that the fundamental delta peak corresponds to gait rhythm. This unique pattern of oscillations associated with walking speed appeared to be independent from the spectral modulations observed in Chapters 6 and 7.

The significance of walking speed findings is that it highlights the critical incidence of behavioural dynamics, in this case the gait cycle, on mobile EEG data acquired during natural behaviour. Critically, the data underline the importance of adopting an integrative interpretation of mobile cognition data, in light of both brain and body dynamics. Moreover, the very distinctive increase of power spectral activity across harmonics was not found in Chapter 6 & 7, in which walking speed remained stable. It should be noted that only substantial walking speed increments (i.e., 1km/h change) yielded significant impact on power spectral power. The absence of motion-related spectral features in these studies may be related to the fact that the effect was most prominent at the fastest walking speeds (4.5 & 5km/h), which were faster than the natural walking pace participants consistently maintained during the spatial navigation experiments. The absence of such a distinctive walking-speed related spectral pattern in the navigation-related EEG data furthermore suggests that the effects reported in Chapter 6 & 7 could not be accounted for by the confound effects of walking-related brain differences.

Taken together these findings provide further evidence for the relevance of mobile brain imaging for the study of embodied and ecological aspects of human cognition. In the following sections, the theoretical implications of the present findings will be discussed along with a reflection about future developments of mobile cognition. Potential research and practical applications for such a mobile cognition approach will be discussed in light of the current state of the wider cognitive research literature, and the exploration of this issue will be illustrated by highlighting some preliminary findings from ongoing research following the mobile cognition philosophy developed throughout this thesis.

9.1.1. Highlighting embodied aspects of human cognition

A recurrent theme in the interpretation of the findings across the different studies relates to the embodied nature of the cognitive effects reported. Indeed, the impact of bodily experiences on the modulation of cognitive EEG markers underlines the relevance of studying human cognition while considering its embodied nature. This work provides additional evidence supporting the embodiment theory, which posits that the nervous system plays a pivotal role at the interface of the body and the environment. From this theoretical standpoint, human cognition serves to adapt the course of actions in real-time according to the feedback of bodily sensations and in face of the dynamic reality of the surroundings. Conversely, a set of actions has the potential to alter the current state of one’s environment, applying a dynamic retroactive interactive loop between one’s body and the environment, from which cognitive experiences emerge. Therefore, integration of both of these interdependent sources of input is crucial in order to produce time adequate behaviours to the situation.

This hypothetical interplay between body, brain and the environment has been observed in the results reported in this thesis. For example, the series of studies on spatial navigation and memory workload have highlighted the fact that one’s position in the environment with respect to the goals pursued yields significant impact on brain dynamics. Furthermore, the series of studies unravelling factors underlying changes in attention (as indexed by the P300 ERP effect) has shown that both bodily experiences and environmental factors have significant impact on one’s allocation of cognitive resources when participants are actively engaged in a complex environment. The confirmation of embodiment effects during real-world behaviours has important implications for cognitive research, making the case even stronger for the consideration of ecological and dynamic aspects of real-world cognitive and physical experiences. Consequently, investigating embodied cognition implies that the relations between behaviour and cognition has to be framed within its environmental context. In order to fully capture cognitive processes and document brain anatomical substrates underlying dynamic and complex behaviours, it is essential to investigate these behaviours under a multidimensional and continuous spectrum of circumstances that genuinely reflect the performance of such behaviours with respect to environmental affordances. Furthermore, the present findings underline the critical importance of considering both brain and body dynamics to capture natural cognitive experience. The mobile cognition approach therefore appears to be an important missing piece in efforts to capture and identify mechanisms underlying embodied cognitive functions in face of a complex reality.

9.1.2. Relevance of natural behaviours

Due to its pervasiveness, walking behaviour was part of most of the experimental conditions in this thesis. Even though the act of walking itself was not the primary focus of the presented research, the findings underlined that even slight variations of walking pace yield important effects on brain dynamics in healthy individuals. This natural behaviour appeared to consistently affect cognitive experiences, both directly (changes of walking speed inducing perturbations of brain dynamics, see Chapter 8) and indirectly (due to the implicit increase of visual and vestibular input as a consequence of locomotion that lead to a recapture of attentional resources, see Chapters 4 & 5). While walking activity in itself may seem to be a trivial behaviour due to its automaticity, it is however generally through a long process that individuals acquire the behavioural expertise that allow them to perform the act of walking seemingly effortlessly (Dominici et al., 2011; Ivanenko et al., 2013). This behaviour, like many others, is therefore not innate and young children have to go through the acquisition of a series of motor skills before being able to walk by themselves (Iosa et al., 2015). Moreover, the physical act of walking, whose cognitive and motor dependencies have been extensively investigated in isolation, takes an additional functional dimension when investigated in real-world context. Indeed, walking is a pervasive behaviour that plays an essential role in most of everyday-life activities throughout human life. Its purpose ranges from the simple exploration of one's environment to serving in more complex schemes that contribute to realize one's intentions. Previous cognitive-motor dual-task research has demonstrated that concurrent walking and cognitive performance mutually affect each other, with detrimental effects on the concurrent activity when the difficulty of one task is increased (Suzuki, Miyai, Ono, & Kubota, 2008; Woollacott & Shumway-Cook, 2002). The findings from the ERP studies presented here are in line with these observations, highlighting that implicit aspects of human locomotion in the real-world capture a substantial part of cognitive resources away from the experimental task, affecting participants' performance.

Although the walking tasks employed in the current thesis were relatively simple, it is clearly possible to envisage more complex experiments as an extension of the present research. The dual-task literature has shown that increasing the difficulty of either of the tasks performed concurrently essentially alter the performance of the other task. It would therefore be hypothesized that increasing the demands related to the act of walking (e.g., by introducing obstacles or increasing walking speed) would likely result in similar effects. However, the present results have demonstrated that the motor cognitive demands of walking only explain a minor part of the cognitive resource reallocation occurring during real-world locomotion. Further investigation, manipulating the demands associated with the act of walking, are therefore required to shed light on what other functions are involved. Regardless, the present findings clearly distinguish the respective effects of the physical act of walking and locomotion-related cognitive experiences on attentional processing and cognitive performance. Therefore, locomotion in the real-world can be conceptualized as a fairly challenging behaviour that involves a certain degree of multitasking and a combination of motor and cognitive functions in order to be executed successfully.

In previous research looking into the interaction of cognitive and motor functions, a common observation was that training and acquired expertise reduces the cognitive cost associated with the execution of related behaviours, eventually freeing up more resources available for the performance of concurrent tasks. It is therefore expected that the sensitivity to cognitive-motor interference will be highly dependent on the expertise of the motor task. For example, the cognitive load associated with walking will be significantly higher for young children making their first steps, whereas almost unnoticeable for healthy adults. In theory, this interference effect can be extrapolated to any cognitive-motor interaction and therefore applies to most, if not all, everyday life behaviours although the neural markers sensitive to these interferences might be different from those reported in this thesis depending on the nature of the behaviours investigated. In a similar way to individuals acquiring motor skills, individuals suffering from motor impairments will have to deploy more resources towards the production of certain behaviours. In this context, a mobile cognition approach appears particularly suited to investigate complex cognitive-motor interplay in clinical populations, especially within the frame of cognitive decline during normal and pathological aging. In addition, neural markers recorded under natural contexts will reveal cognitive fragilities with greater sensitivity than traditional assessment tools that are limited in terms of ecological validity (e.g., paper and pencil tests). Conceptually, mobile brain imaging offers a novel way of characterizing brain dynamics in dual motor-cognitive tasks, allowing a wider range of physical activities to be examined, and importantly allowing their recording in natural contexts. The departure from stereotypical movements (e.g., such as grasping and pointing tasks or treadmill walking) to corresponding behaviours in real-life settings will provide a more ecologically valid understanding of the allocation of cognitive resources under everyday life circumstances. The following section explores the relevance of a mobile cognition approach for neuropsychology research but also potential clinical applications.

9.1.3. Applications to the study of problematic behaviours and cognitive deficits

An important methodological aspect to consider is that the sample of participants tested across the different studies presented in this thesis was entirely composed of relatively young and healthy individuals (age range across studies: 18-51). While we previously highlighted the incidental role of walking across the different studies, and acknowledged its impact on cognitive function, all the participants tested were free of any motor impairment. The dual-task literature has extensively documented increased interference effects in motor-impaired populations. Typically, individuals with either cognitive deficits or physical impairments exhibit poorer performance in the context of dual-tasks related to their deficits. The general interpretation of this interference is explained as an increased amount of resources required to compensate for the person's dysfunctions, at the expense of the resources allocated to the performance of the concurrent task. Therefore, it is expected that individuals presenting gait disorders will have different patterns of neural activity and concurrent task performance than healthy individuals under situations requiring any sort of locomotion.

