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**Performance monitoring during action observation and
auditory lexical decisions**

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Table of Contents

Chapter I. General Introduction	5
1.1 Performance Monitoring	7
1.1.1 <i>What is performance monitoring?</i>	8
1.1.2 <i>Neural signatures of performance monitoring</i>	9
1.1.3 <i>Role of anticipation in performance monitoring</i>	11
1.2 Action observation	12
1.2.1 <i>Neural evidence of action observation and anticipation</i>	14
1.2.2 <i>Expertise and Action Observation</i>	15
1.3 Links between performance monitoring in language comprehension and in action observation	16
1.4 Outline of the thesis	17
 Chapter II. Predicting the fate of basketball throws: an EEG study on expert action prediction in wheelchair basketball players.	 20
2.1. Introduction	22
2.2. Methods and Analysis	24
2.3. Results	30
2.4. Discussion	34
 Chapter III. Predictive monitoring of actions, EEG recordings in virtual reality	 40
3.1 A commentary on the role of virtual reality for the study of the predictive monitoring of one's own actions	42
 Chapter IV. Observed and performed errors in auditory lexical decisions	 47
4.1 Introduction	49
4.2 Methods	53
4.3 Behavioural Pilot Study Results	56
4.4 EEG experiment	57
4.5 Results	59
4.6 Discussion	62
 Chapter V. General Discussion	 66
5.1. Action observation and expertise	68
5.2. Performance monitoring and language comprehension	71
5.3 Experimental Scenarios	72
5.4 Limits and future directions	73
 Appendix: Additional Studies	 75
A. Motor errors in Parkinson's Disease: neural correlates of actions observed in immersive virtual environments	76
B. Theta tACS over the frontal midline modulates behavioural adjustment during human-avatar motor interactions	96
 References	 118

Chapter I: General Introduction

How does the brain monitor performances? Does expertise modulate this process? How does an observer's error related activity differ from a performers own error related activity? How does ambiguity change the markers of error monitoring? In this thesis, I present two EEG studies and a commentary that sought to answer these questions. Both empirical studies concern performance monitoring in two different contexts and from two different personal perspectives, i.e. investigating the effects of expertise on electroencephalographic (EEG) neuromarkers of performance monitoring and in terms of monitoring own and others' errors during actions and language processing. My first study focused on characterizing the electrophysiological responses in experts and control individuals while they are observing domain-specific actions in wheelchair basketball with correct and wrong outcomes (Chapter II). The aim of the commentary in the following chapter was to highlight the role of Virtual Reality approaches to error prediction during one's own actions (Chapter III). The fourth chapter hypothesised that the error monitoring markers are present during both one's own performance errors in a lexical decision task, and the observation of others' performance errors (Chapter IV), however, the results suggested a further modulation of uncertainty created by our task design. The final chapter presents a general discussion that provides an overview of the results of my PhD work (Chapter V). The present chapter consists of a literature review in the leading frameworks of performance monitoring, action observation, visuo-motor expertise and language processing.

1.1 Performance Monitoring

The vast majority of human activity is goal-directed (Locke 1969). To ensure the success of the goal, one must continuously monitor their performance. This process involves being able to detect when a performance fails, and that the outcome is worse than expected. Performance monitoring mechanisms is not isolated only to the monitoring of one's own performance, but also external factors that might affect the outcome of the goal (Ullsperger et al 2014a). For example, an expert basketball player might shoot a free throw and succeed in making the ball go through the hoop almost every time, but during a match, players have to monitor also the potential interference from other's actions to advance in the game. A critical aspect of the environment is represented by the outcomes of the actions of people around us. Seminal studies have shown that similar behavioural and neural responses apply to errors that individual commit on their own, as well as to errors observed in others' actions. Thus, performance monitoring is thought to work in a way that allows learning from observed errors.

One benefit of research that focuses on neural mechanisms of performance monitoring is that it leads to tailoring better treatments for patients with a variety of motor and cognitive disabilities (Cools 2006). For example, in individuals with Attention Deficit and Hyperactivity Disorder (ADHD), a specific neural signal of performance monitoring might appear altered compared to healthy individuals (Ehlis et al 2018). This result carries the potential to be used as proof of success for a new ADHD medication, supporting behavioural improvements. Embedded in a broader social context, the ability to learn by monitoring own and other's performances is relevant in developing correct social interactions (Tomasello et al 1993). This is dependent on performance monitoring mechanisms that allow one to learn from the consequences of actions, because if the mistakes can be detected (through monitoring), then the future performance can be improved (Holroyd & Coles 2002; Bellebaum & Colosio 2014). The more neural markers of performance monitoring are known, the better learning environments can be created to promote such cognitive skills (e.g. video game-based trainings; Olfers & Band 2018). Last but not least, the daily human-machine interactions require its own stream of performance monitoring research. Automatization of processes such as

driving, piloting or supervising systems draw attention to how better train people for these roles, as well as how better to design systems to work well with our cognitive structures (Somon et al 2017).

1.1.1 What is performance monitoring?

The ability to change ones' behaviour upon the detection of an error is crucial to human and other animals' social lives. Performance monitoring can be described as a mechanism in which a goal directed action is continuously monitored. It is closely tied to other cognitive processes such as attention (Alexander & Brown 2010; Nelson et al 2017) and the integration of multimodal sensory information to recruit muscles, to carry out a goal, namely motor control (Rushworth et al 2004). This ability to monitor ongoing performance (e.g. action) is necessary for efficient goal completion and it is essential for adaptation when the goal is compromised (e.g. when an error occurs). Several cognitive models have been used to study performance monitoring such as reinforcement learning (Holroyd & Coles 2002; Bellebaum & Colosio 2014) error monitoring and response conflict monitoring (Ullsperger & von Cramon 2004) and predicted response outcome (Ullsperger 2014a). Error detection, or the detection of a discrepancy between the intended response versus the performed response are suggested to have similar computational demands but potentially varied consequences (Ullsperger & von Cramon 2004). For instance, the detection of errors can result in online corrections via further engagement of cognitive control processes, as well as resulting in adjustments of behaviour in situations with similar demands in the future, which is a prerequisite for learning. For the learning to be achieved, not only monitoring of own performance is used but also external feedback of that performance (Holroyd & Coles 2002; Bellebaum & Colosio 2014). Regardless of the model, it has been demonstrated that attention (Kok et al 2006; van Veen & Carter 2006; Alexander & Brown 2010), error awareness (Nieuwenhuis et al 2001; Shalgi et al 2009; Wessel 2012; di Gregorio et al 2016), on-line sensorimotor processes (*i.e.* visuo-motor transformations and continuous observed and performed action anticipation) affect the neural correlates of performance monitoring (Aglioti et al 2008; Avenanti et al 2012; Amoruso et al 2014; Bansal et al 2018).

1.1.2 Neural signatures of performance monitoring

Performance monitoring is one of the key processes of cognitive control. Evidence from studies in humans have identified a neural network comprised of frontal regions for cognitive control mechanisms (Ullsperger et al 2014b; Ridderinkhof et al 2004). This wide network of frontal regions includes posterior medial frontal cortex (pmMFC) and dorsal prefrontal cortex (dlPFC) (Ridderinkhof et al 2004; Cohen 2011a; Ullsperger et al 2014b). Furthermore, the anterior cingulate cortex (ACC) has been consistently reported as a crucial area for performance monitoring, and been defined as critical in error monitoring processes (Carter et al 1998; Swick & Turken 2002; van Boxtel et al 2005; Oliveira et al 2007; Jessup et al 2010; van Noordt & Segalowitz 2012; Foti et al 2015). In detail, prediction error signals that stem from the mismatch between prior prediction and perceptual input is thought to be projected from the frontal areas to ACC via dopaminergic structures originating from subcortical structures such as the striatum and the basal ganglia (Schultz 2002; Bloom et al 2009). In electrophysiology and neuroimaging studies, the ACC has been reported to be involved in error monitoring (Carter et al 1998; Swick & Turken 2002; Brown & Braver 2005). ACC is also thought to be the source of the Error-Related Negativity that is reported in EEG studies during performance errors and error prediction (see below; Carter et al 1998; Oliveira et al 2007; Keil et al 2010).

Performance monitoring has been studied extensively using time-restricted choice tasks (Luu et al 2004; Trujillo & Allen 2007; Cavanagh et al 2009; Cohen 2011b). EEG studies have identified several event related potentials (ERP) that are thought to be correlates of performance monitoring (Falkenstein et al 1990; Nieuwenhuis et al 2004; Shalgi et al 2009; Wessel 2012). Among performance related ERPs, the error related negativity (ERN), as a mid-frontal negative peaking potential was first found to be an initial and automatic response to error commissions during a speeded choice reaction task (Falkenstein et al 1990). The ERN following erroneous responses has been consistently shown to operate on internal monitoring of performance slips (Falkenstein et al 1990; Gehring et al 1992; Gehring et al 1993). Crucially, its peak amplitude is larger during errors compared to correct responses, with maximal amplitude in the mid-frontal region (Gehring et al 1993). Moreover, in motor tasks the ERN has been suggested to index the prediction of errors, namely, the ERN may arise before errors even occur (Joch et al 2017). The ERN is typically followed

by the Error Positivity (Pe) (Shalgi et al 2009), a positive deflection that is thought to be a marker of error awareness (Nieuwenhuis et al 2001; Wessel 2012). Furthermore, following feedback upon error commissions, another EEG marker is observed (e.g. the FRN, Feedback Related Negativity; Walsh & Andersen 2012; Luft 2014). The FRN is larger for negative than positive feedback (Nieuwenhuis et al 2004) and for unexpected rather than expected feedback (Von Borries et al 2013). The ERN, Pe and FRN have been linked to general top-down monitoring mechanisms (Holroyd & Coles 2002; Cavanagh et al 2010; Ullsperger et al 2014b; Ozkan & Pezzetta 2017). These ERPs have also been reported to be present in observation of others' performances. For example, the ERN was present following the observation of others' errors (van Schie et al 2004; de Bruin et al 2007; Pezzetta 2018), though with smaller amplitude and later latency. Similarly, the FRN was also present for the negative feedback of others' observed responses (Yu & Zhou 2006; Kobza et al 2011; Koban et al 2012). Also, a slow wave called the Contingent Negative Variation (CNV; van Rijn et al 2011) in the central electrodes is thought to reflect sensory anticipation and movement preparation (Bender et al 2004). Initially thought to reflect the temporal preparation after a cue stimulus and maximal at the moment of response, it was later related to planning processes (Zaepffel & Brochier 2012) and the error correction performance during the delay period between a cue stimulus and an imperative stimulus, peaking at the action onset (Jang et al 2015). The CNV was further suggested to reflect anticipatory motor simulation of an observed partner's action (Kourtis et al 2013). It should be noted that the specific features of these performance related ERPs (*i.e.* magnitude and latency) are affected by factors such as probability (Pezzetta et al 2018), learning (Bultena et al 2017), valence (Weismüller & Bellebaum 2016), and awareness (Nieuwenhuis et al 2001).

While the components described above are performance-dependent (e.g. larger when an error is occurring), electrophysiological studies have also identified performance-independent (*i.e.* stimulus related) markers associated with monitoring. Errors may refer to motor processes and their outcomes, but also deviations from expected sensory events (in the absence of any performed or observed motor errors), as well as a combination of the two. For instance, in auditory and visual modalities, Mismatch Negativity (MMN; Pazo-Alvarez et al 2003; Ylinen et al 2017; Stefanics et al 2018) has been identified over central electrodes, elicited 150-250 ms following rare, deviant (but

not wrong) stimuli (Wacongne et al 2012; Näätänen et al 2007). MMN is suggested to reflect an incorrect prediction of the sensory input (Garrido et al 2009). Similarly, N400 is a negative deflection maximal at parietal electrodes and peaks at around 350-400 ms after target onset that is sensitive to semantic violations such as an incongruent word in a sentence (Federmeier 2007; Kutas & Hillyard 1980). N400 is suggested to reflect a higher-level semantic prediction error (Jack et al 2019). Both MMN and N400 are found to be weighted by the precision level of predictions, which means less weight is given to bottom-up signal if the predictions are reliable, and therefore the amplitude of the component is reduced (Bornkessel-Schlesewsky & Schlewsky 2019). These ERPs help to understand to what extent the performance monitoring mechanism is shared in its processing of events that are due to both performance and stimulus, and in both yes/no discrete responses (Holroyd & Coles 2002; Cavanagh et al 2010) and continuous events such as actions' kinematics (Pavone et al 2016; Panasiti et al 2016; Pezzetta et al 2017). This can be studied by segmenting actions into smaller chunks where significant events occur (*i.e.* the moment of missing to grasp a cup).

1.1.3 Role of anticipation in performance monitoring

When one performs a movement, it is argued that there are predictive mechanisms that help form perception of our own actions as well as when we observe other's actions (Kilner et al 2007). During movements, motor system sends a copy of the motor command back to the sensory brain areas as an internal feedback (Bansal et al 2018). These internal feedbacks are then compared to external signals which are the brain's monitoring of action consequences. This mechanism monitors whether the motor commands (*i.e.* speech or body movements) have occurred as intended, or whether they should be modified upon errors (Bansal et al 2018). Without exception, the detection of errors during continuous monitoring of behaviour helps to adjust actions in all kinds of natural interactions with others and with objects (Vogt & Thomaschke 2007; Constantini et al 2010; de Bruijn et al 2011; Cavanagh & Frank 2014). The continuous nature of performance monitoring also affords anticipation of deviations in order to ensure goal success during movement execution (Ullsperger et al 2014a, Ullsperger et al 2014b) and supports anticipation during the observation of other's actions (Aglioti et al 2008). The integration of sensory information with the motor output supports the

prediction of consequences of actions (Bastian et al 2006). This can be illustrated with a recent action observation paradigm where a virtual agent throws a ball, with various combinations of the action preferences of an agent (i.e. the probability of action or contextual information), and the movement kinematics (Helm et al 2020). Observers optimize the anticipatory process for the consequence of actions by integrating these two sources of information. Integration of both top-down and bottom-up signals are modulated by factors such as expectation and attention (Gordon et al 2019).

Performance monitoring can be viewed as the process of continuous comparison of outcome expectation and the actual outcome (Ullsperger et al 2014a) that is sensitive to violations in predictions (Oliveira et al 2007). Performance errors elicit well-established neural signals in the brain (Ullsperger et al 2014b). These signals have been widely studied using tasks that require discrete responses such as yes/no responses on Flanker type tasks (Ullsperger et al 2014a), but also tasks that are dependent on the continued monitoring of action sequences, such as movements' kinematics (Aglioti et al 2008; Urgesi et al 2010; Amoruso 2014). In other words, some of the signals defined on performance errors are shared also during the prediction of motor errors, even before they occur (Maidhof et al 2009, Ruiz et al 2009, Joch et al 2017). These error signals provide us with the opportunity to test monitoring of our own task performances, monitoring of deviations in external stimuli as well as monitoring of the performance of others (Kok 2014; Ylinen et al 2017; Maurer et al 2019). Both empirical studies presented in this thesis use performance monitoring, but from different approaches; one from the modulation of anticipatory processes involved in expert action observation, and the other from the context of monitoring own and others' errors during lexical decision performances. The commentary on Chapter III on the other hand, highlights a research paper that used a paradigm that required to anticipate the consequences of own actions.

1.2. Action observation

Studies have shown that the fundamental neurophysiological mechanisms that are involved in action execution are also involved in action observation (Rizzolatti & Craighero 2004; de Bruijn et al 2007; Kilner et al 2007a; Kilner et al 2007b). It was proposed that the actions are simulated

internally during planning, control, and learning (Wolpert et al 1995, Kawato 1999). From passively observing others' movements and actions, it has been proposed that through these internal simulations, humans are able to infer intentions (Kilner et al 2007b; Blake & Shiffrar 2007) and learn from their peers (Vogt & Thomaschke 2007; Hodges et al 2007; Harris et al 2018).

In the past two decades, studies have identified a large-scale network of brain regions including occipito-temporal, frontal and parietal cortex that activated by action observation: The Action Observation Network (AON). Theories trying to understand the cognitive and neurophysiological architecture of the systems activated by action observation are largely influenced by the evidence from mirror neuron research (Rizzolatti et al 1996), which lead to the idea that the system that is involved in action execution is also activated during action observation. Supporters of a role of these shared mechanisms during action execution and observation propose that reactivating the sensorimotor system during action observation is the functional mechanism that allows humans to infer intentions from observed actions, and that the neural activity in these networks reflects the simulation of the observed action (Gallese & Goldman, 1998; Rizzolatti & Craighero, 2004). The activity of the AON has been proposed in predictive coding accounts of action understanding as supporting the communication between areas where visual, action-related, inputs are matched against simulation of predicted actions based on models of inferred intentions (Neal & Kilner 2010). This suggests that the activity in the motor system is linked to activity in the visual system during action observation (Kilner et al 2007b; Neal & Kilner 2010). These motor representations of intentions are used to create a model to predict the visual and somatosensory representations of action kinematics via the backward connections, where they are compared with sensory input (in the predictive coding framework a mismatch between predictions and sensory inflow produces a prediction error that is used to update the predictions). In this framework, actions are not only monitored but also anticipated (Umiltà et al 2001; Amoruso et al 2014; Denis et al. 2017; Abreu et al. 2017). Anticipation can be crucial in interacting with others, as the predictions that are generated of others' observed actions can be used to coordinate with them. Anticipation is also useful in competitive sports to avoid being fooled by deceptive movements. An observer tries to anticipate the consequences of an agent's movements based on an anticipatory simulation of the

observed movement. To advance in a match, players try to trigger a wrong anticipatory action simulation to cause the opponent to be misled in understanding the real goals (Tomeo et al 2012).

1.2.1 Neural evidence of action observation and anticipation

A large number of studies have provided evidence on sensorimotor brain regions' involvement in action observation (Fadiga et al 1995; Cochin et al 1999; Babiloni et al 2002; Pineda, 2005; Hari 2006; Orgs et al 2008; Perry & Bentin, 2009; Press et al 2011). Evidence on AON emerged from studying motor facilitation during implied action observation (Urgesi et al 2010; Avenanti et al 2012) and highlighted the anticipatory nature of motor simulation which was originally proposed from studies on monkeys (Umiltà et al 2001). The main brain regions of AON are identified as the occipitotemporal regions which are activated during action observation, premotor cortex and inferior parietal lobule (di Pellegrino et al 1992; Gallese et al 1996; Rizzolatti et al 2001; Umiltà et al 2001; Fogassi et al., 2005).

Action observation has been shown to be related to central electrodes/primary motor cortex μ rhythm suppression in the time-frequency domain (8-13 Hz; Arnstein, et al 2011; Denis et al. 2017; Dumas et al 2012), as well as to modulation of several fronto-parietal observed motor error ERPs' amplitude in the time domain (oERN, van Schie et al 2004; oPe, Panasiti et al 2016; oFRN, Koban et al 2012). However, the properties of these markers may vary depending on which aspect of action observation we consider. Observational ERPs related to performance monitoring (e.g. not related to a performed action, but to the observed performance) are typically smaller in amplitude and delayed in latency, compared to the ones elicited by performed errors (Koban 2012; Panasiti et al 2016). Observation of action errors from a first-person perspective avatar (e.g. when a virtual arm reaches to grasp a cup and fails) can elicit oERN and observational Pe (oPe) (Pezzetta et al 2018). Likewise, observed Pe (oPe) a positive deflection that is topographically similar to the response related Pe was present after the observation of erroneous piano finger movements (Panasiti et al 2016). Similarly, CNV can be present both for performed motor responses and for observed movement planning of a partner (Kourtis et al 2010; Kourtis et al 2013). Altogether, performance monitoring mechanisms seem to extend to the observed actions.

1.2.2 Expertise and Action Observation

Motor practice can shape prediction and action simulation mechanisms and their neural underpinnings (Brass et al 2007; Aglioti et al 2008; Sebanz and Shiffrar 2009; Abreu et al 2012; Badino 2014; Huberth et al 2018; Novembre et al 2013; Novembre & Keller 2014; Makris & Urgesi 2014). Arguably, with physical expertise comes also the expert eye meaning that motor expertise is often associated to perceptual expertise too. Expert basketball players (visuo-motor experts) are able to predict the outcome of basket shots earlier and more accurately from body kinematics compared to expert watchers (visual experts) and novices (Aglioti et al 2008); expert watchers, while also good at predicting the outcome of basket shots, they use cues from the ball trajectory instead of body kinematics. This suggests that the motor expertise improves the perceptual expertise through the motor simulation of observed body kinematics. Similarly, sport expertise equips the players with the ability to detect deception from body kinematics (Sebanz and Shiffrar 2009; Fujii et al. 2014; Aglioti et al 2008). ERP results have supported this claim by detecting modulation in several neuromarkers. For instance, observing others' erroneous piano fingering movements, Pe was elicited in expert piano players EEG signal (Panasiti et al 2016). Similar results have been found in expert tango dancers; the dancers differ in their anticipatory activity in the fronto-parieto-occipital network in the observation of realistic tango steps compared to naïve observers (Amoruso et al 2014, 2017). Larger N400 responses are present during the perception of incorrect movement executions in expert basketball players (Proverbio et al 2012) and dancers (Orlandi et al 2017) compared to naive controls. The above-mentioned ERP studies suggest that the observed-error related signals might reflect the modulation of expertise that can be detected during incorrect motor execution. Echoing the tendency of the brain to change due to physical expertise, motor and auditory expertise in musical instruments can lead to enhancement of auditory-evoked potentials (Bauman et al 2008). To study the EEG correlated for anticipation of action outcomes, it was shown that ERN related to the execution of piano errors anticipates the mistake by about ~ 100 ms in experts (Maidhof et al 2009), regardless of the presence of auditory feedback (Ruiz et al 2009). This suggests that the error signal of self-monitoring system can be indexed before the errors even occur. In sum, it can be argued that the motor expertise and contextual information contribute in allowing the simulation of

observed actions to be used in anticipation of the actions to follow (Kilner et al 2007b). The chapter II of the thesis focuses on the neural activity of domain-specific action observation for motor expertise.

1.3 Links between performance monitoring in language comprehension and action observation

Language comprehension is a complex cognitive function which consists of a set of cognitive processes such as semantic knowledge (e.g. meaning of words) and cognitive control (for a review, see Ralph et al 2017). Semantic cognition relies on both representations of non-verbal behavior through the encoding of the sensory, motor, linguistic and affective contexts, and on cognitive control. Most of the contemporary theories of language comprehension and production include executive control mechanisms, which contribute to the processes of lexico-semantic selection and retrieval (Walker & Hickok 2016; Nozari et al 2016). Previous research highlighted similar neural markers (ERPs) for action and language processing in the context of semantic violations (Amoruso et al 2013; Zachau et al 2014). Others have argued that language comprehension does not share computational demands with action observation or execution (Pritchett et al 2018), that the domain-general sensorimotor processes for language comprehension are organized differently than for understanding actions (Tremblay & Small 2010; Zhang et al 2017). The neural signatures of performance monitoring, however, have been shown to be present both for tasks that make use of language semantics (Kutas & Hillyard 1980; Butterfield & Mangels 2003) and actions that form a meaningful sequence (or rather the violation of it; Reid & Striano 2008; Balconi & Caldiroli 2011; Amoruso et al 2013). An example of an action chain semantics and its violation is given by the observation of a cup full of water being grasped and brought to the mouth to drink from it. If the cup is dropped and the water is spilled, or if the grasping fails, the expectation will have been violated, much like a semantically unexpected word at the end of an otherwise meaningful sentence. In particular, the N400, which is considered a marker of semantic violations (Kutas & Hillyard 1980) has been found to be present also for violations of the semantics of observed actions (action-N400; Amoruso et al 2013). Further evidence on the shared mechanisms between actions and language processing comes from the finding that the N400 marks violations in both spoken and sign language

processing (Zachau et al 2014). Moreover, lexical decision errors (Bultena 2017; Sebastian-Gallés et al 2006), just like error commissions in Flanker tasks (Eriksen 1974) elicit the ERN. Based on the above-mentioned evidence, one of the core questions addressed in this thesis: are error monitoring ERPs present in observed and performed actions (Gehring et al 1993; van Schie et al 2004) in the context of lexico-semantic processing?

When we hear sounds that form words, perception is formed by comparing the speech input with the context dependent predictions for phonological rules (Norris & McQueen 2008; Ylinen et al 2017). For instance, Ylinen et al (2017) have found that phonologically incorrect pseudowords that violate predictions elicit larger MMN response than pseudowords that do not violate phonological rules (does not violate predictions), supporting the idea that incorrect phonological predictions are coded as a prediction error and reflected in the MMN signal. As a result of the predictive nature of lexical perception in such tasks word ambiguity can lead to sub-optimal lexical integration (Strauß et al 2014; Proverbio & Adorni 2008). Ambiguity in this example refers to the difficulty in which a non-word can be classified as a non-word. In order to study the effects of ambiguity in spoken word recognition, Strauß et al (2014) have used an auditory lexical decision task (LDT), in which subjects were presented with real German words ('Banane' *Banana*) and ambiguous words ('Banene') and pseudowords ('Bapossner') and were expected to respond with a button press to indicate whether the stimulus word is a real word or not. In order to address the question of whether the performance monitoring ERPs are present for both observation of lexical processing, we have adapted this task with a similar manipulation (Chapter IV).

1.4. Outline of the thesis

The presented evidence suggests that adaptive behaviors depend on own and others' performance monitoring. This thesis encapsulates two of the main projects I have worked on during my PhD, with the binding framework being the ERP correlates underlying performance monitoring. In the empirical chapters, the main points investigated were:

- Can we specify an ERP that marks the prediction of action outcome? What are the EEG correlates of the prediction of an action outcome from the body kinematics of a wheelchair

basketball player by individuals who do or do not share the same motor expertise? This question focuses on the prediction of an action outcome by processing the body kinematics of a wheelchair basketball player.

- Is the ERN-Pe pattern during erroneous responses in lexical decision tasks comparable to the classical ERN-Pe pattern that are typically found in speeded-choice tasks? This question is embedded in performance monitoring in two-fold; *(i)* monitoring of the word meaning - mismatch between what was predicted and what happens at the end of pseudowords, *(ii)* monitoring of own performance on the response to task due to this manipulation.
- Is there an oERN even when the action of an observed partner violates a lexico-semantic prediction?