In Chapter 4, healthy participants did not present substantial attenuation of attention associated with the physical act of walking. It is hypothesized that patients with gait disorders would present an attenuation of neural responses to task-related stimuli because of the increased cognitive load associated with the act of walking. However, the presence and extent of these potential differences have yet to be determined under natural ambulatory situations, and may differ depending on the nature and severity of the motor impairment. As mentioned previously, while walking is taken as an example because of its relevance in the interpretation of the findings presented in this thesis, these observations are not limited to walking behaviour but also extend to other complex behaviours. These considerations make the case for the application of a mobile cognition approach to study the expression of motor impairments in the context of natural behaviour.

In the future, neural markers of natural behaviour could be used as sensitive measures for the diagnosis and assessment of motor impairments associated with different neurological aetiologies: within the frame of neurodegenerative disorders (e.g., Parkinson's disease) or following acquired brain lesions (e.g., head traumas, stroke). Conversely, a mobile cognition approach could be used to detect cognitive fragilities within the context of early onset of cognitive disorders by placing individuals in natural situations whose complex nature would uncover potential difficulties that classic neuropsychological testing batteries would not be sensitive to. For example, individuals suffering from executive functions and attentional disorders (e.g., developmental disinhibition in young adolescents (Iacono, Carlson, Malone, & Mcgue, 2002), or neuropsychological disorders following brain lesions (Liua et al., 2011), may present delayed and attenuated neural markers reflecting attentional processing during concurrent motor activities. Therefore, the present findings raise following questions about how natural behaviours affect cognitive processing in clinical populations. Reciprocally, altered cognitive functions is likely to yield negative impact on the performance of everyday life activities. In the context of cognitive decline, the cognitive load related to everyday life activities, relative to the pool of cognitive resources available, may increase the risks of behavioural failures (e.g., falls). Therefore, neural signatures acquired during natural behaviours may provide an indication of how likely the individual is prone to fall, and could inform the deployment of preventive interventions accordingly.

In the frame of this thesis, cognitive aspects related to walking have been investigated. As discussed previously, walking is an essential behaviour of our daily life, and is "cognition-wise" inexpensive for healthy subjects under normal circumstances (i.e., natural speed, flat terrain). Previous research has however shown that walking activity is sensitive to cognitive load (either temporarily in relation to the demands of a specific task or due to long-lasting cognitive impairments following neurological lesions), with increased cognitive demands leading to variations in stride length, changes in walking pace, and loss of stability (Rajagopalan, Litvan, & Jung, 2017). Therefore, gait dynamics may be used as an index of the interplay between motor-cognitive aspects of natural behaviour. These measures may prove value in the assessment of cognitive fragilities and mobility issues with greater sensitivity than current assessment methods. Furthermore, as discussed in the General Introduction, one of the challenge of real-world brain imaging lies in the acquisition of event timing. The use of pressure-sensitive foot insole recording the plantar pressure distribution across an array of sensors allow the timing of gait events, such as heel strike and toe off to be measured (Crea, Donati, De Rossi, Maria Oddo, & Vitiello, 2014). Additional measures from motion sensors and accelerometers can be used to determine stride length and gait velocity (O'Connor, Thorpe, O'Malley, & Vaughan, 2007). From these measures, gait dynamics can be characterized and used in conjunction with mobile brain imaging to map brain dynamics related to walking activity. The disruption of walking activity in clinical populations may be of interest to highlight cognitive difficulties and investigate the impact of such difficulties on cognitive capacity.

While the relevance of brain imaging methods for the study of cognitive impairments following neurological aetiologies does not need much argumentation, neural correlates of problematic behaviours such as addictions (e.g., substance abuse, gambling, etc) and obsessive-compulsive disorders have also been subject to neuroscientific investigations. With regards to the expression of these problematic behaviours that are intimately linked to particular contexts, a mobile cognition approach appears particularly suited to capture brain and body responses provoked by specific stimulation. Indeed, capturing brain dynamics related to the occurrence of inadequate behaviours may help build an understanding of the mechanisms that drive the generation and maintenance of such behaviours. Moreover, monitoring brain activity and body dynamics in specific contexts related to the occurrence of these behaviours would also provide a way to identify factors triggering or reinforcing inadequate behaviours, which would eventually help in devising appropriate therapeutic interventions.

The study of pathological aging is a field of research that could significantly benefit from a mobile cognition approach. The current practice for the screening of neurodegenerative disorders consists of a neuropsychological assessment, sometimes complimented by brain imaging measures. The sensitivity of the commonly used paper and pencil tests is however limited and usually only detects changes in cognitive functions when the neurodegenerative syndrome is already well established. When classic neuropsychological outcome assessment is not clear, MRI scans have been used to assess the presence of physiological markers of neurodegenerative syndrome. Such measures are not always effective however. For example, it has been demonstrated that beta amyloids plates, that are thought to indicate Alzheimer's disease, are also present in healthy individuals (Chételat et al., 2013). Therefore, recent evidence suggests that expensive brain imaging measures, such as PET and fMRI, may lack diagnostic accuracy. The lack of assessment tools to identify the onset of abnormal cognitive decline is of particular importance because early diagnosis allows the patient to benefit from appropriate care, which further helps reducing the risks of falls and slowing down overall functional decline that are commonly associated with neurodegenerative diseases.

Due to the high comorbidity of pathologies typically observed in the aging population, it is often difficult for practitioners to distinguish the origin of dysfunctions, and mild cognitive impairments are often overshadowed by other more apparent pathologies. In addition, progressive decline of cognitive and physical functions is commonly observed within the frame of healthy aging, which makes the diagnosis of degenerative disorders even more challenging. In that context, combined measures of body and brain dynamics during the execution of natural behaviours could provide additional insight on the nature of the deficits observed. Following the same rationale as that for clinical populations, contrasting the expression of cognitive functions between healthy and pathological aging populations during natural behaviours could provide novel insight into the mechanisms associated with the development of neurodegenerative disorders. For example, a similar step-by-step approach as the one used throughout the series of ERP studies (Chapters 3, 4 & 5) to identify the specific factors impacting behavioural and/or cognitive performance could be applied to a wide range of everyday life activities. In the case of an extension of the P300 investigation to aging populations, a reasonable hypothesis would be that a concurrent motor activity such as walking, which cost in terms of cognitive resources has been shown to be relatively low in healthy young subjects, may be more taxing for older subjects. This increased workload related to the physical activity of walking would therefore translate into a significant modulation of attentional responses to target stimuli in older subjects, highlighting a reallocation of attentional resource towards gait and balance monitoring at the expense of other cognitive processes. In the elderly, a shift from automatic to controlled processing of motor behaviour has been observed (Heuninckx, Wenderoth, & Swinnen, 2008; Heuninckx, Wenderoth, Debaere, Peeters, & Swinnen, 2005). This finding suggests that the cognitive demands related to motor control are increased in aging population. This increased cognitive load further limits the adaptability of older individuals in terms of neural resource distribution in the face of multi-tasking challenges. Therefore, assessing the ability of individuals to deploy attentional resources functionally would help identifying potential difficulties that may eventually lead to behavioural failures in the context of everyday life activities.

Previous research has shown that neural markers of cognitive processing such as the P300 present features that changes across the lifespan, such as the latency and the amplitude of the neural responses (Smith, Michalewski, Brent, & Thompson, 1980). In the elderly, marked differences in ERP components have been found between healthy individuals and patients suffering from dementia (for a review see Schiff, Valenti, Pellegrini, Lot, & Bisiacchi, 2008). However, the studies reporting differences in EEG dynamics contrasted healthy individuals with patients that were already at an advanced stage of the cognitive decline process and who were already presenting a large range of cognitive deficits. To date, and despite being a central subject of research efforts, predictive EEG markers of the onset of pathological cognitive decline have not been reliably identified yet. The identification of neural markers associated with cognitive decline may however be a critical element in the development of sensitive and reliable diagnosis at early stages of neurodegenerative disorders. Building upon neuropsychological research that has underlined neural correlates and cognitive markers of mild cognitive impairments, ecological adaptations of the paradigms will likely increase the sensitivity of existing diagnostic methods and possibly reveal measures specifically sensitive to the onset of different stages of neurodegenerative syndromes. For example, the effects of real-world locomotion in healthy subjects presented in this thesis could be investigated in populations presenting difficulties to cope with the increased cognitive load of a real-world experience (elderly populations, patients with cognitive impairments). The following findings would therefore inform the design of clinical applications aiming to prevent risky locomotion behaviour and focus the rehabilitation of problematic cognitive functions. Ultimately, using a mobile cognition approach could provide greater insight into cognitive-motor interference during real-world behaviours which could reveal markers of early onset of dementia but also reveal sensitive measures for the diagnosis and rehabilitation of cognitive impairments. Eventually, the definition of such markers could be translated into portable and user-friendly neuroimaging tools that can be integrated in assessment routines by practitioners outside of specialized institutions that would not require substantial technical and economic cost.

9.2. Future of mobile cognition

In this thesis, a vision of what mobile research methods can be utilized for has been described from a cognitive science viewpoint and illustrated by series of experiments that capitalized on the portability of mobile EEG to characterize cognitive effects during natural behaviours, in the real-world. As stated in the General Introduction, mobile brain imaging techniques have emerged from collaborative efforts involving different fields of research (including neurosciences, engineering, computer science, psychology, medicine, and physics). It is therefore not surprising that the literature and research community related to mobile brain imaging technologies is heterogeneous. While some research has been more technically oriented to address methodological aspects of the technology, other investigations focused on theoretical or practical applications of mobile brain imaging methods, which makes the body of research on the subject somewhat lacking in coherence to this day. The studies presented here are part of this developing field of research. Although the experiments presented in this thesis have essentially focused on addressing fundamental research questions about human cognition, the results of these investigations have nevertheless potential implications for real-world applications. The following sections will discuss foreseeable ways forward for the application of mobile research methods from a cognitive science perspective and how these methods could be translated into clinical applications.

9.2.1. Multimodal brain and body imaging

In the present thesis, mobile electroencephalography was used to capture brain dynamics associated with cognitive events in real-world contexts. As stated in the introductory chapter, mobile EEG is however not the only portable brain imaging technique. Recently developed functional Near Infrared Spectroscopy (fNIRS) is another non-invasive technique that can be used outside of the lab (Ferrari & Quaresima, 2012; Quaresima & Ferrari, 2016). The main difference between these two brain imaging methods lies in the nature of the data recorded. EEG captures electrophysiological activity of neuronal populations, whereas fNIRS registers changes in brain's vascular dynamics. These different measures of brain dynamics present distinct properties that define the strengths and limitations of both methods (see General Introduction for more details). A simplistic comparison would contrast the high temporal and low spatial resolutions of the EEG to the low-temporal but higher spatial resolution of fNIRS. The selection of mobile brain imaging method is therefore dependent on the object of the research. Nevertheless, these two techniques allow researchers to capture complimentary aspects of brain activity. For this reason, the joint use of mobile EEG and fNIRS has the potential to reveal relationships between electrophysiological and haemodynamic markers of cognition. By capitalizing on the strengths of both imaging methods, information regarding the spatial mapping and time course of cognitive processes can be recorded. Therefore, the use of multimodal brain imaging may be particularly valuable to capture the different aspects of brain activity underlying real-world behaviours. While multimodal brain imaging has become more common in laboratory setups (e.g., fMRI-EEG), examples of the application of this approach using mobile brain imaging techniques are scarce.

Recently, Zich, Debener, Thoene, Chen, & Kranczioch (2016) explored relationships between brain haemodynamics and electrocortical activity within the frame of a neurofeedback intervention based on mental imagery for motor rehabilitation purposes. The oxygenated (HbO) and deoxygenated hemoglobin (HbR) concentrations recorded through fNIRS and spectral dynamics (ERD) acquired from EEG sensors were compared and used to provide online feedback to the participants based on the lateralization of their brain activity. The findings highlight complex relationships between vascular and electrophysiological patterns of brain activation during mental imagery and motor activity. Movement-related electrical potentials (recorded using EEG) and vascular responses (recorded using fNIRS) offered complimentary information regarding brain dynamics underlying motor execution. Within the frame of a real-world approach to the study of human cognition, the combination of EEG-fNIRS measures is likely to be of critical importance to extract complementary dimensions of brain dynamics by capitalizing on the respective strengths of both techniques. The high temporal and spectral resolutions provided by the EEG coupled with the spatial resolution of fNIRS and its sensitivity to long-term changes (effectively extending the frequency range of investigation) will potentially provide additional information about embodied cognitive experiences. Furthermore, such a multimodal brain imaging approach could be applied to model the relationships between electrophysiological and haemodynamic changes associated with real-world cognitive experiences, which may be a key solution toward the development of real-world neurofeedback interventions (Pinti et al., 2015). Following the same rationale, coupling mobile brain imaging methods with brain stimulation techniques (e.g., transcranial Direct Current Stimulation, tDCS) may be interesting within the frame of mobile cognition investigations. For example, links between brain dynamics and functional changes induced by electrocortical stimulations could therefore be investigated in real-world contexts, potentially providing novel insight on the impact of brain lesions on cognitive functions supporting complex behaviours (e.g., spatial navigation, sensorimotor integration, social cognitive abilities).

With regards to the findings presented in the present thesis, the combination of EEG and fNIRS dynamics recordings would provide further insight into the unique relationships between electrocortical potentials and haemodynamics involved during real-world navigation and supporting locomotion. Another strength of fNIRS relative to EEG is its sensitivity to changes in brain dynamics beyond the range of seconds that are typically filtered in EEG data. Within the frame of spatial navigation, fNIRS would allow to quantify low frequency changes (sub 1Hz) reflecting sustained changes of blood flow associated with embodied and spatial cognitive processing. Moreover, the degree of spatio-temporal coherence between EEG and fNIRS dynamics would be informative about the relationships between the two types of neural dynamics. Modelling the relationships between these dynamics would reveal haemo-electrocortical networks underlying the expression of cognitive functions in the real-world. Such multimodal approach may be particularly useful in the definition of neural markers associated to cognitive function in the face of natural environments as the relationships between different types of brain dynamics may be more sensitive than isolated measures. Moreover, the classification of brain dynamics reflecting motor deficits in the context of neurofeedback interventions may benefit from the additional insights provided by models of cognitive functions based on multimodal neural dynamics relationships to achieve greater accuracy and better efficiency overall.

The work presented in this thesis has focused on the capture and interpretation of brain and behavioural data of individual subjects involved in a range of experimental tasks. The recording of brain and body dynamics from multiple individuals simultaneously (referred as hyperscanning, Babiloni & Astolfi, 2014) is another promising direction for real-world cognitive science research. In the context of individuals performing joint actions, investigating brain dynamics related to critical events during both collaborating (e.g., dancing) or competing (e.g., fencing) behaviours will shed light on the nature of the cognitive processes involved. As such, investigating brain activity of individuals performing a joint action has the potential to reveal brain dynamics associated with adaptive sensorimotor integration with regards to the current state of the interaction. Moreover, successful collaborative and competitive behaviours within the frame of joint action requires to account for partner’s/opponent’s perceived intentions (theory of mind) to successfully adapt ongoing behaviours. From this perspective, joint action paradigm offer a framework to study neural dynamics underpinning adaptive motor execution from a theory of mind perspective.

In a recent study, Ko, Komarov, Hairston, Jung, & Lin (2017) have recorded brain activity of 18 students attending the same lecture. At various times over the course of the lecture, slides containing target visual stimuli were presented. The students were instructed to respond to the presentation of these stimuli as quickly as possible by pressing a corresponding image on a smartphone. The reaction time of the participants was correlated with the activity recorded within the delta, theta and beta frequency bands, suggesting that the tonic variations of spectral power reflect cognitive fatigue. A similar approach could be adopted to investigate brain dynamics of “students” learning motor schemes (e.g., dance choreography) from a “teacher” through action observation, with the potential to identify neural correlates underlying motor learning of complex behaviours.

From a methodological standpoint, the hyperscanning approach also provide more control over the contribution of confounding environmental variables to the results during real-world data acquisition as many participants can be tested at once (same place and at the same time) effectively reducing the variance in the experimental setting. In the future, the multimodal capture of brain and body dynamics of multiple subjects interacting with each other will offer new insight on human cognition. However, considering the additional dimensionality of the data implied by such hyperscanning approach, the conceptualization and interpretation of the resulting information will require novel approaches in how experimental events related to meaningful joint actions between individuals are extracted. The richness of such data (commonly referred to as ‘big data’ in data science vernacular) pose new analytical challenges that demand novel solutions to be applied with regards to the modelling and interpretation of the data. In that sense, multimodal brain imaging of multiple participants is in line with the ongoing development of data science solutions for large-scale continuous data. The hyperscanning approach to the study of human to human interactions will therefore naturally benefit from the development of analytical solutions in the near future.