The first point is based on the idea that becoming a motor expert modulates performance monitoring processes in the domain of expertise. This is explored in Chapter II that includes the first empirical project I have conducted within my PhD, by using an action observation task presented to an elite team of Wheelchair Basketball players. In this study, the players had to predict the outcome of free-throw, and the results show an effect of expertise in the ERP waveform when compared to non-experts. Chapter III includes a commentary in response to a research article about the ERP activity to action related errors, discussing its implications of the predictive monitoring of actions. In this commentary we consider different approaches to explore this topic, while also making use of virtual reality techniques. Chapter IV presents an experiment that aims to study error processing when the errors are due to the incorrect prediction of whether a word is real or not during an auditory lexical decision task, both for performance and for the observation of other persons' lexical error performance. All three chapters specifically make use of anticipatory processes in performance monitoring, first from an expert action observation standpoint, second from a general prediction of own action's outcomes perspective, and third for performance errors on incorrect prediction of language-based stimuli. The difference between the two empirical studies is that while one focuses on the prediction of an action outcome and the potential differences from the kinematics of the observed actions, the other one focuses on the observed response to a word stimulus that may be incorrect. While the shared point of origin is the broader umbrella of performance monitoring, they

differ in terms of the type of monitoring required (prediction from observed action kinematic vs observation of lexical decision errors). This prohibits an integrated interpretation of results. While the first study provides further discussion on the modulation of shared motor expertise on the prediction of action from the observed kinematics, the second study attempts to clarify whether the so-called domain-general error monitoring mechanism can be identified by the typical markers for also lexical-decision errors. Chapter V discusses the general findings of the experiments presented in this thesis. In the Appendix, two additional studies I've worked on during my PhD are presented. Appendix A consists of an error observation study in the immersive Virtual Reality Cave, in which Parkinson's patients were tested on and off dopamine medication, in order to examine the role of dopamine network in error processing. Appendix B includes a tACS study that investigated the potential effect of theta stimulation in an action adaptation task, by targeting the individual theta frequency in each participant, obtained from the analysis of resting state EEG data. Overall, the presented results aim to further the knowledge regarding performance monitoring processes, and to create new experimental designs to have a deeper insight into our interaction with the others.

Chapter II. Predicting the fate of basketball throws: an EEG study on expert action prediction in Wheelchair Basketball Players

Abstract

The ability to anticipate and detect changes in human movement helps people to modify their behaviors in ever changing environments. Studies indicate that expertise modulates observation of domain-specific actions in sports - a process that is crucial for adapting rapidly to a new situation, often before awareness of environmental changes is achieved. Here, we explored the electrophysiological underpinnings of wheelchair basketball players predicting the fate of free throws performed by wheelchair basketball athletes. We performed electroencephalography (EEG) in semi-professional wheelchair players with different degrees of expertise (Players) and in ambulant, non-expert people (Controls) while they observed movie stimuli of a free throw that could land inside or outside the basket. On each trial participants were asked to predict the outcome of the throw. For each group, Event-related Potentials (ERPs) were averaged as a function of condition, using only the trials that were correctly predicted. Results show that compared to controls, expert players exhibit a greater negative amplitude of oCNV over Pz (an observational Contingent Negative Variation-like waveform which is considered a marker of action effect prediction) during the wrist movement preceding the ball release (the last 100 ms of the shot), which carries the most crucial kinematic information regarding the fate of the throw. Our data provide further support to the view that functional modulation of the Action Observation Network is associated with expertise.

2.1 Introduction

People invent games to advance their physical and mental abilities, just as much as sheer enjoyment. To succeed in many sports one has to efficiently use available information and predict what can happen next. Will the rival player in a basketball match go for a shot or make a pass to his teammate? The outcome of the game depends on how efficiently we can make decisions, or how good and fast we are at predicting the action outcomes (of other people's/players actions). For instance, experienced basketball players might focus on body kinematics in order to successfully predict the next event, whereas beginners tend to make uninformed predictions based solely on ball trajectory (Aglioti et al. 2008). For experts in sports and music, body kinematics can be even more informative than other environmental factors that unfold around them. In this study, we explore the electrophysiological signatures of domain-specific action observation in wheelchair basketball athletes. In particular, we focused on the event related potential (ERP) waveform during the kinematically informative moments of a free throw.

When we observe actions the Action Observation Network (AON) becomes involved (Hardwick et al. 2017). This network is comprised of premotor and inferior parietal regions that are also activated during action execution. Findings suggest that action observation is supported by our own motor capacities; for instance, TMS studies show corticospinal facilitation of the hand muscles measured via motor evoked potentials when observing grasping pictures with implied motion (Urgesi et al. 2006). It has also been suggested that anticipating the actions of another person might rely on a finely tuned and partially implicit perceptual mechanism (i.e. an inner motor simulation process) supported by embodiment and predictive coding (Abreu et al. 2017). At the electrophysiological level, ERP evidence from the parietal electrodes, specifically a negative deflection, has been associated with action effect prediction (Hughes and Waszak 2011; Jin et al. 2011; Savoie et al. 2018). Related to this, a slow negative deflection over fronto-central regions, the so-called Contingent Negative Variation (CNV) has been proposed to reflect cue-initiated motor response preparation (Gomez et al. 2003), with variations in amplitude and topography due to task requirements (Rohrbaugh et al. 1976). CNV has been generally proposed to reflect the retrieval of a motor program from memory, and the late CNV (lCNV) to reflect sensory anticipation as well as movement preparation (Bender et

al. 2004). The CNV is thought to be involved in both low- and high-level motor (movement) planning (higher order motor planning would refer to the shaping of a motor program, while lower level refers to the overt release of the motor command: Leuthold et al 2004; Zaepffel and Brochier 2012). Kourtis et al (2010; 2013) showed that the CNV waveform pattern corresponds to the planning period of a partners' action in a joint action task, suggesting that motor simulation might occur for observation and anticipation of an action. Overall, the evidence suggests that our own movement capacities influence action anticipation and that it might be reflected in the CNV waveform. For ballet dancers, experience-dependent modulation of alpha power can be shown while they watch dance moves compared to novice groups (during action observation and motor imagery; Di Nota et al. 2017). Crucially, for the present study, there is evidence that elite basketball players can predict successful free throws more rapidly and accurately based on cues from body kinematics, as reflected by a difference in corticospinal facilitation between experts and novice groups during the observation of successful and unsuccessful basket shots (Aglioti et al. 2008). Unlike amateurs, expert basketball players can detect deception from kinematics and postural cues (Fujii et al. 2014; Sebanz and Shiffrar 2009), and when a part of the body kinematics is disguised, it reduces the experts' accuracy to the level of amateurs (Rowe et al. 2009). Furthermore, studies on ERPs show a larger N400 during the perception of incorrect execution in basketball players but not in naïve controls (Proverbio et al. 2012), with similar results found in expert dancers (Orlandi et al. 2017). Complementary findings suggest that differences in neural activity related to experience can be unique to sensorimotor areas: expert tennis players have a greater accuracy in anticipating the outcome of tennis related actions and greater event related desynchronization in *Mu* rhythm (8-13 Hz) and beta (14-30 Hz) frequency bands, associated with activation of the AON (Denis et al. 2017). In a sport-specific attentional cueing task, CNV has also been found during action observation in the context of expertise (Wang and Tu 2017). Accumulating information from different samples of population and expertise converges towards the evidence that AON processes are imperative to understanding how predictive processing works. In the current study, we focused on wheelchair basketball athletes.

Wheelchair basketball, just like standard basketball, is an open-skill sport where the environment changes constantly and it requires rapid adaption and response flexibility in disabled

athletes (Di Russo et al. 2010). In wheelchair basketball, athletes are functionally classified from 1 (most severe disability) to 4 (least severe disability) according to the level of trunk movement and stability (De Lira et al. 2010; Maynard et al. 1997). During competition, the functional classification of the players is balanced in order to achieve comparable levels of physical ability across the competing teams, as the ability to throw a ball from a wider range of distances and upper arm circumference are related to success in scoring (Cavedon et al. 2015; Malone et al. 2002). Players are required to be exceptionally strong and able to recover from harsh falls as well as to adapt quickly to the demands of the game. Their expertise moves beyond their respective injuries, especially for an action such as a free throw (which requires movement mainly from the upper body).

Our paradigm focused on action prediction from body kinematics and investigated the electrophysiological correlates of action anticipation in expert wheelchair athletes. We expected the neurophysiological signals of action observation to be modulated by basketball expertise, specifically at the most informative moments of a basketball free throw kinematics, as shown by previous research (Abreu et al. 2012). Moreover, we expected the signals to be modulated by the fate of the basketball shot (i.e., whether it was successful or unsuccessful). To test this, we asked players from the Santa Lucia wheelchair basketball team to observe movies of another player and predict the outcome. We tested expert wheelchair basketball players, amateur wheelchair basketball players and naïve walking controls to investigate how specific motor handicap and motor expertise might impact motor prediction and the electrophysiological markers that accompany expertise. We attempted to investigate how motor expertise might impact prediction of the consequences of a motor action and the electrophysiological markers that accompany such expertise.

2.2 Methods and Analysis

2.2.1 Participants

The study was approved by the local Ethics Committee at the Fondazione Santa Lucia Research Hospital (Rome, Italy), and followed the ethical standards of the 1964 Declaration of Helsinki. The sample consisted of 16 players, recruited from the Santa Lucia Wheelchair Basketball Team in Rome. Sixteen Expert players (Male, age: mean=28.94, \pm SD=9.51; expertise: mean= 9.14, \pm SD=9.59; years since injury: mean= 18.86, \pm SD=10.11) were tested.

The Players were comprised of athletes who actively took part in matches of the “Serie A1”, the highest level of the Italian Wheelchair Basketball Championship, within the Italian Wheelchair Basketball Federation (FIPIC), and athletes within the “Serie B”, with less years of experience compared to “Serie A1”.

All players had deambulation issues and were full-time wheelchair users with reasons ranging from thoracic-back injury, paralysis, or amputation of two limbs. The only exception was one participant who could walk short distances with the aid of crutches, and another who could walk with prosthetic legs.

24 control participants were recruited from La Sapienza, University of Rome. Three participants were excluded due to an accuracy below 55%, and four more were excluded due to technical failure to send triggers; therefore, EEG analyses were conducted on a total sample of 17 basketball naïve Control participants (7 Male, 10 Female; Age = 26.4, SD = 5.99) and 16 Wheelchair Basketball players. One player was left handed. All participants had normal or corrected-to-normal vision and did not report head traumas or psychiatric disorders.

2.2.2 Stimulus selection

The movie stimuli consisted of movie recordings of a wheelchair basketball player (Point 1) of the Santa Lucia Wheelchair Basketball Team (Figure 1b). The movie stimuli were recorded from a sagittal viewpoint and displayed the shooting execution up to the first frame of the ball leaving the hand. In these stimuli, it was possible to observe and discriminate clearly between a shot that would or would not be successful for both experts and completely naïve participants.

The movement of the actor started, on average, 789 ms before the movie stimulus ended (SD = 170.9). The videos started by a preparation of the player sitting still and holding the ball in preparation. Preparation lasts until approximately 80 ms (SD = 22.6) before the video offset, when the player extended the arm, closed the wrist and let go of the ball. In the “IN” shots, this extension ends on a higher point compared to the “OUT” shots. During the baseline part of the movie stimuli (mean = 1105.5 ms, SD = 185 ms), the player was seated on a wheelchair with the ball at hand with a slight rocking movement. The baseline part of the movie stimuli was validated to make sure that

the kinematics were uninformative by asking 8 naïve participants to try to guess the outcome of the actions. The pilot participants performed at chance level and with no significant difference between the likelihood of correct response for either condition ($\text{Mean}_{\text{IN}} = 42.3\%$, $\text{SD}_{\text{IN}} = 22.3$; $\text{Mean}_{\text{OUT}} = 51\%$, $\text{SD}_{\text{OUT}} = 24.4$; $\chi(1) = .989$, $p = .320$). These participants were not included in the actual study. According to the Pearson Chi Squared likelihood ratio tests, the accuracy rates did not change from the first block to the last during piloting, which indicated that feedback did not result in learning effects (Accuracy per block from 1 to 4: 82.8%, 78.2%, 85.7%, 83.5%; $\chi(3) = 5.043$, $p = .169$). This pilot helped to ensure the neutrality of the baseline part of the stimuli, as well as confirming the absence of a learning effect.

2.2.3 Procedure

Participants were seated comfortably in front of a computer in a well-lit room. Before the experiment, the participants completed the practice phase and became familiar with the task (6 trials: 3 IN, 3 OUT). The movie stimulus was classified as IN when the ball went in the basket, and OUT when it failed. A total of 208 trials were delivered in 4 blocks with 3 breaks, lasting 35 to 40 minutes. Each block included 52 movie stimuli comprised of 26 free throws repeated twice. The movie stimuli had a proportion of 30% "IN" and 70% "OUT", in order to obtain the maximum amount of trials where there was an error in prediction. The stimuli included two players, however, 5 of the elite players recognized and reacted to one of the players of the movie, and we were forced to discard the data obtained from that stimulus. Data from 104 movie stimuli were considered during the analysis. Participants were required to predict whether the ball was going to be "IN" or "OUT", which they expressed by pressing the left or right arrow buttons for "IN" and "OUT" respectively. On average, each trial lasted 8 seconds. Each movie stimulus started with the wheelchair basketball player, holding the ball for 1895 ms on average ($\text{SD} = 63.2$). One session was approximately 10 minutes, and the full task duration was approximately 40 minutes.