9.2.2. Brain and gaze dynamics in the real-world

The first series of studies presented in this thesis (Chapters 3, 4 & 5) has focused on the manipulation of factors related to real-world locomotion on attentional processing. For practical reasons (i.e., issues related to the acquisition of accurate visual events timing in the real-world), experimental stimuli were presented in the auditory modality. The present findings highlight that the continuous flow of visual information, which is inherent to real-world locomotion, has an important impact on the attentional resources allocated to the processing of information presented in the auditory modality. This cross-modality interference does not really come as a surprise considering the prominent influence of visual experiences in our interactions with the environment. Indeed, the visual modality is an important source of sensory input that is used to plan actions and adjust motor control. Therefore, even though the visual information may not be related to the ongoing task, a significant proportion of our cognitive resources are automatically dedicated to the processing of this rich information. An interesting extension of the research presented in this thesis would be to investigate visual processing within the frame of real-world behaviours.

A common trend in lab-based gaze tracking studies is the progressive switch from static images to dynamic visual scenes as stimuli. While it has already been argued in the General Introduction that static visualization of videos does not provide all the characteristics of three-dimensional real-world visual experiences, analysis of gaze during dynamic scenes present challenges that require solution in order to allow effective investigation of human gaze during natural behaviours. A main issue in the analysis of dynamic eye-tracking data is the definition of moving areas of interests that match the position of moving objects throughout the course of a video (Schöning, Gundler, Heidemann, König, & Krumnack, 2017). In experimental setups in which of set of specific dynamics scenes will be used, these

Regions Of Interests (ROI) can be defined manually or by using built-in software shortcuts (e.g., drawing a rectangle or an ellipse that will share the same trajectory as the object based on key positions throughout the video).

The first solution is highly time-consuming and is practically considered for short sequences of limited number of ROIs. The latter solution, while economic in terms of time and effort, is not ideal for accurate analysis of the data as the matching between object and ROI may not be consistent across the length of the recording, especially if the objects do not preserve a linear and monotonic trajectory. This problem is even more relevant for mobile eye-tracking data, where objects of interests are not only moving around the point of view, but the perspective of the participants is also changing as they move around. Therefore, object of interests may appear and disappear from the participants field of view as they move across the environment in an unscripted way. Manually defining ROI in real-world eye-tracking data would therefore have to be done on a trial by trial basis, as every recording would differ to some extent.

To address this issue, mobile eye-tracking manufacturers have included pattern recognition technology that are built-in to the analysis software packages. By placing barcode-like patterns around experimental objects, the software can automatically mark objects and delimit certain areas of the environment automatically in the continuous video recording. In practice, however, this solution has several limitations. First, the objects delimited by such barcodes have to remain static, which severely limits the application of this delimitation method. Secondly, the initial recognition by the software of these signals do not match the entrance of the objects in the field of view of the participants. This is mostly related to the necessity of the code to be presented in a certain orientation to the external camera (with more or less angular freedom) to be effectively recognized. Therefore, it is possible that participants may have already visually explored an object included in an experimental ROI before the software recognize its delimitations and effectively picks it up, which would eventually invalidate any analyses based on initial fixations and the timing of reactions to the presentation of such stimuli. Another limitation lies in the contamination of the visual environment by these barcodes, which oddness can potentially grasp one’s attention away from other stimuli and therefore indirectly inflate the proportion of exploration time within the ROI. These analyses issues are additional to the hardware limitations of current mobile eye-tracking systems (e.g., low sampling rate and lower data acquisition reliability, for more details see General Introduction). While the current hardware limitations are likely to be resolved in the near future by the increasing demands for concurrent eye-brain recordings in natural settings, efforts will still be required to allow for the extraction of gaze dynamics in mobile eye-tracking data. The rapid progress in the fields of machine learning and computer vision suggest that analysis tools able to recognize dynamically changing patterns will become available in the foreseeable future. Applied to mobile eye-tracking data, AI-based object recognition algorithms have potential for automatic, adaptive and highly accurate definition of ROI of real-world gaze data.

As covered in the General Introduction, carrying experimental research outside of the lab poses multiple challenges. Amongst the issues raised, the acquisition of accurate experimental event timing, necessary for time-resolved analyses, can be solved through the use of computerized paradigms if appropriate (running on tablets and mobile phones), motion tracking and EMG for the definition of behavioural responses onset and the use of eye-tracking to retrieve the initial exploration of visual stimuli. In addition to these solutions, novel signal-processing methods present promising developments towards solving the reverse inference problem (i.e., retrieving accurate experimental events timing based on EEG dynamics) of real-world EEG data (Su, Hairston, & Robbins, 2018). While current data-driven methods operate on a-priori time series in order to identify stereotypical EEG components, the development of unsupervised machine learning algorithms may help uncovering patterns of brain dynamics that are specific to cognitive processing in the real-world. A related issue is the conceptual definition of what constitutes a cognitive event in the real-world. In the tradition of functional brain imaging research, brain dynamics elicited by experimental events are interpreted based on the nature of the paradigm used. These artificially evoked neural responses may not be reflected during the experience of much complex and dynamic environments. In contrast to the dichotomic and reductionist nature of experimental stimuli in laboratory settings, meaningful visual information within the frame of a particular behaviour may be declined over the range of a spectrum of forms in the real-world. In order to truly investigate the expression of human cognition in the real-world, it is therefore necessary to address the questions relative to what is “eventful” within one’s continuous and dynamic experience of the environment. For this purpose, it is critical to adopt novel approaches to the interpretation of real-world EEG data while departing from practice that are inherent to laboratory research.

A second major challenge of a mobile cognition approach lies in the acquisition of enough data to perform averaging-based analyses with sufficient signal-to-noise ratio. While sports and workplace contexts offer applied situations where scripted routines can be repeated numerous times over a limited period of time, other natural behaviours may not be so convenient for EEG research purposes. A partial solution to the issues related to the presentation of stimuli can be found through the use of augmented reality and holograms. Through the use of such technologies, the experimenter would therefore have control over the nature, timing and number of stimuli that are projected in front of the participants, directly in the real-world with minimal collateral alterations to the embodied experience of the environment. Moreover, tablets and smartphones can also be used to trigger and present stimuli as participants are performing the experimental task (e.g., instructions are given based on participants position within the frame of a spatial memory task). It could however be argued that using such mixed-reality devices would sacrifice ecological validity, defeating the very purpose of carrying research in real-world environments. This trade-off should definitely be considered, and the invasiveness related to the presentation of virtual images should be minimal to not interact with the experience of the real-world. This section does not attempt to provide an extensive listing of existing solutions to the issues related to the acquisition of event-related data in the real-world. Furthermore, it is expected that upcoming technologies may offer novel solutions to address these issues in the near-future.

9.2.3. Altering real-world experiences through neurofeedback

A modest contribution of the presented work to the issue of real-world Brain-Computer Interfaces (BCIs) lies in the characterization of environmental factors that impact the strength of EEG signals commonly used within the frame of BCI applications. The results presented within this thesis are therefore a first step towards the characterization of neural signatures commonly used in BCIs under real-world conditions. The development of portable and relatively inexpensive brain imaging system offers unprecedented opportunities to apply brain-computer interfaces and neurofeedback directly to real-world contexts. BCIs interpret brain signals elicited by specific paradigms to identify meaningful signals for the production of a behaviour from other brain dynamics. The thresholds used for classification are tailored to the specificities of single subject brain activity. In practice, this is done by feeding machine learning algorithms with data collected during initial training (or familiarization) sessions. Essentially, the algorithm is optimized over successive iterations of the learning process as different thresholds are tested, compared and readjusted in offspring generations of the parameters, until a classification rate deemed satisfactory is consistently reached.

The field of BCI has made important progress in the interpretation of brain dynamics to allow the users to interact with their environment through a machine. For example, BCIs have been developed to interpret specific brain signals (e.g., the P300 ERP and steady-state visually evoked potentials "SSVEP") recorded from locked-in patients, allowing them to communicate through the selection of letters without requiring the performance of any movement (Dal Seno, Matteucci, & Mainardi, 2010; De Vos, Kroesen, et al., 2014; Käthner et al., 2013). Another practical application is the manipulation of prosthesis through cortical motor commands in patients suffering from spinal cord injuries and motor defects resulting from different aetiologies. Brain-Computer Interfaces ultimately aim to compensate functional deficits and ease patients' interactions in their everyday life. Paradoxically, despite the applied focus of BCI research, the current literature mostly consists of theoretical work exploring subtle variants of successful lab-based paradigms. Therefore, the current state of functional BCI clinical applications is mostly limited to patients' bedside.

At the occasion of the 7th Graz Brain-Computer Interface Conference (Austria, 2017), leaders in the BCI field have conveyed the message that while extensive empirical support has been provided for existing paradigms, the field now needs to move towards real-world applications. For this purpose, innovation is required to extend the range of applications and existing paradigms needs to be confronted to challenges of real-world brain imaging. To effectively make the big leap towards truly real-world BCI applications, it is necessary to build an understanding of how human brains operate in such circumstances, and to identify neural signals of relevance to the realization of natural movements and selective processing of relevant information. According to this objective, the present work provides insights on how attentional processing is modulated by environmental and embodied factors during real-world locomotion which can be used as a foundation for gathering novel insight human cognition but also to help design a new generation of neurofeedback applications that operates in the real-world. In addition to the definition of neural signals that can be used effectively and consistently, other methodological aspects of mobile brain imaging require further improvements in order to be translated into successful BCI applications in the real-world.

Current BCI research has heavily focused on the classification of neural signals reflecting selective attention and initiation of motor responses. For this purpose, BCI studies have used paradigms eliciting robust responses to increase the salience of relevant cognitive markers from other signals. Due to its robustness, the P300 elicitation paradigm has therefore been widely used within the frame of BCI research and most of the existing BCI solutions are based on the identification of the attentional processing signatures (e.g., P300-based spellers). Although some examples of successful BCI and neurofeedback solutions have been applied to real-world issues (e.g., locked-in patients), their operation remains confined to highly controlled and restraining settings (i.e., patient's bedside, involving static equipment). In order to fully embrace its ambition to develop real-world solutions, the BCI field has to move towards the characterization and classification of meaningful neural signatures recorded under natural circumstances. In light of the present findings, however, it appears that environmental factors of the real-world may alter the allocation of cognitive resources, which eventually is reflected by modulations of attentional markers used within the frame of BCI paradigms. It is therefore crucial to model what factors will impact the expression of such markers during natural behaviours. Future work should therefore further address the identification and classification of neural markers of attention directly in natural contexts.

The main and perhaps most complex aspect requiring improvement with regards to the current state of BCI, relates to the processing and classification of EEG data. In order to provide users with informative feedback that will allow them to change their behaviour appropriately, as in the case of neurofeedback-based rehabilitation tools, it is crucial to reduce the delay between the elicitation of relevant cognitive markers and the feedback provided as much as possible. Ideally, algorithms would discriminate brain signals on a single-trial basis. In practice, however, classification accuracy may be jeopardized by the introduction of noise in the data. To circumvent issues related to lower SNR, lab-based BCI classification is currently performed on averaged series of single-trials. This practice implies a trade-off between classification speed and accuracy. While this approach allows reliable classification in EEG recordings recorded in controlled experimental setups, its application may not be suitable within the frame of real-world EEG data.

The second chapter of this thesis provided an illustration of the methods required to address the noise issued from active behaviour in the EEG. While most of the processing steps included in the pipeline may be automatically performed at a relatively low cost in terms of computation time, other processing steps such as ICA-based pruning of artifactual components require manual inspection of the data and complex decision-making. In the absence of automatized substitutes to manual procedures, BCI classification of mobile EEG data has therefore to be performed on partially cleaned data that will likely present significantly lower signal-to-noise ratio than data acquired in laboratory settings. This lower SNR will necessarily result in either slowing down the feedback process (lower bitrate) due to additional trials being required to warrant a consistent classification of neural signals, or it will preclude the classifiers from reaching any reliable interpretation of the data altogether. The application of BCI to real-world situations will therefore greatly benefit from the optimization and inclusion of signal processing methods that are critical to deal with the challenges of mobile brain imaging data.

In addition to the major fundamental and methodological problems, practical issues related to the current state of mobile brain imaging hardware will also require substantial improvements before being effectively ported into real-world BCI solutions. Indeed, the preparation procedure preceding actual acquisition of EEG data would need to be simplified and shortened in order to allow for user-friendly and autonomous BCI experience. For this purpose, EEG systems using dry electrodes fitted in an elastic cap significantly reduce the time dedicated to capping. Indeed, the positioning of the electrodes only requires minor adjustments and conductive gel is not needed. The main downside of state-of-the-art dry-EEG is their substantially higher impedance in comparison to wet electrodes (Oliveira et al., 2016b). Dry-EEG sensors are therefore more prone to pick up signals from artifactual sources and present higher degree of variance in the recording of brain activity. Current attempts to solve the SNR issues of dry sensors have only marginally reduced sensor impedance by exacerbating their invasive aspect (i.e., dry electrodes present microscopic claws that are grounded into scalp epidermis) (Chi et al., 2012; Dias et al., 2012).

The quality of the user experience is a crucial aspect to consider in the development of consumer-based BCI solutions. Another important aspect to consider relative to the usability of real-world BCI is how intrusive the equipment is. Indeed, within the frame of the studies reported in this thesis, EEG sensors were fitted in a swimming-like cap, a style which is definitively eye-catching and arguably not elegant. Although the appearance of the EEG equipment had little incidence within the frame of the experiments reported here, the increased self-consciousness related to wearing the cap may offset the increased ecological validity of studies investigating social interactions in natural contexts. Moreover, in the context of the aforementioned neurofeedback interventions, patients’ brain states will have to be monitored over long periods of time. The visual intrusion of the equipment may discourage the users to engage with the intervention. Therefore, reducing the visibility of the equipment is an important step towards increasing patients’ adherence to neurofeedback interventions and extend their application to situations where the caps presently used may not be deemed socially acceptable. The invisibility of intra-aural EEG sensors (Mikkelsen et al., 2015; Goverdovsky et al., 2016) and the discretion of “around the ear” EEG electrode arrays (Bleichner & Debener, 2017; Debener et al., 2015; Mirkovic et al., 2016) are promising solutions to this aesthetic problem. Recent evidence has shown the reliability throughout day-long recordings of such method (Bleichner et al., 2016) and their relevance for capturing activity of neuronal populations in the vicinity of the electrodes (i.e., brain signals projecting to the temporal lobe). The downside of this discretion is that these small sensors arrays are not evenly distributed across the scalp and are therefore mainly receptive to local field activity while far-field potentials (e.g., motor cortical potentials commonly recorded at midline electrodes) may not be captured with sufficient sensitivity (Pacharra, Debener, & Wascher, 2017). This issue drastically limits the range of cognitive markers that can be identified using such electrode arrays, and may therefore only be relevant within the frame of certain BCI applications.

9.2.4. Future directions

Coming from an experimental laboratory research tradition, analyses carried out on EEG data are based on the assumption that the signals recorded are event-related (see sections 2.2.6). As discussed before, retrieving the timing of experimental events is one of the technical challenges of acquiring real-world brain activity (see section 1.4). An additional, perhaps more metaphysical issue related to the investigation of event-related cognitive processes in natural environments, is the actual definition of what constitutes an event in the real-world. As opposed to the artificial way of “inducing” or “evoking” cognitive events by the repetitive presentation of stimuli in laboratory-based experiments, the definition of “cognitively meaningful” events in the context of natural behaviours is at the very heart of what motivates a real-world approach to the study of human cognition. Such “eventfulness” is however difficult to conceptualize within the frame of dynamic and complex environments where relationships between objects states and cognitive experiences remain to be investigated. While solutions to retrieve experimental events (i.e., stimuli purposefully placed and manipulated by the experimenter in the environment) in the real-world have been discussed (see Figure 1.3) and even applied within the frame of this work (motion sensors used in Chapter 7, see section 7.2.3), delimiting the boundaries of natural cognitive events in the time domain (i.e., when does the cognitive experiences related to the stimuli initially start and its duration) would require a different approach.