Participants were instructed to keep their muscles relaxed as they watched the movies. They started the task by pressing the space bar. Each trial began with a fixation cross on the location where the player would then appear, and participants were instructed to fix their gaze on this cross, and the player's body, throughout the trial. The movie stimuli were delivered in a pseudo-random

order (i.e. more than two clips belonging to the same condition (IN/OUT) were not presented consecutively). After each movie clip, there was a black screen (range: 500-1500 ms), followed by

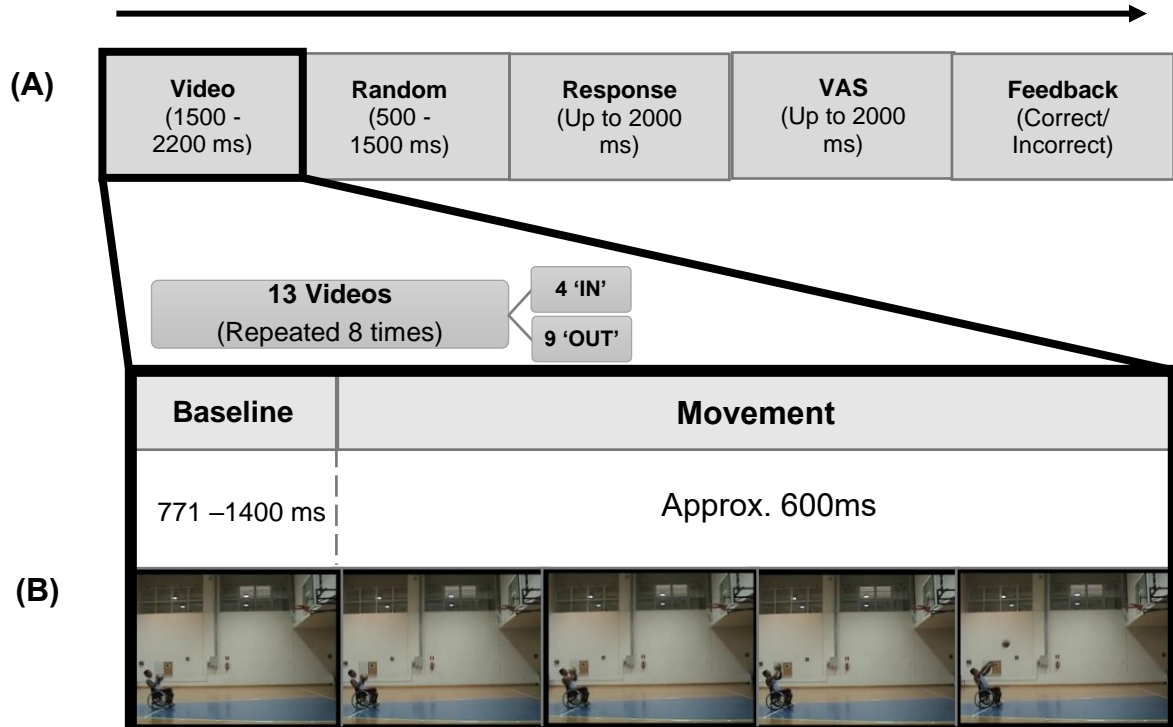


Fig. 1 (A) Timeline (B) Procedure: A representation of the movie progression, first, middle and last frames of the movie (1st frame – the player sits still; 2nd frame – the player initiates the movement; 3rd and 4th frames – the player moves to execute the throw; 5th frame – the movement is completed when the player's wrist is closed and the ball is let go)

the response screen (Please see Figure 1a for the trial sequence, and Figure 1b for the movie properties). After their response, the participants rated how confident they were with their response in a Visual Analog Scale (VAS) from “Not Confident at All” to “Very Confident”. Each trial ended with the feedback (correct or incorrect). Figure 1 describes the timeline of one trial.

2.2.4 EEG recording

The triggers containing timing information for EEG recordings were sent via a photodiode, a device that delivers triggers activated by a white patch placed on the bottom right corner of each movie at the last frame. Time 0 was fixed at the end of the movies, since it was the same movement within each movie, presenting a mutual event in time. EEG signals were recorded by using a Neuroscan SynAmpsRT amplifier system (Compumedics, Ltd) with a 60-electrode elastic headband (Electro-Cap, International, Eaton, OH) positioned according to the international 10-10 system. The signals were acquired from the channels: Fp1, Fpz, Fp2, AF3, AF4, F7, F5, F3, F1, Fz, F2, F4, F6,

F8, FC5, FC3, FC1, FCz, FC2, FC4, FC6, T7, C5, C3, C1, Cz, C2, C4, C6, T8, TP7, CP5, CP3, CP1, CPz, CP2, CP4, CP6, TP8, P7, P5, P3, P1, Pz, P2, P4, P6, P8, PO7, PO3, PO1, POz, PO2, PO4, PO8, O1, Oz, O2. The ground electrode was positioned on the scalp for ALF derivation, while the reference electrodes were applied to the left (digital reference) and right (physical reference) earlobes. A Horizontal Electro-Oculogram (HEOG) was recorded bilaterally, and a Vertical (VOEG) was recorded with electrodes positioned under the left eye. The signal was recorded with an online low-band filter 0.01-200 Hz and digitized at a sampling rate of 1000 Hz. Impedances were maintained under 5 K Ω by applying gel (ElectroGel) to all electrodes. After the data collection, the raw files were down sampled to the rate of 500 Hz. Independent components were calculated for each participant using continuous EEG data to identify and remove eye movement and muscular artifacts (ICA; Jung et al 2000) a mean of 3.6 components (range 1:6) were removed, using the MATLAB toolbox EEGLab (Delorme and Makeig 2004).

2.2.5 Behavioral Analyses

Statistical analyses for the behavioral data were performed with SPSS (IBM SPSS Statistics for Windows, Version 20.0. Armonk, NY: IBM Corp.). The mean accuracy rates were calculated for each group. We ran a mixed ANOVA design with Condition and Group as the within and between groups factors, respectively. The accuracy of the data guided our trial selection in our EEG analysis (See Figure 2 for the error frequencies of each group). Trials that were not correctly identified as “IN” or “OUT” by the participant were removed. A mean of 86.3% of the trials was kept for the EEG analysis.

We also determined that the accuracy rates were free from perceptual bias: to assess whether the participants might have a bias towards giving the “IN” or “OUT” responses more often, we ran a signal detection analysis (McFall and Treat 1999). We also controlled for the learning effect and measured the accuracy rates throughout each block of trials. We determined that performance did not improve with time.

We ran a Spearman's rank-order correlation to determine the relationship between the Confidence Ratings and Accuracy of each group.

2.2.6 ERP Analysis

Preprocessing of the EEG data in the time domain was performed using the Brain Vision Analyzer 1.05 software (Brain-Products, GmbH). The data were band-pass filtered to 0.5-30 Hz. Epochs were time locked to the end of the players' movements, meaning that the signal was epoched in wide windows of 2200 ms, from -1500 to +700 ms relative to stimulus offset and were baseline corrected with a chosen interval of 200 ms during the baseline period of the movie stimulus, when the player in the video sat still (from -1400 to -1200 ms relative to stimulus offset). Only correctly predicted trials were included in the analysis. Each epoch was visually inspected for artifacts and residual epochs with eye blinks or epochs exceeding -100/+100 μ V amplitude were manually removed. Overall, 86.7% of the correctly classified trials were analyzed (~2560 trials in total). Bad channels were interpolated only when necessary (Perrin et al. 1989). ERPs were calculated with the *erpR* package (Arcara and Petrova 2014) in R Studio (R Core Team 2014).

In line with previous literature, we focused our analyses on the parietal area (Amoruso et al. 2013; Jin et al. 2011; Proverbio and Riva 2009) and mainly on the electrode Pz. We chose the window for analysis according to the part of the movie stimulus that carried the most information about the fate of the throws occurring in the last 100 ms of each movie, where the player bends his wrist and lets the ball go. Our focus on this window stems from research on how visuo-motor expertise provides advantage in reading kinematic cues (Ridderinkhof and Brass 2015; Savelsbergh et al. 2002), and that the release of the basketball is informative for experts and not novices (Abreu et al. 2012).

We used a 2X2 factorial design to analyze EEG amplitude over Pz with (i) Condition: "IN" and "OUT", and (ii) Group: "Players", "Controls" as factors. ANOVA was conducted with the *ez* package (*ez: Easy analysis and visualization of factorial experiments*, version 4.2–2; Lawrence 2013). We also ran a Spearman correlation analysis only on the Player group's amplitudes for both "IN" and "OUT" conditions with their years of expertise.

2.3 Results

2.3.1 Behavioral Results

Figure 2 shows the mean accuracy rates for each group and each condition. The mean accuracy of the “IN” movies was 88.25% for the Players and 80.76% for the Controls (SD = .09, .10; respectively). In the “OUT” movies, the Players were accurate in 92% of the trials and Controls were 85.59% accurate (SD = .09, .12; respectively). There was a significant main effect of group on accuracy rates $F(1,31)=5.61$ $p=.024$, with no surviving effects on the post-hoc tests.

No significant main effect of the condition (“IN” or “OUT”), or a significant interaction between the condition and group ($p=.153$ and $.479$; respectively) was found.

According to the t tests that were run on signal detection analysis values, the overall perceptual sensitivity of the Players was significantly higher than the Controls, $t(31) = 2.866$, $p = .007$ (d' Players= 2.95, SE = .25; d' Controls = 2.09, SE = .17). Analysis of the C values for bias showed

that neither group had any bias towards either the “IN” or “OUT” responses, due to the stimulus frequency, $t(31) = -.04$, $p = .970$.

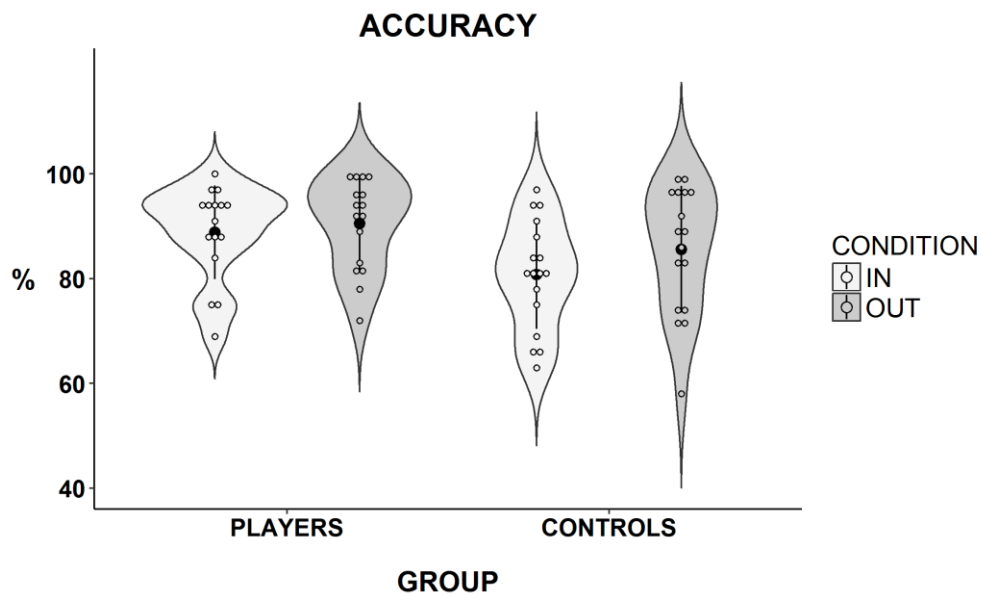


Fig. 2 Accuracy rates of each group in each condition. Players were significantly better than Controls ($p < .001$), but no other main effect or interaction was observed. Individual dots represent the score for each subject

There was a positive and statistically significant correlation between the VAS Scores and Accuracy Rates, in Players ($r_s(16) = .630$, $p = .009$) and Controls ($r_s(17) = .554$, $p = .021$). The Players had VAS scores of 69.40% (SD = 10.33), whereas Controls had 60.76% (SD = 13.57).

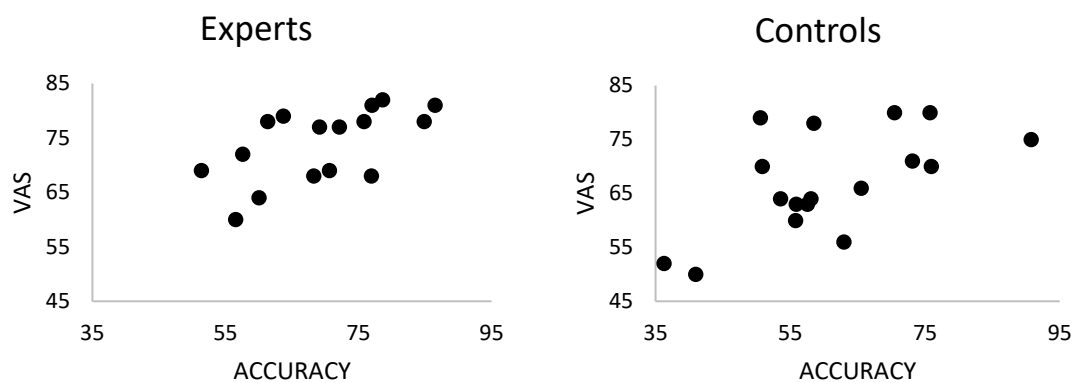


Fig. 3 Scatterplots for correlations between VAS scores and Accuracy rates of each group

2.3.2 ERP Results

A repeated measures ANOVA on the ERP waveform from electrode Pz, with the factors Group (Players, Controls) and Condition ("IN", "OUT"), revealed a significant main effect of group on the mean amplitude of the signal $F(1,31)=6.17$, $p=.019$ during the last 100 ms of the movie stimuli (which carried the crucial kinematic information about the basketball throw). The main effect of condition ($F(1,31)=3.58$, $p=.069$) and interaction of group X condition ($F(1,31)=2.28$, $p=.141$) did not reach significance. FDR corrected post-hoc tests showed that Players had significantly more negative in amplitude than the Controls in the "IN" movies ($\text{Mean}_{\text{Difference}}=-3.35$, $p=.035$), but not in the "OUT" movies ($\text{Mean}_{\text{Difference}}=-2.62$, $p=.056$). Figure 3 (B) shows the topography of the average signal (-100 ms to 0); Figure 3 (D) shows the scalp distribution of the ERP waveforms from the electrodes around the midline. In neither the "IN" nor the "OUT" conditions were amplitudes significantly correlated with expertise ($r_{\text{IN}} = -.366$, $p_{\text{IN}} = .082$; $r_{\text{OUT}} = -.246$, $p_{\text{OUT}} = .179$).