As a starting point, the studies reported in this thesis have resorted to laboratory-based paradigms and a-priori hypotheses to define experimental events presented in the real-world. Building upon the present work, another step towards the capture of natural cognitive events could be achieved by looking at cognitive effects related to stimuli naturally embedded in the real-world instead of experimentally superposed to it (e.g., tracking the occurrence of visual events recapturing attentional resources in the real-world using eye-tracking). The context should however be favourable to the collection of many trials. Furthermore, another challenge in the quest of capturing natural cognitive events is their identification in continuous time series data streams. The development of novel data-driven approaches (i.e., unsupervised machine learning applied to multimodal “big” data recorded across brain and body imaging methods) holds promises to address these issues. Indeed, modelling the complex relationships between measures reflecting environment, body and brain states may provide indications towards the identification of cognitively meaningful events in the real-world. It is plausible that hypothesis-driven approaches based on previous laboratory findings may be inadequate to model these complex relationships, therefore the application of data-driven approaches would reduce (even though not completely eliminate) the impact of potential biases that would hold the field of cognitive sciences back. This reflection underlines what separates the current state of real-world cognitive research to the vision developed in the General Introduction.

The body of work presented in this thesis contributes to the development process required to eventually achieve a real-world approach in the study of human cognition. The implications of capturing natural cognitive experiences as they occur in the real-world are far-reaching from both theoretical and practical standpoints. The insight provided by the characterization of such cognitive experiences could then be translated into real-world actions (e.g. informing the architectural designs to improve users’ experience and accessibility, prevention of falls, rehabilitation or help in the acquisition of skills). The present studies and the quality of the signals reported demonstrate that mobile brain imaging technology, even though still requiring further improvements, is effectively suitable for real-world cognitive investigations in its current state. The conceptual and theoretical challenges aforementioned indicate that the process of progressively departing from the traditional ways of conducting cognitive sciences research in the laboratory, while on its way, still require further innovations. The role of cognitive science investigations will be instrumental in this process, as it will interface between technology and real-world applications by defining what, how and when cognitive processes occur during natural behaviours.

9.3. Conclusion

A recurring theme that can be drawn from of the findings presented in this thesis is the importance of understanding the embodied aspects of cognitive experiences. Indeed, factors underlying the capture of attention (investigated in Chapters 3, 4 & 5) and modulations of oscillatory brain dynamics associated with spatial cognitive functions (investigated in Chapters 6 & 7) are bound to one’s position and experience of the environment. The results reported across the different studies all point towards the complex interplay between physical and cognitive experiences of the environment, and its impact on how the brain operates, and processes information in a real-world context. The ERP studies have demonstrated that both visual and vestibular input are essential factors of real-world experience that significantly affect the allocation of attentional resources. These results provide novel insight into seemingly easy (i.e., cognitively inexpensive) aspects of real-world cognitive experiences that actually require significant reallocation of processing resources. Critically, these findings also provide strong evidence against models of cognitive load that segregate cognitive processing resources on a modality specific basis.

The second strand of studies exploring neural spectral dynamics associated with spatial navigation (see Chapters 6 & 7) has shown distinct pattern of brain activation associated with spatial memory and spatial navigation. The results highlight the role of frontal low-frequency oscillations during spatial navigation and the context-dependent nature of the processes associated with real-world navigation. The spatial memory condition was associated with increased gamma activity at parietal electrode Pz, which is commonly observed during the retrieval of information. Taken together these findings shed light on previous knowledge issued from invasive recordings and animal literature, further demonstrating the feasibility of recording spatial cognition dynamics during navigation in natural environments. In a final study, rhythmic changes associated with walking speed were investigated (see Chapter 8). It appeared that low-frequency power and peak frequency increased as a function of walking pace. The significance of this discrimination is twofold, a) brain dynamics involved in different aspect of complex behaviours can be distinguished in mobile brain imaging data, b) the presence of brain and non-brain effects can be effectively separated despite recording contexts prone to movement-related artifacts. In the context of a mobile cognition approach, these results emphasize the impact of both natural behaviours and the experience of a real-world environment on cognitive processing.

The original contribution of this work resides in the demonstration of the relevance of mobile brain imaging for cognitive research investigations. Throughout the different studies presented in this thesis, empirical evidence highlighted embodied aspects of human cognition during natural behaviours. The theoretical implications of the findings question previous cognitive models (e.g., modality-specificity of concurrent cognitive processing) and advocate for a study of cognitive experiences in real-world contexts. Indeed, the present results highlight both implicit factors of natural behaviours affecting neural signatures of cognitive processing and dynamic changes of cognitive markers associated with one's position in the environment. Even though the present studies have focused on the investigation of fundamental aspects of human cognition, examples of mobile cognition applications for the creation of neurofeedback-based interventions have been discussed with a specific focus on their relevance for clinical purposes. In this context, multimodal brain and body imaging appears particularly relevant as a way forward to map cognitive markers onto the occurrence of natural behaviours and real-world experiences by combining behavioural and neuroimaging measures (e.g., gait dynamics and ERPs). This knowledge could eventually be applied to design sensitive assessment methods for the diagnosis of cognitive impairments and used to develop real-world neurofeedback interventions. Brain-computer interfaces could therefore be applied to the monitoring of patients, facilitating the rehabilitation of problematic behaviour through brain and body states informed feedback directly in everyday life context. The low-cost and relative ease of operation of mobile brain imaging are additional incentives that warrant the development of user-based devices that would benefit the greatest number of patient populations.

Over the course of this PhD, the field of mobile brain imaging, which initially consisted in proof-of-concept experiments, has evolved towards more applied research. As illustrated by the signal processing methods applied throughout the different studies presented in this thesis, progresses have been made to partially address the technical challenges of mobile brain imaging. It is, however, important to acknowledge that despite this rapid progress, there are still many issues holding back the application of the true vision of real-world cognition research that have yet to be resolved. These current limitations have been expressed by researchers from different fields interested in applying mobile brain and body imaging to their research at the occasion of the International MoBI meeting (July 2018). Most of these issues concern the processing of noisy signals and the synchronization of multimodal data streams to which solutions are already in development phase. Moreover, due to inherent limitations of certain techniques and the increased noise brought by the recording of natural behaviours, this mobile cognition approach may not be suitable to capture some aspects of human cognition. The study of human cognition in natural contexts is nevertheless a promising field of research that is still in its infancy. There is still a lot of room for improvements with regards of how mobile cognition data is acquired and analysed, and the range of research questions that can be addressed will continue to expand following technological and technical breakthroughs. The results reported in this thesis converge with findings from other research groups using mobile brain imaging methods to study various aspects of human cognition. This growing body of research makes the case for exploring uncharted territories of cognitive experiences in the real-world, and further development will likely lead to innovative paradigms and the design of pervasive and accessible tools that will be beneficial in the rehabilitation of impaired cognitive functions, or even the enhancement and optimization of human behaviours.

Appendix A.

Chapter 7: Exploratory data analyses results

A.1. Mean spectral power across recording site

Similar to the approach used in Chapter 6, power spectra were computed within a consistent time window centred on the middle of the corridors. Each trial contained three segments for which power spectra were computed independently. The mean power spectral activity at frontal and parietal sites was computed across the entire length of the trials of each condition. Relative power spectral activity was then averaged within frequency bands, before being subjected to statistical comparisons.

Repeated measures ANOVAs were then used to assess the effect of the experimental task manipulation on power recorded across a-priori frequency bands at frontal and parietal midline electrodes. The following sections report the results issued from the analysis of variance applied to each frequency band and electrode separately (that were not included in the initial hypothesis-driven analyses). Main effects of the task were further investigated through post-hoc analyses (paired-sample t-tests).

A.1.1. Frontal Delta Power

Repeated measures ANOVAs were used to assess the impact of the type of task on power recorded within the delta band. The type of task yielded a significant impact on delta power [$F(2, 44) = 8.839$, $p < .001$, $\eta^2 = .287$]. Post-hoc paired-sample t-tests revealed that delta power was significantly larger in the wayfinding condition (mean = .663, SD = .844) than recorded in any other condition [direction: mean = -.439, SD = 1.281, $t(22) = 3.160$, $p = .005$, $d = .659$, $BF_{10} = 9.578$; numbers: mean = -.429, SD = 1.253, $t(22) = 3.337$, $p = .003$, $d = .696$, $BF_{10} = 13.708$], suggesting a distinct pattern of spectral activity is elicited during navigation.

A.1.2. Frontal Alpha Power

Repeated measures ANOVAs were used to assess the impact of the type of task on power recorded within the alpha band. The experimental task manipulation yielded a significant impact on alpha power [$F(2, 44) = 11.39$, $p < .001$, $\eta^2 = .341$]. Post-hoc paired-sample t-tests revealed that alpha power was significantly larger in the wayfinding condition (mean = .596, SD = .763) than recorded in any other condition (direction: mean = -.102, SD = .804, t(22)

= 4.157, $p < .001$, $d = .867$, $BF_{10} = 77.333$; numbers: mean = -.429, SD = 1.253, $t(22) = 4.176$, $p < .001$, $d = .871$, $BF_{10} = 80.645$). The Bayes Factors indicate very strong evidence in support of higher frontal alpha power recorded during the wayfinding condition.

A.1.3. Frontal Beta Power

The type of task yielded a significant impact on beta power [$F(2, 44) = 3.256$, $p = .048$, $\eta^2 = .129$]. Post-hoc paired-sample t-tests revealed that beta power was significantly larger in the wayfinding condition (mean = .244, SD = .644) than recorded in the numbers condition [mean = -.068, SD = .704, $t(22) = 2.645$, $p = .015$, $d = .552$, $BF_{10} = 3.542$]. The directions memory workload condition (direction: mean = .143, SD = .579) did not significantly differ from the numbers [$t(22) = 1.679$, $p = .107$, $d = .350$, $BF_{10} = .736$] or the wayfinding conditions [$t(22) = .778$, $p = .445$, $d = .162$, $BF_{10} = .287$].

A.1.4. Frontal Gamma Power

The type of task yielded a significant impact on gamma power [$F(2, 44) = 4.766$, $p = .013$, $\eta^2 = .178$]. Post-hoc paired-sample t-tests revealed that gamma power was significantly larger in the directions condition (mean = .387, SD = 1.064) than recorded in the numbers [mean = -.136, SD = 1.505, $t(22) = 2.265$, $p = .034$, $d = .472$, $BF_{10} = 1.808$] and wayfinding [mean = -.378, SD = 1.059, $t(22) = 3.471$, $p = .002$, $d = .724$, $BF_{10} = 18.044$] conditions.

A.1.5. Parietal Delta Power

Similar results were found at midline parietal electrode site (Pz), with a significant main effect of cognitive task on overall delta power [$F(2, 44) = 7.836$, $p = .001$, $\eta^2 = .263$]. Following paired-samples t-tests revealed significantly higher delta power in the wayfinding condition (mean = .961, SD = 1.462) than in any other condition [direction: mean = .115, SD = 1.152, $t(22) = 2.909$, $p = .008$, $d = .607$, $BF_{10} = 5.841$; numbers: mean = -.308, SD = 1.149, $t(22) = 3.151$, $p = .005$, $d = .657$, $BF_{10} = 9.410$].

A.1.6. Parietal Theta Power

In contrast to the results observed at frontal recording site, the experimental task did not have a significant effect on parietal theta power [$F(2, 44) = 2.566$, $p = .088$, $\eta^2 = .104$].

A.1.7. Parietal Alpha Power

Similar results were found at midline parietal electrode site (Pz), with a significant main effect of cognitive task on mean alpha power [$F(2, 44) = 3.920$, $p = .027$, $\eta^2 = .151$]. Following paired-samples t-tests revealed significantly higher alpha power in the wayfinding condition (mean = .074, SD = .605) than in any other condition [direction: mean = -.208, SD

= .585, t(22) = 2.440, p = .023, d = .509, BF_{10} = 2.447; numbers: mean = -.085, SD = .596, t(22) = 2.223, p = .037, d = .463, BF_{10} = 1.684]. These results, although following the same pattern, are less statistically robust than what is observed at the frontal electrode

A.1.8. Parietal Beta Power

A main effect of the experimental condition was observed on mean beta power recorded at midline parietal electrode [F(2, 44) = 6.700, p = .003, η^2 = .233]. Following paired-samples t-tests revealed significantly lower beta power in the numbers condition (mean = -.196, SD = .396) than in the direction [mean = .026, SD = .403, t(22) = 3.116, p = .005, d = .650, BF_{10} = 8.760] and the wayfinding conditions [mean = .082, SD = .505, t(22) = 2.843, p = .009, d = .593, BF_{10} = 5.137].

It can be noted that a significant increase in parietal beta activity was found for both the spatial memory and spatial navigation conditions in comparison to the non-spatial memory condition. This difference was not found at frontal site, suggesting a parietal effect. This beta band effect may be related to the more statistically robust effect (as indexed by the Bayes factors) observed in the gamma band. Indeed, the two neighbouring frequency bands present similarities in terms of the spatial distribution of the effect. Moreover, the definition of the gamma frequency band essentially spans over a wide range of frequencies (ranging from 30 to 80Hz), and the parietal gamma modulation was found to be spread over the whole range of the frequency band (see Figure A.2). Therefore, taking these considerations into account, the modulation observed in the beta band is likely an extension of the effects reported across the whole gamma band (most likely extending its lower limit to the higher-end of the beta band, as seen on Figures 7.7 & 7.8).

A.2. Time course of spectral dynamics across recording sites

In the previous study, time-resolved spectral analyses highlighted an increase in frontal theta activity throughout the course of trials involving spatial memory. To determine whether this temporal dynamic is associated with memory or spatial cognitive processes the following analysis contrasts spectral perturbations recorded throughout different trial segments of each experimental condition. The following subsections will present segment-based power spectral activity, recorded at frontal and parietal sites for each of the *a-priori* frequency bands investigated (see Figures A.1 & A.2 for a visual representation of spectral perturbations recorded at the frontal and parietal electrodes respectively).

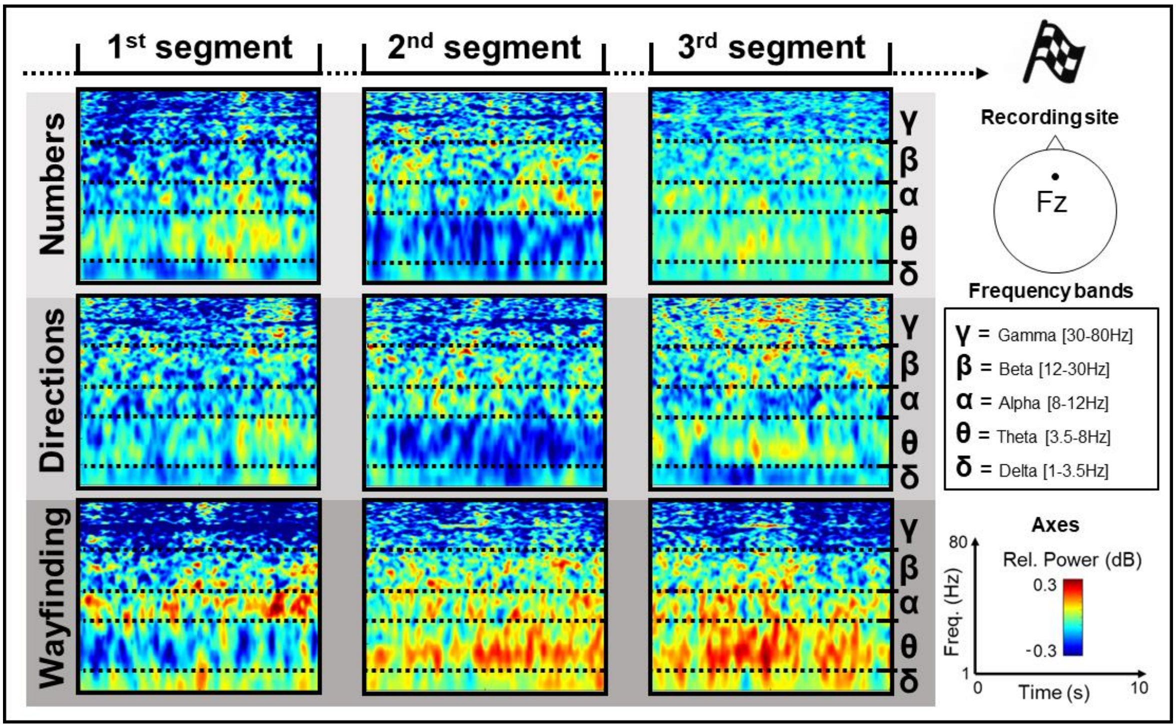

Figure A.1. Grand average Event-Related Spectral Perturbations (N=23) relative to control condition recorded at frontal electrode "Fz". The time-frequency plots present power spectral dynamics across the three segments of a trial for each condition (wayfinding, directions, numbers). The wayfinding condition presents a distinct pattern of spectral activity. An initial increase of alpha coupled with decrease of theta activity is observed at the beginning of the wayfinding trials and is then followed by a gradual increase of theta throughout the middle and last portions of the trials. Frontal low-frequency activity is significantly increased during the wayfinding condition in comparison to the non-spatial memory (numbers) and spatial memory (directions) conditions.