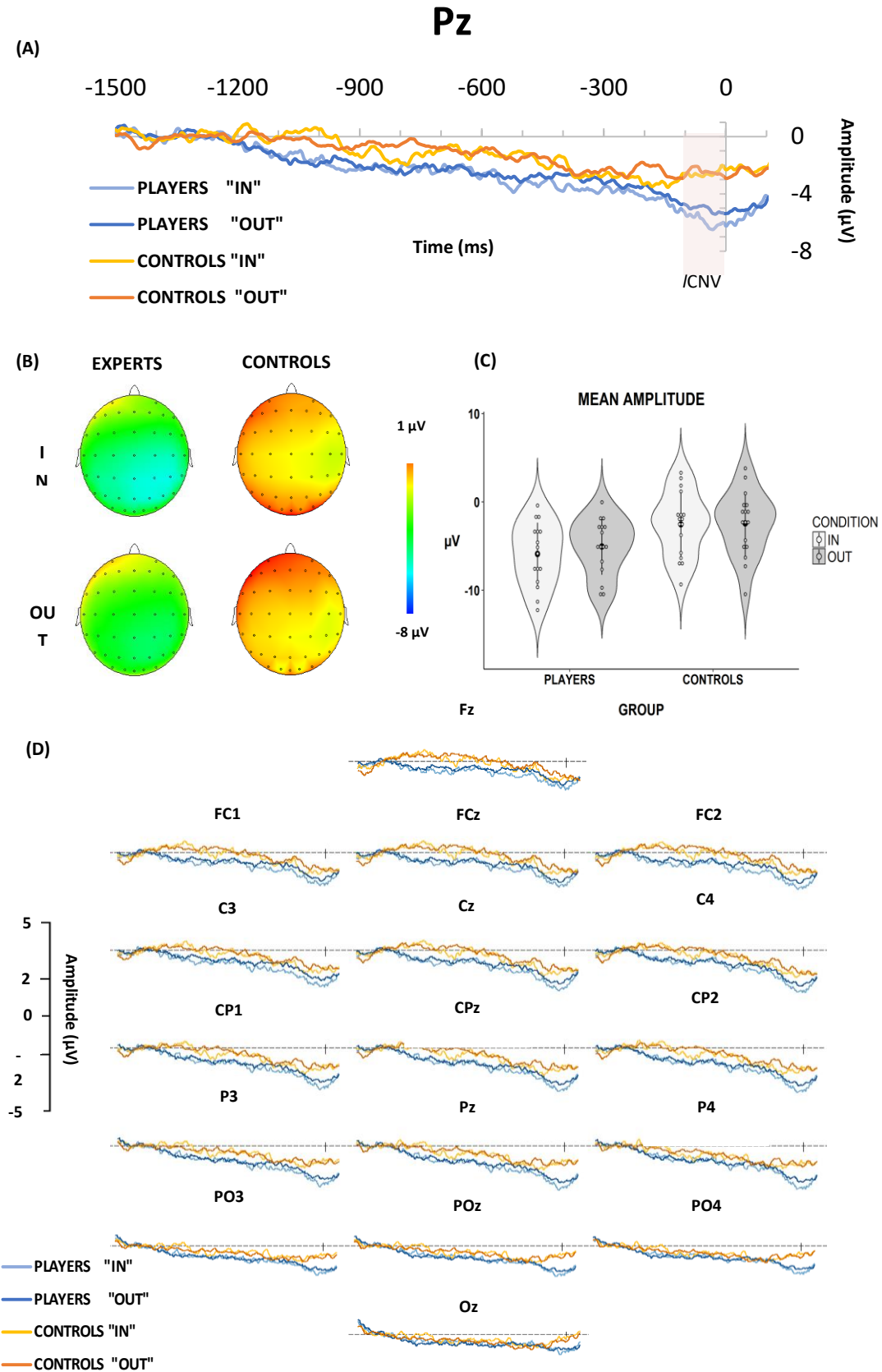


Fig. 4 (A) ERP waveform between Players and Controls – The area marked in red specifies the 100 ms time window in our analysis. The waveform starts from -1500 ms before the end of the video and stops 100 ms afterwards. (B) Topographic view. (C) The mean amplitudes of each group in each condition (D) ERP waveforms recorded in the electrodes, Fz, FC1, FCz, FC2, C3, Cz, C4, CP1, CPz, CP2, P3, Pz, P4, PO3, POz, PO4, Oz.

2.4 Discussion

Experts differ from amateurs since they rely on more refined sources of information when it comes to navigating within their domain of expertise (Aglioti et al, 2008; Abreu et al. 2012). Consequently, they are better able to predict and adapt to sudden changes in the environment. In the present study, we aimed at identifying ERPs during action observation in an expert population. To do this, we tested elite athletes from the Santa Lucia Wheelchair Basketball team (Players) and walking novice controls. All subjects were asked to predict the outcome of free throws presented in movie stimuli. This task allowed us to examine the neural activity with respect to domain-specific actions, as well as to record behavioral responses. Indeed, our data shows a different neurophysiological pattern for Expert athletes in comparison to Controls.

2.4.1 Accuracy rates

As expected, the Players (with a mean of 9 years of expertise) were significantly more accurate than the Controls. It should be noted that the success rate across both groups of participants is 86.3%, suggesting that the shot outcome was relatively easy to predict, as was the aim of the task. However, expertise did play a significant role in the accuracy of the prediction of the fate of the basketball shots.

2.4.2 ERP signals

Our main hypothesis was that the neurophysiological correlates of predicting the outcome of an action through observation of kinematics are modulated due to motor expertise. Our analysis shows that the Players had a significantly larger parietal EEG negative amplitude compared to Controls during the key point of the observed throw: when the wrist closed to complete the shot. This may be reminiscent of the results that expert basketball players focused on the kinematics of the shot while the expert watchers (i.e. non-players) used later cues like the ball trajectory in order to reach successful predictions (Aglioti et al. 2008). Upon visual inspection of the topography and the scalp distribution of the waveform (Figure 4) we have found similarities with the analyzed waveform and the oCNV.

Action effect prediction has been associated with a negative deflection over the parietal electrodes (Hughes and Waszak 2011; Jin et al. 2011; Savoie et al. 2018). Our task had some

similarities and some differences with respect to the traditional set up that elicits a CNV. In our task, the cue (the beginning of each clip) was uninformative as to the required response and it only indicated that there was going to be a response from the participant in roughly 1.5 seconds. Then the actual information regarding the response was carried within the last ~100 ms of each clip. Nevertheless, the slow negative waveform is present for both groups. The oCNV amplitude in experts is significantly more negative compared to the controls. This result aligns well with the idea that a CNV is elicited not only during the observation of a partner's action (Kourtis et al 2010; 2013), but also during the observation of an expert's domain of expertise (Wang and Tu 2017). Wang and Tu (2017) found that CNV was smaller in badminton players compared to controls when predicting the height of badminton shots with a high uncertainty. Increased CNV amplitudes in controls has been interpreted as a greater need for attentional control. While this finding seems in contradiction with our results, in our task we aimed to have a ceiling effect, which meant that for the players, there was little uncertainty. Although, a stronger argument for this might be possible with further analysis on selecting the trials in which the participants had high confidence as well as being accurate versus the ones that they had low confidence while being accurate. Overall, we believe that the parietal negativity we report has similarities with CNV, in terms of its occurrence during action prediction and latency.

Contrary to our prediction, our results did not show a difference in the ERP waveform regarding "IN" and "OUT" shots within groups. However, there was a main effect of group in the amplitudes, which survived the post-hoc tests for the "IN" condition. In other words, the Players had greater negative parietal activity compared to the Controls in the "IN" condition. We speculate that the difference revealed in the oCNV might be due to the observed domain-specific activity (i.e. observational /CNV). We suggest that this negative amplitude is associated with higher activity in sensorimotor areas associated with expertise during the observation of a domain-of-expertise action (Hughes and Waszak 2011; Jin et al. 2011; Savoie et al. 2018), but further investigation is required to validate this claim. The correlation analysis regarding expertise and ERP amplitude was not significant for either "IN" or "OUT" conditions. This is likely due to the small sample size, as differences in amplitude are very small, and would require a greater sample of experts.

By occluding the ball trajectory, the present study builds on Aglioti and collaborators' previous findings (Aglioti et al. 2008) and highlights the EEG correlates associated with action outcome prediction based on movement kinematics (i.e. arm and wrist movements). When compared to the Controls, the Players show significantly more negative deflection in parietal regions during the observation of the kinematics of a basketball shot for the "IN" condition compared to the 'OUT' shots, but the significance does not survive the post-hoc tests. The significant difference between these two groups in the "IN" shots may stem from the uncertainty that exists for non-players, especially in the 'IN' shots. Once the decision for the 'OUT' shot has been made, the observer will no longer have any uncertainty, whereas for the 'IN' shots, even for mere milliseconds, there may be more attention necessary until later in the movie. Thus, a scenario where Players -who do not seem to experience uncertainty in either condition- compared to Controls have a more negative ERP signal regarding the 'IN' shots can be tentatively interpreted as occurring due to the continued uncertainty which the Controls might experience. However, a stronger claim for this point would if such effect existed for feedback. It has to be listed as a limitation in statistical strength for this study that the difference for 'IN' and 'OUT' shots might have been effected by the more extensive action simulation of the basketball players. We did not observe any clear peak that could be considered an error-specific component such as a frontal observed error-related negativity (oERN) for the "OUT" shots (where an error in kinematics occurs for the shot to fail). This may stem from the overlap of other components such as error positivity (Pe) over ERN, dependent on specific task features (e.g. Panasiti et al. 2016). It may also be due to the continuous nature of our task, making a clear event-related potential difficult to extract. Furthermore, the timing of the movements building up to the shot varied across our movie stimulus.

It has been shown that visual and motor training have different implications in action observation (Casile and Giese 2006; Inuggi et al. 2018). In the seminal research from Aglioti et al (2008), expert basketball commentators who had much visual familiarity with basketball were found to focus on the ball kinematics, whereas players were reading the body kinematics with comparable success in outcome prediction. Furthermore, basketball players use both visual and proprioceptive cues when it comes to their own movements. Maglott et al. (2019) tested basketball players from a

university team (experts) and recreational basketball players (non-experts) and asked them to predict the fate of their own shots (verbally indicating “in” or “out”) without seeing the actual outcome. Their results showed that university team players – compared to recreational ones - were more accurate in predicting their own correct throws, but worse in predicting their missed shots (i.e. worse than chance level). Performance advantage of experts can be considered in terms of better prediction to unexpected which may be visible already in the neural markers of known monitoring processes. Furthermore, action anticipation based on biological kinematics can have an impact on neural activation; experts are able to simulate the observed domain specific action (Senna et al. 2014; Tomasino et al. 2012). Amoruso et al. (2014) demonstrated, in expert tango dancers, that anticipatory neural activity regarding movement recognition differed between groups of experts and novices, and that semantic neural responses such as N400 predicted motor expertise. In our study, we investigated how the level of expertise might impact a specific domain of action observation. An alternative mechanism for the effects of expertise may be efficient visuo-motor integration. In expert dancers, the parietal region was shown to contribute to integrating kinesthetic perception with the representation of the dance syntax during the observation of the moving body (Bachrach et al. 2016).

In this study, we have shown a parietal negativity (on electrode level) during the crucial moments of action cues for anticipation during a basketball shot. While it is true that we are not able to directly compare our results to neuroimaging studies that specify the parietal region in the context of expertise (due to sensor-level analysis), we find it important to acknowledge that source localization should be performed in the future. For instance, it has been shown that subtle intention-specific kinematic information can be decoded from a network that involves parietal regions (Koul et al. 2018). In our study, we focused our analyses on the electrode-level, which prevents direct comparison to neuroimaging studies that specify the parietal region in the context of expertise. Nevertheless, our results are in line with those of other studies that have shown different brain activation for experts with various imaging techniques and tasks. Successful action integration and prediction allows expert players to more rapidly and more effectively adjust in situations that require their expertise (Hack et al. 2009; Wu et al. 2013). Experts are therefore better in action execution during unexpected situations that may arise in the domain of their expertise, and show different AON

activation during action perception tasks (Wang and Tu 2017; Wang et al. 2017). However, in studies that use tasks such as the Flanker task (not directly relevant to the particular domain of expertise), the neurophysiological signals from expert athletes do not always display differentiating patterns compared to non-athletes, even in the presence of better reaction times or performance (Di Russo et al. 2010; Wang et al. 2017). Moreover, the type of expertise (e.g. in the kind of sport that is the focus of a study) drives which cognitive skills are enhanced, such as cognitive control or spatial abilities (Chan et al. 2011; Yamashiro et al. 2015), and a better understanding of these measures might lead to better skill specific training.