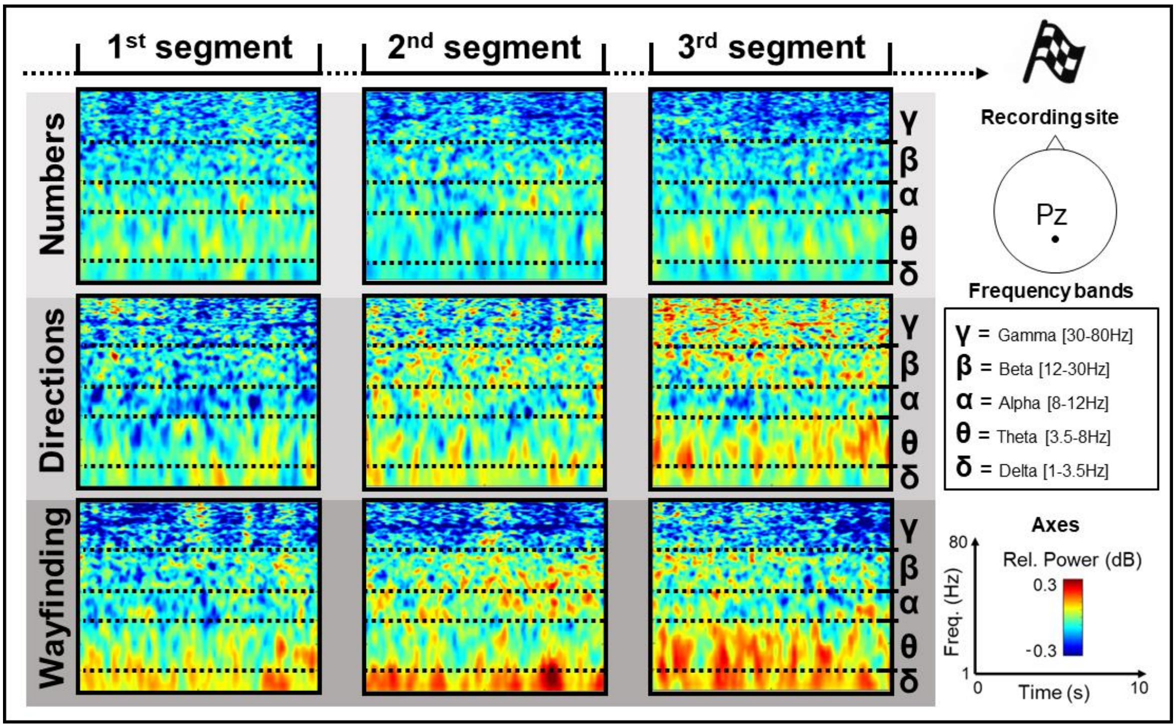

Figure A.2. Grand average Event-Related Spectral Perturbations (N=23) relative to control condition recorded at frontal electrode "Pz". The directions condition presents a distinct pattern of spectral dynamics with an increase of gamma power over the course of the trial. Similar to what was observed at frontal electrode, the wayfinding condition present a progressive increase of low-frequency power across segments.

A.2.1. Frontal Delta Power

A repeated measure ANOVA including task (directions, numbers, wayfinding) and recording position relative to the destination (start, middle, end) was carried out to investigate the effect of the experimental manipulations on mean normalized delta power throughout the different segments of the trial. The experimental manipulation had a significant main effect on overall delta power [F(2,44) = 5.552, p = .007, η^2 = .202]. Moreover, participant's position within a trial had a significant main effect on overall delta power [F(2, 44) = 11.156, p < .001, η^2 = .336]. There was, however, no significant interaction between the factors on delta activity [F(4, 88) = 1.067, p = .378, η^2 = .046].

A.2.2. Frontal Alpha Power

The same repeated measure ANOVA was used to investigate the effects on frontal alpha. The experimental manipulation had a significant main effect on overall alpha power recorded [F(2,44) = 9.364, p < .001, η^2 = .299]. Moreover, participant's position within a trial had a significant main effect on overall alpha power [F(2, 44) = 7.870, p = .001, η^2 = .263]. There was, however, no significant interaction between the factors on frontal alpha activity [F(4, 88) = .937, p = .446, η^2 = .041].

A.2.3. Frontal Beta Power

The experimental manipulation did not have a significant main effect on overall beta power recorded [F(2,44) = 1.944, p = .155, η^2 = .081]. Although participant's position within a trial had a significant main effect on overall beta power [F(2, 44) = 12.755, p < .001, η^2 = .367],

there was, however, no significant interaction between the factors on beta activity recorded [F(4, 88) = 1.244, p = .298, η^2 = .054].

A.2.4. Frontal Gamma Power

The experimental manipulation had a significant main effect on overall gamma power recorded [F(2,44) = 3.682, p = .033, η^2 = .143]. Moreover, participant's position within a trial had a significant main effect on overall gamma power [F(2, 44) = 11.725, p < .001, η^2 = .348]. There was also an interaction between the aforementioned factors on gamma activity recorded [F(4, 88) = 3.138, p = .018, η^2 = .125]. When participants performed the task following the directions instructed, gamma spectral power was significantly lower in the middle segment than both at the beginning [t(22) = 3.157, p = .005, d = .658, BF_{10} = 9.523] and at the end [t(22) = 4.425, p < .001, d = .923, BF_{10} = 138.318] of the trials. There was no significant difference in gamma power recorded at the beginning and end of trials within the directions condition [t(22) = 1.657, p = .112, d = .345, BF_{10} = .714]. For the numbers condition, frontal gamma power recorded within the middle segment was significantly lower than within the first segment [t(22) = 2.598, p = .016, d = .542, BF_{10} = 3.249]. There was however no significant difference between the first and last segments [t(22) = .965, p = .345, d = .201, BF_{10} = .332] nor the second and last segments [t(22) = 1.301, p = .207, d = .271, BF_{10} = .461] in terms of mean frontal beta activity. In the wayfinding condition, lower gamma activity was found in the middle segment of the trials in comparison to the first [t(22) = 3.935, p < .001, d = .821, BF_{10} = 48.049] and last sections [t(22) = 3.346, p = .003, d = .169, BF_{10} = 13.967]. There was no significant difference in frontal beta activity associated with the wayfinding condition was found between the first and last segments [t(22) = .808, p = .428, d = .169, BF_{10} = .293].

A.2.5. Parietal Delta Power

Equivalent analysis of the data for Pz electrode revealed that the experimental manipulation had a significant main effect on mean parietal delta power recorded [F(2,44) = 7.436, p = .002, η^2 = .253]. However, participant's position within a trial did not yield a main effect on parietal delta activity [F(2, 44) = 1.029, p = .366, η^2 = .045] and there was no significant interaction between the aforementioned factors on delta activity recorded [F(4, 88) = .468, p = .759, η^2 = .021]. Post-hoc paired-samples t-tests did not reveal difference in parietal delta power recorded throughout trials for any of the experimental conditions.

A.2.6. Parietal Theta Power

There was no main effect of the experimental manipulation on mean theta activity recorded at parietal site [F(2,44) = 2.443, p = .099, η^2 = .100]. However, the position within the trial had a main effect on parietal theta power [F(2, 44) = 11.080, p < .001, η^2 = .335]. There was no significant interaction between the factors on theta activity recorded [F(4, 88) = .758, p = .556, η^2 = .033].

A.2.7. Parietal Alpha Power

The experimental manipulation had a main effect on parietal alpha power [F(2,44) = 4.893, p = .012, η^2 = .182]. Moreover, participant's position within a trial also yielded a main effect on parietal alpha power [F(2, 44) = 5.737, p = .006, η^2 = .207]. Again, however, there was no significant interaction between the two factors on alpha activity recorded at parietal site [F(4, 88) = .237, p = .917, η^2 = .011].

A.2.8. Parietal Beta Power

Beta activity recorded at parietal site was affected by the experimental manipulation [F(2,44) = 6.150, p = .004, η^2 = .218]. However, participant's position within a trial did not yield a significant effect on parietal beta power [F(2, 44) = .507, p = .606, η^2 = .023]. Moreover, there was no significant interaction between the factors on beta activity [F(4, 88) = 2.099, p = .088, η^2 = .087].

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