Finally, while the heterogeneity of the athletes' physical ability impedes addressing straightforward questions regarding the effects of actual physical ability/disability on the AON as well as the necessity for source analysis, it still provides a setting in which physical expertise can be studied. Wheelchair basketball requires skills acquired with more difficulty than regular basketball, and perceptual-motor training (obtained by a visual constraint that forced participants to use target information as late as possible) has a positive impact on future successful shooting percentages (Oudejans et al. 2012). There is a lot of interest in how expertise affects not just the behavior but also plasticity in the brain, and research focusing on the effects of many hours of practice has had a valuable impact on the understanding of the mechanisms underlying learning, skill acquisition, and the rewiring of the brain after an acquired motor disability.

3.4.3 Future directions and conclusions

The relationship between expertise and AON engagement has been modelled within different frameworks. Recently, a quadratic relationship between increasing familiarity and the accuracy of predictions was proposed (Gardner et al. 2017). Gardner and his colleagues trained participants in guitar movements. They demonstrated that BOLD activity in the AON is present during both highly familiar and highly unfamiliar observed actions, either due to more accurate predictions in the former, or due to continuous updating in the latter. It may be beneficial for future EEG/MEG studies to examine how parietal negativity during domain-specific action observation due to sports expertise might be affected with a manipulation that could result in a quadratic relationship. In our study, we compared subjects that were expert Players and completely naïve Controls. We aimed to describe

expertise-related observational properties, but we did not induce expertise acquisition (e.g. through learning) within our paradigm. It is necessary for future studies to assess how motor skill learning occurs, or more specifically, how motor expertise acquisition induces changes in the brain (Ossmy and Mukamel 2018), in order to have on-line information about training-induced brain plasticity. The timing of the crucial wrist movement for the basket shot that determines the fate of a shot in our videos were not positioned at the same moment in each video down to the millisecond. Instead, they varied within the same 100 ms window. This has limited our ability to take full advantage of the temporal properties of ERP data. However, in other action observation tasks that are done using virtual avatars has the benefit of pinpointing the event (in our case) movement of interest with complete sensitivity. Furthermore, with a virtual arm that executes a basket shot from the first person perspective instead of the third person perspective there would be the possibility to detect prediction related activity with higher precision (Pavone et al 2016; Spinelli et al 2018; Pezzetta et al 2018), targeting specific features of action observation in expert groups with certain physical abilities, with the aim of making effective comparisons.

Overall, we report ERP signals evoked by action observation in wheelchair basketball expertise. While we acknowledge that the sample of athletes in this study is comparatively small, our data supports and extends the literature by demonstrating more negative activity in elite athletes, especially when the expert players focus on crucial information. Crucially, our data also further supports the relation between motor experience and anticipation expertise via embodiment mechanisms and raises new questions regarding the acquisition of motor skills after injury and the different levels of expertise.

Chapter III. Predictive monitoring of actions, EEG recordings in virtual reality

A commentary on: Brain negativity as an indicator of predictive error processing – The contribution of visual action effect monitoring

By Michael Joch, Mathias Hegele, Heiko Maurer, Hermann Müller and Lisa Katharina Maurer

Abstract

Error-related Negativity (ERN) is a signal that is associated with error detection. Joch and colleagues (*Journal of Neurophysiology* 118:486-495, 2017) successfully separated the ERN as a response to online prediction error from feedback updates. We discuss the role of ERN in action, and suggest insights from VR techniques; we consider the potential benefit of self-evaluation in determining the mechanisms of ERN amplitude; finally, we review the oscillatory activity that has been claimed to accompany ERN.

3.1 A commentary on the role of virtual reality for the study of the predictive monitoring of one's own actions

Error detection is a crucial ability for learning and implementing adaptive behavior. Several MEG/EEG studies have investigated the cortical signatures of error monitoring in a variety of tasks, ranging from the widely known speed-response tasks (i.e. Flanker task, go no-go) to more finely-tuned motor tasks such as grasping an object or hitting a target (Maier, Di Pellegrino, & Steinhauser, 2012; Meyer, Braukmann, Stapel, Bekkering, & Hunnius, 2016). EEG studies indicate that execution errors as well as errors of observed action are indexed by specific electro-cortical markers in the time and time-frequency domains. Specifically, in the time domain, when an error is detected but the result of an action is still explicitly unknown, an ERN is observed in the mid-frontal regions. Moreover, when the external feedback about the performance is provided, a so-called Feedback-related Negativity (FRN) is elicited. As the ERN appears before the feedback, it may represent a signal of prediction error. However, this conclusion becomes less straightforward in complex tasks where many other “low level” - action execution related - factors can contribute to the generation of this negative event-related potential. In fact, despite the error prediction process itself, in many studies the participants could still execute corrections while the action is in progress, or they could visually observe the trajectory that leads to the goal, which makes the contribution of these later factors to the ERN generation unclear. Furthermore, the temporal proximity of any external feedback overlapping with the error detection itself makes it difficult to pinpoint the neural bases of action outcome prediction.

In a recent issue of *Journal of Neurophysiology* Joch and colleagues (2016) addressed some of these issues by recording EEG from healthy individuals while they performed a complex motor task. Their aim was to investigate whether the ERN represents a high-level (action outcome related) prediction error or whether this signal is generated by the detection of low-level (i.e. kinematics) discrepancies. The task they proposed was a quasi-virtual ball-throwing task inspired by the pub game called Skittles. In this game, a ball was attached to a rope on the top of a stick; the participants were instructed to decide when to pick up and release the ball by simply pressing and letting go of a virtual lever that controls it, with the aim to hit an external target. In the current paradigm, the ERN

signal is elicited by missing the target. By preventing the knowledge of the result (namely the feedback), movement correction and action effect monitoring, the authors excluded three possible confounds of the ERN generation that were observed in previous research (Maurer, Maurer, & Müller, 2015). Specifically, in the target study, Joch and colleagues prevent the effects of online feedback of the action itself by occluding the vision of the ball trajectory once the movement has been executed (namely when the subject lets go of the lever). As a consequence, movement corrections were avoided as well as action effect monitoring due to ball flight visibility.

In the target article, when they compared the mean amplitude in both the hit and error trials on electrode FCz, they detected a negative deflection between 200 and 350 ms following the ball release for the erroneous trials (ERN). They also found another deflection occurring between 1000 and 1200ms as a reaction to feedback (FRN), also in the mid-frontal regions. While in their previous study, Maurer and colleagues (2015), found a broad negative event-related potential (that was interpreted as the neural response to action effect monitoring of the ball flight trajectory, in the target article, they observed no significant broad negative deflection in the interval between the ERN and the FRN unlike in Maurer et al (2015). Therefore, the aforementioned confound was eliminated in the present work by Joch and colleagues (2016).

This efficiently verifies that the previously observed negativity was related to the action effect monitoring of the ball flight trajectory. The findings are important because they center upon an issue in the error field that focuses on the action observation network (AON), since it involves both visual and proprioceptive information. As this study clarifies, the error signals can indeed continue to be generated due to action effect monitoring; by focusing on what happens in the brain when an action is produced before any immediate external feedback (as the ball trajectory represents), one is able to focus on the prediction of an error based on the pure action kinematics. When an action is observed (visual), the pre-existing sensorimotor network (AON) is engaged, especially more robustly when the observed action is familiar. In a way, this resembles the information from the “memory” of a proprioceptive component of the very same action. Thus, if an individual is executing an action while observing the consequence visually, but not observing the outcome, it is possible to narrow

the window in which the error signal occurs. Below we discuss how this quasi-virtual paradigm and the results pave the way to find out the fine nuances of error detection, and even the prediction of an error.

We have three points to make about the implications of this study, and the further opportunities it presents. Firstly, the target article paradigm emphasizes the distinction on whether the error signal codes the error prediction itself, the knowledge that an error has happened, or it is a more general signal that occurs in both types of situations. Tellingly, the study is embedded in the context of the forward model of action prediction, which comprises the efferent information derived from the muscles and the afferent information from the action trajectory. According to the forward model, a prediction is generated by integrating available sources. In this paradigm, the informative sources are: i) the throwing movement, which produces an efference copy and ii) the visual and proprioceptive online information about the very same movement (Aglioti, Cesari, Romani, & Urgesi, 2008). Specifically, in the target article, the efferent copy is represented by the lever press (release of the ball), but it is still coupled with the observed trajectory until the movement of the press ends, even though the following observation is prevented. Therefore, as mentioned by the authors themselves, the online sensory information here is both visual and proprioceptive. There are several ways to approach the issue, building upon the target article. The intention to separate the efferent and afferent copies of error prediction lead us to propose an alternative use of the augmented reality techniques, coupled with motion tracking (for a similar paradigm, see Yazmir & Reiner, 2016). With a motion tracking system (e.g., cyber gloves), it is possible to carry the movement of hands to the virtual environment without the need to utilize a lever as an intermediary apparatus. If the real-time movement can be translated into a virtual environment in another sensory prediction task, the visual cues from the virtual environment can be manipulated to create a scenario in which sensory information can be congruent with visual information and where the visual information is unavailable after the movement itself is learned by heart (similarly applications on animal studies, Schwartz, 2004). In the unavailable visual information condition, it would be possible to observe whether there is a point in which the participants can detect their executed error. Thus, the pure effect of proprioceptive information on error detection can be separated from the visual information that

relates to the AON. By means of virtual reality, strong control over the environment and reliable sensory information can be obtained and new discoveries can be made regarding cortical signatures of error prediction in adaptation, such as in the cases of expertise, where the absence of efference copy (by means of a paradigm similar to the target article's) is easily compensated due to the simulated action based on the learned domain-specific kinematics (Aglioti et al 2008).

Secondly, the ERN reported by Joch et al (2016) had a later latency and smaller amplitude compared to choice-reaction time tasks. The authors explain that task complexity leads to less accurate predictions. Collecting confidence ratings prior to the external feedback could also help address this issue. Di Gregorio, Steinhauser, & Maier (2016) proposed a paradigm in which participants respond with one of the three options in a visual-color matching task. Each response was followed by a self-evaluation of performance: participants judged whether the response provided was correct or incorrect and, if incorrect, to indicate which of the wrong targets they responded to. This allowed the authors to sort trials by the level of confidence on error commission and disentangle implicit and explicit correctness of the predictions. From the neuro-electrical point of view, this confidence about the prediction and thus, the level of awareness about the performed action, was previously linked to the error positivity (Pe – a positive signal that peaks ~100–200 ms after an error; Ridderinkhof et al 2009). We think in future research, findings regarding a late positivity after ERN or FRN would clarify this point. This can create an informative picture of predictive processes, and confirm whether the certainty of error prediction and the amplitude of ERN co-vary with the Pe, or, whether the two mechanisms underlying the two cortical potentials are independent.

Lastly, aside from the evidence based on ERPs, a growing literature based on time-frequency domain analyses reveal interesting results on the link between error prediction processes and brain oscillatory activity. For future research, we think that the current paradigm is well suited for analysis that aims to separate the phase-locked and non-phase locked features of the theta-band activity, which may be related to the on-going events after an action. It is important to recognize that ERP components have a complex heterogeneous structure composed of frequency-specific oscillations (Yordanova, Kolev, & Kirov, 2012). In the time-frequency domain, delta (< 4Hz) and frontal midline

theta (4–8Hz) has been considered a key mechanism in the generation of ERN and FRN. Moreover, an extensive literature support theta involvement in behavioral and cognitive control (Luu, Tucker, & Makeig, 2004; Cavanagh, Cohen, & Allen, 2009), so the oscillatory theta activity may be a consistent neurophysiologic marker of the mismatch (error) information by the monitoring system.

To conclude, the elegant paradigm in the target paper temporally localizes the action related ERN by obscuring the visual action effect monitoring and delaying the feedback. The authors' paradigm and similar motor tasks could provide fruitful opportunities to disentangle the neuro-electrical patterns of error prediction processes in controlled virtual environments. The mentioned ERPs and the related oscillatory activity are useful to understand the neuropsychological mechanisms for coordinating different cognitive processes involved in predictive processes.

Chapter IV. Observed and performed error signals in auditory lexical decisions

Abstract

This study investigates the observation of errors using a speeded auditory lexical decision task, on pairs of participants (performer and observer), using language processing as a realistic setting. Monitoring one's own errors yields a response-locked EEG component for errors relative to correct responses, known as the Error Related Negativity (ERN), that is followed by an error positivity (Pe). Similar components have been shown for the observation of errors. While these effects have been widely studied for performance errors in speeded decision tasks, relatively little is known about the performance monitoring signatures in language comprehension observation. Some recent studies indicate a similar ERN effect for errors in linguistic performance, but so far, the observed ERN and Pe have not been examined during lexical decision tasks. In our task, native speakers listened to Dutch words, obvious non-words, and crucially, long pseudowords that resembled words until the final syllable, which were shown to be error-prone in a pilot study because they were responded to too soon. In this paradigm, we manipulated the length and deviation point of non-words in order to prevent the participants from forming a strategy based on timing expectations. Consequently, errors can be (i) obvious upon response (expected for real words and obvious non-words), or (ii) revealed upon the completion of the word, after response (expected for long pseudowords). We hypothesised that the errors on an auditory lexical decision task would result in a response locked ERN-Pe pattern both for the performer and for the observer.

4.1 Introduction

Performance monitoring lies at the base of many processes including adaptation and learning (Cavanagh & Frank, 2014; Koban et al 2012; Luu et al 2004; Ullsperger et al 2014b). Specifically, fast error detection in own and others' actions are fundamental for subsequent adaptation, flexible behaviours and learning of goal directed actions (de Bruijn et al 2007; de Bruijn et al 2011; Navarro-Cebrian et al 2016). Although much of the error monitoring research focuses on speeded choice tasks or performed motor errors, similar electrophysiological markers in the brain during observation of others' motor errors have also been found (van Schie et al 2004; Pezzetta et al 2018; Moreau et al 2019 *in press*). Furthermore, these markers of the error monitoring system have been shown to be present both in action errors (Joch et al 2017; van Schie et al 2004) and in language comprehension (Sebastian-Galles et al 2006; Ylinen et al 2017). The present study brings together the well-established literature of error monitoring during action observation with the brain responses associated to auditory language comprehension, with the aim of exploring the extent of how much the monitoring mechanisms are shared or specialized.

Subprocesses of performance monitoring have been studied extensively using EEG (de Bruijn & von Rhein 2012; Luu et al 2004; Ullsperger et al 2014a). In the time domain, two event related potentials (ERPs) have been identified to be related to error monitoring processes (Luck & Kappenman 2011): The Error Related Negativity (ERN) and Error Positivity (Pe). ERN is a negative deflection peaking fronto-centrally around ~100 ms after an error is committed. It is thought to be generated in the anterior cingulate cortex (ACC) which is involved in cognitive control and adaptive functions (Holroyd & Coles 2002). The Pe is a positive deflection that usually follows ERN, with maximal amplitude over central-parietal area (Shalgi 2009; Wessel 2012), and is thought to reflect error awareness, and context updating (Nieuwenhuis et al 2001). Typically, ERN seems to be present during speeded choice tasks such as Flanker, Stroop and Go-No Go, time-locked to errors (Riesel et al 2013).

In the past two decades, the action observation literature has been mainly based on motor simulation hypothesis, in which the basis of action understanding relies on our own motor capabilities

(Keysers & Perret, 2004; Rizzolatti & Craighero 2004; Kilner et al 2007b). Namely, action understanding relies on the individual's ability to predictively simulate the observed movements by reactivating the same neural machinery that would be used in case the observer performs the observed action themselves. In keeping with this account, during from the observation of motor errors from first- and third-person perspective has been shown to elicit similar activation in neural activity (Pavone et al 2016, Pezzetta et al 2018). For instance, the errors that are not our own, but are observed have been reported to elicit the so-called observational ERN (oERN) as well as the observational Pe (oPe; Bediou et al 2012; Koban & Pourtois, 2014; Panasiti et al 2016). Seminal research from van Schie et al (2004) demonstrated the presence of oERN, with longer latency and smaller amplitude compared to classical ERN, during the observation of a Flanker task performance. In their task, a participant had to choose whether the presented arrowhead in between distractors were pointing left or right by using the joysticks on each side. In the observation condition, the observer was presented the correct response on a screen separate from the actors, who were performing the task without any feedback. In the last decade, error monitoring signals such as the oPE have been shown to be present in various tasks such as observation of incorrect piano movements (Panasiti et al 2016), a virtual avatar committing errors in a game (Kobza & Bellebaum, 2013), of key presses for oERN (Weller et al 2018), or even of a computer algorithm performing a Flanker task for oERN and oPe (de Visser et al 2018). While some error observation studies did not find oERN possibly due to the same frequency of error and correct trials (de Bruijn et al. 2007; Panasiti et al. 2016), recent findings show the oERN to be present for erroneous trials regardless of frequency (e.g. same amount of (Kobza & Bellebaum, 2013) or more erroneous trials than correct ones (Pezzetta et al 2018)). oERN was found in patients with schizophrenia while ERN was absent, suggesting these patients might be sensitive to others errors while monitoring of own errors was compromised (de la Asuncion et al 2015). Furthermore, it has been recently shown that being observed increases the amplitude difference in the ERN between errors and correct responses (Huang & Yu 2018). Overall, ERN that is elicited by both erroneously performed and observed actions has been shown to be affected by task characteristics and requirements as well as individual differences. Crucially, the literature calls for testing performance monitoring in more realistic settings

(Wessel, 2014) (e.g. not guiding the observer in the monitoring process such as in van Schie et al), while also being mindful of the effect of various task manipulations. In the present study, we have aimed to create a realistic setting to address the performance monitoring processes involved in observation of language processing.

In EEG studies in the auditory domain, several response and stimulus related monitoring ERPs have been found that seems to be shared with the language comprehension processes. The ERN was elicited by erroneous responses to an auditory lexical decision task with words and non-words in Catalan, in Catalan-dominant bilinguals (Sebastian-Gallés et al 2006). In their paradigm, the non-words were created by changing one vowel from existing words in Catalan. When Spanish-dominant bilinguals performed the task in Catalan, they did not show any ERN effect between error and correct trials despite having committed many errors. This was interpreted as due to the Spanish-dominant bilinguals' unfamiliarity with the vowel contrast, as such, being unable to 'hear the error'. Recently ERN was found in also errors of language switching tasks (Zheng et al 2018). Furthermore, manipulated vowel harmony can result in MMN, depending on task requirements (Ylinen et al 2017). Ylinen et al demonstrated that MMN was elicited 340 ms after the presentation of an auditory stimulus comprised of words that violated Finnish vowel harmony, such as in oddball paradigms, highlighting the presence of mismatch monitoring markers specialized for language processing. Their task did not involve response to stimuli, only passive listening. Overall, evidence suggests that the auditory stimuli can elicit several ERPs due to performance related effects. In other words, just hearing different types of words, such as a deviant word in a sequence of other words can elicit MMN (Li et al 2019; Ylinen et al 2017).

Based on the presented evidence, the current study hypothesised that the mechanism for error monitoring is shared throughout modalities during observation of even the performance on a lexical decision task. This mechanism might not be only shared with performed errors in speed choice tasks, motor actions, and verbal error commissions, but also with the process of making lexico-semantic decisions. To investigate this hypothesis we have created an auditory lexical decision task that requires the listener to make a speeded decision on whether the stimuli they hear

are words or non-words, and the observer to be attentive to this procedure. The non-words were purposefully created to either be obvious (obvious non-words; e.g. blij/blooi – happy/heppee), or to be revealed to be non-words once the listener has predicted the stimulus to be a real word (pseudowords; e.g. *universiteitsbibliotheek/universiteitsbibliotheekui* – university library + ui). The rationale in having pseudowords distinct from the regular non-words was to ensure the participants would commit enough errors. Thus, by task design, errors were intended to occur due to the tendency of internal completion of a word, or prediction of it from the initial few correct sounds (Norris & McQueen 2008), only then for the participants to realize that they are mistaken.

We were guided in the choice of the stimuli by the assumptions of the Bayesian perspective of word recognition. A recent model of speech recognition, Shortlist B (Norris & McQueen 2008) posits a Bayesian perspective of word recognition which sets forth a claim that listeners adopt an approximate optimal strategy in word recognition, guided by predictive coding framework. In this model, optimality is described as the best recognition that can be achieved by the listener, constrained by the potential ambiguity of perceptual input, combined with phonological and lexical knowledge. If there is an ambiguous amount of perceptual input (e.g. if a word isn't easily recognizable to distinguish from a non-word, or when the deviation point that makes a word into a non-word is at the very end which creates ambiguity until the word is completed) in a task that requires a speeded response decision, the most probable word will be selected as the correct response (Bogacz et al 2006). Thus, words are recognized by prediction before they are revealed in full. However, depending on the ambiguity of the input, spoken word recognition process may or may not result in certainty. On the one hand, if a non-word is presented to a listener with an immediate obvious deviation from all known words, the listener can recognize with optimal probability that the word is non-existent. On the other hand, if a non-word is recognized to be a word only at the last sound (i.e. when a sound is added, which makes the real word a non-word), the optimal response will have been made with certainty, only to then realize the error in the decision. Therefore, it would be possible to test predictive mechanisms of word recognition, which according to Shortlist B is based on (incorrect) prediction with a set of stimuli comprised of Real words, filler words that are obviously non-words, and Pseudowords that become non-words in the last syllable. Pseudowords

were the target words in which we manipulated to make the participants to commit errors, and the Obvious non-words were included to prevent the participants forming a strategy expecting which syllable the error would be at. As per previous evidence, we hypothesized that the erroneous responses (yes-response to Pseudowords) in the present auditory lexical decision task will be marked with response-locked ERN. On the other hand, the correct responses are not expected to have ERN (yes-response to Real words). We expect the ERN for errors to be followed by stronger P_e for errors marking the subject's awareness of the error. This would suggest the error monitoring mechanism is also shared for the errors that are committed during language comprehension. No-response to real words were not used as errors because it might include a slightly different process that might confound the results if averaged over with the yes-response to Pseudowords. Furthermore, we expected to demonstrate the presence of oERN during the observation of another individual performing an error in the auditory lexical decision task, with smaller amplitudes compared to the performance ERN.

4.2 Methods

4.2.1 Participants

20 pairs of participants have been tested, all native Dutch speakers between the ages of 18-35, recruited through the SONA system (M_{Age} : 22.4, SD : 4.2, 28 Females). The inclusion criteria comprised of right-handedness, having no hearing issues, normal or corrected to normal vision, no color-blindness, no dyslexia or reading problems, no neurological issues, and not having learnt a second language from birth.

4.2.2 Materials

In order to select stimuli for the experiment, first a database of 4000 Dutch words was created from CELEX (Max Planck Institute for Psycholinguistics, 2001) and SUBTLEX-NL (Keuleers, Brysbaert, & New, 2010). 720 words (nouns, verbs and adjectives) between 1-10 syllables were then selected from within this set based on several exclusion criteria. Among these were: phonotactic violations, certain derivations (*-heid*, *-teit*, *-isch*, *-lijk*, *-ig*), generic compounds and reduction of derivations, names, inflected word forms and taboo words, as well as infrequent and emotionally

loaded (Moors et al 2013) words. 120 Pseudowords were created of the following manipulations: Added syllable (as with *universiteitsbibliotheek* → *universiteitsbibliotheekui* – university library + ui), added consonant, changed last sound or syllable, (*scheikundelaboratorium* → *scheikundelaboratoriuf* – chemistry library + uf), replaced vowel (*diplomautrekingsceremonie* → *diplomautrekingsceremona* – graduation ceremony), replaced consonant (*onafhankelijkheidsverklaring* → *onafhankelijkheidsverklarinkt* – declaration of independence), added consonant (*verantwoordelijksheidsgevoel* → *verantwoordelijksheidsgevoelt* – feeling of responsibility). Pseudowords were identical to real words until the last syllable, and were always between 7-10 syllables, and non-words were 1-6 syllables. Obvious non-words were created to be phonotactically sound (i.e. theoretically possible Dutch words) while not being identical to any existing Dutch word. The words varied in length (number of syllables), lexical frequency, and the position of stressed syllable. Words with strong phonological similarity to German or English were also avoided in order to avoid confusion due to the high chances of familiarity to these languages. Most of the obvious non-words were assembled by changing existing words from the initial set until they became a clear nonword. A total of 250 Obvious non-words were created by adding a single sound, replacing several syllables or combining parts from multiple words, such as *spak*, *kleuzelschetter* or *abanteurenmaroon*. Contrary to obvious non-words, pseudowords were set to be longer to allow the predictive process to complete the word before the end was known. The Obvious non-words were created as filler non-words so that the participants wouldn't be able to form an expectation on where and when the deviation from a real word would occur.

We have recorded the words spoken by a female native Dutch speaker. Recordings were done in sound proof audio labs and were edited in PRAAT software (Boersma & Weenink, 2019). The audio files were segmented at word boundaries, at the zero crossings right before stimulus onset and after stimulus offset respectively (Avg. 1100 ms; Min. 342 ms, Max. 2302 ms). We balanced two lists for both participants in the pair to have the role of Observer and Performer. Each list had 240 real-words, 90 obvious non-words, 30 pseudowords, and the items were distributed over different

syllable lengths. Obvious non-words were easy to recognize immediately, so they served as fillers to mask the fact pseudowords always had the manipulation at the very end.

4.2.3 Procedure

The set-up included a touchscreen that was embedded in a table, in which the buttons were presented. The task was a simple two-alternative forced choice auditory lexical decision task. The stimuli were delivered via speakers by Presentation® software (Version 20.0, Neurobehavioral Systems, Inc., Berkeley, CA, www.neurobs.com). The participants sat facing each other, with a table placed between them. The buttons were presented via a touchscreen placed between the two participants. Performers had to respond by touching the green box on the right side of the touch screen if they thought it was a real word, and red box on the left side if not. Performers had their hand on the planks placed over the touch screen, with their index finger hovering over the response buttons. Observer's task was to pay attention to the auditory stimuli, as well as the Performer's response on the touch screen (green for 'word', red for 'not a word'). Additionally, both partners had to keep track of the number of incorrect responses to ensure the errors were being attended to. Response hands were not counterbalanced to make it simpler for the Observer to discriminate the Performer's response on the touch screen. The participants were informed that they could respond as soon as they were sure, and that they did not need to wait until the end of the word. As determined by behavioural pilot sessions (see below), the time out duration was set to 400 ms after the offset of the word. If they were within the time limit, a white screen for inter-stimulus-interval between 500-1000 ms was presented before the next sound file played simultaneously with the buttons presented. If they were too late to respond, they saw a message ('Sneller A.U.B.!' – 'Faster please!') that told them to be faster before the next trial started. The task lasted ~25 minutes comprised of 4 breaks and 5 blocks. In each break, participants were asked approximately how many trials they thought they observed/committed depending on their role, to ensure the observer's attention throughout the session. Upon the completion of the first task, the participants changed roles, and were presented with the second word list.

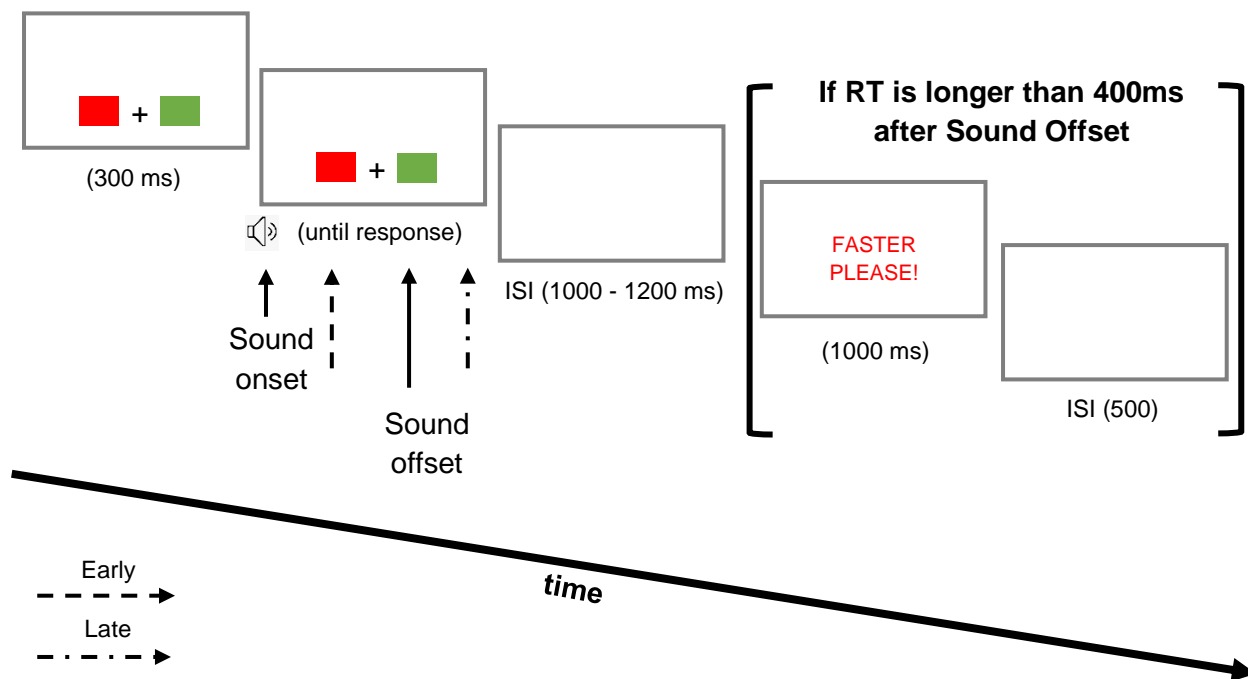


Figure 1 Sequence of one trial. Each trial started with a presentation of the buttons and fixation cross for 100 ms, followed by the sound presentation. Response could be given either during (early response) or after (late response) the sound, and upon response, the buttons disappeared from the screen, and a blank interval screen was presented. Duration of the sound files varied between 394 - 2468 ms. Note: The blank screen after response was jittered, and so was the interval after the 'Faster Please!' message. When the response was within the time limits and there were no 'Faster Please!' message presented, the first blank screen was the only jitter between trials.

4.3 Behavioural Pilot Study Results

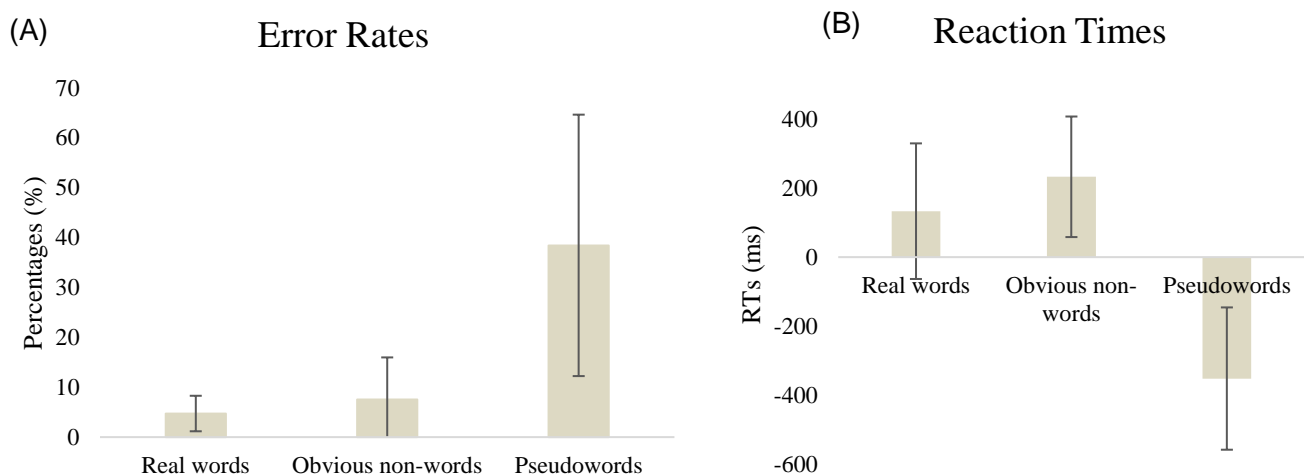


Figure 2 Results of the pilot study: **(A)** Error rates for each type of stimuli **(B)** RTs to each type of stimuli (Time 0 represents the sound offset. Negative reaction times represent the responses that were given before the sound offset.)

In order to assess the validity of the stimulus and to estimate the appropriate time pressure for the participants to commit enough errors throughout the experiment, we have conducted a pilot experiment. This also helped us to get a sense of the type of the errors committed as well as the reaction time information. Participants were tested in sound-proof cubicles and were asked to fill in

a questionnaire about the clarity of the stimuli. We have tested 34 participants with various time limits enforced (250 ms, 400 ms, 1000 ms), and decided on a 400 ms time pressure to respond to 400 ms after stimulus offset for our final sample of 20 participants. The task differed from the EEG experiment in the way that the participants were tested individually and using a buttonbox. Overall, in this pilot study participants were 91% accurate of 360 trials. We had aimed for at least a minimum of 6 error trials for pseudowords and correct trials for real words as a criterion to include the participant in the analyses, which proved possible by the pilot results (Olvet & Hajack et al., 2009; Pontifex et al., 2010). On average, the number of errors for real words were ~11 out of 240 (SD = 8.5), for obvious non-words were ~6 out of 90 (SD = 7), and on pseudowords were ~11 out of 30 (SD = 6). Reaction time to real words was ~133 ms after the stimulus offset (SD = 196 ms), to obvious non-words was ~232 ms (SD = 174 ms), and to pseudowords were exclusively before the stimulus offset ($M_{RT} = -350$, SD = 206 ms). Independent samples t-tests revealed that there were no differences between the error rates and the reaction times to the two lists of stimuli (all $ps > .9$).

4.4 EEG Experiment

Participants were recruited in pairs and were seated in a comfortable chair. After having signed the consent forms, they were explained the procedure and mounted with the EEG caps simultaneously by two researchers. The session was comprised of two parts: Observation and Performance. The order of the Observer/Performer role was assigned randomly. After the completion of the tasks, they were asked to fill out a post-experiment questionnaire. The full experiment lasted 2 hours. Each participant was compensated with 20 € for their time.

4.4.1 EEG recordings and Preprocessing

The EEG recordings were done using two Brain Products ActiCaps. Each cap had 32 electrodes including the external ocular and reference electrodes. The signals were acquired from channels: FP2, F4, F8, FC6, C4, T8, CP2, CP6, O2, P4, Cz, Pz, Oz, O1, P3, CP5, CP1, T7, C3, FC1, Fcz, FC2, Fz, FC5, F7, F3, FP1. The reference electrodes were applied to the left (digital reference) and right (physical reference) mastoids. All electrodes were algebraically re-referenced offline to the average of both mastoid electrodes. The Horizontal Electro-Oculogram (HEOG) was recorded bilaterally, and Vertical (VEOG) with electrodes positioned under the left eye. The signal

was recorded with an online band-pass filter 0.01-250 Hz with a sampling rate of 500 Hz. Impedances were maintained under 5 K Ω by applying gel (ElectroGel) to all electrodes. All preprocessing of the EEG data was carried out using FieldTrip, an open source toolbox (Donders Institute, Nijmegen; Oostenveld et al 2010) in MATLAB (The MathWorks, Inc.). Removal of visual artifacts was done in two steps. First, a blind source separation method, the Independent Component Analysis (ICA; Jung et al 2000) was applied to remove the components that are related to eye movements. Then, all trials were visually inspected and all trials with artefacts including residual eye blinks were excluded from the analysis. Furthermore, the trials with longer response times than 2 standard deviations were removed from both behavioural and EEG analysis, matched between the Performers and the Observers. On average 22.8 trials per participant were removed. The ERPs were calculated time-locked to the response, obtained by segmenting the signal into epochs of 1000 ms length (-200 ms to +800 ms, relative to response time) and were band-pass filtered offline (0.1–30 Hz). Baseline correction was done using the time window from 200 milliseconds before the stimulus, which were well before the response. The number of correct trials (from the Real words category) were matched to the number of erroneous trials (from the Pseudowords category).

4.4.2 ERPs

Statistical analyses on response-locked ERPs were performed with R Software (R Studio Team 2014), using the *erpR* package (Arcara and Petrova 2014). The data were segmented locked to the response of the Performer (Figure 4). Based on the ERN and Pe literature the analyses will be focused on FCz and Pz electrodes, respectively. Mean amplitudes for each participant and for each condition in the time windows of interest were fixed from 0 to 150 ms for ERN for the Performer (Danielmeier et al 2009; Kaczurkin 2013; Zambrano-Vazquez & Allen 2014) and from 250 to 350 ms for the Observer relative to the response of the Performer (covering the peak following ERN). The early Pe was defined as the mean amplitude in the 150–250 ms post-response time window at FCz for the Performer and 350-450 ms for the Observer. The late Pe was determined as the mean amplitude in the 300–500 ms post-response time window at Pz for both groups (de Bruin 2017). Data from the Obvious non words were not included the analysis, as there were filler words to prevent the participants from expecting the deviation from a real word to be at the end of the words each time.

Performer's and Observer's data were analysed separately, and *t*-tests were used to compare the mean amplitude difference between correct (yes to Real-words) and error trials (yes to Pseudowords). In order for both of the participants in a pair to be assigned to each role within one session, the number of stimuli was kept to a minimum. This meant that several other comparisons beyond the main hypothesis was not possible due to the small number of trials. Thus, comparisons between the stimulus types were beyond the scope of this study.

4.5 Results

4.5.1 Overview of Task Performance (EEG)

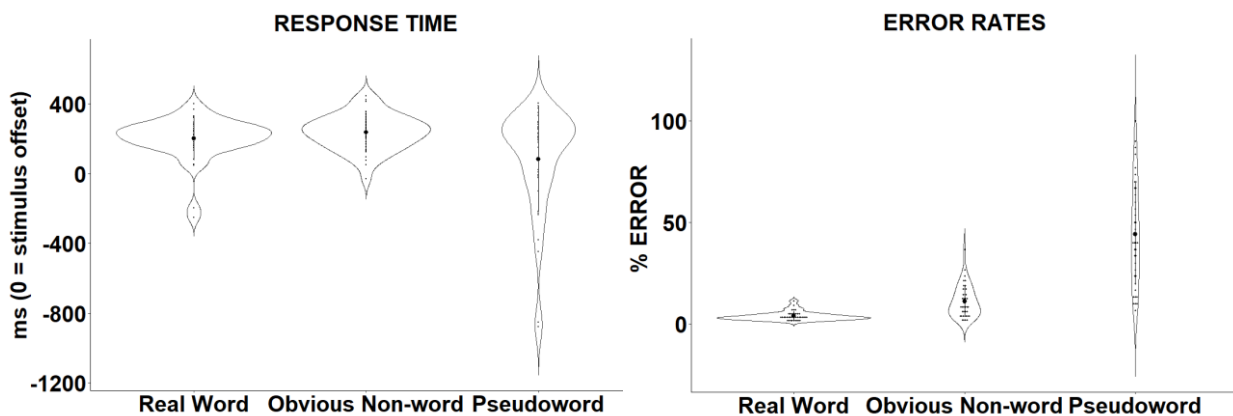


Figure 3 Behavioural data from the Experiment: **(A)** Error rates for each type of stimuli **(B)** RTs to each type of stimuli (Time 0 represents the sound offset. Negative reaction times represent the responses that were given before the sound offset.)

Response times were analyzed relative to the stimulus offset, of which could be before (resulting in negative response times) or after (positive response times) the end of the stimulus. Overall, participants were 91% accurate of 360 trials. On average, the number of errors for real words were ~9 (SD = 5) out of 240 (4%), for obvious non-words were ~10 (SD = 7) out of 90 (11%), and on pseudowords were ~13 (SD = 7) out of 30 (44%). Error responses were executed faster than correct responses (137 ms after the sound offset (SD = 205 ms) vs 209 ms (SD = 116 ms); $t(39) = -3.85$, $p < 0.001$). Response times (RTs) to pseudowords were significantly faster (83 ms, SD = 303) than RTs to real words (201 ms, SD = 125; $t(39) = 3.8$, $p = 0.001$). Participants' estimating accuracy for own errors was .02 and for partners errors was 2.6 out of 360 trials (even though with some variability SDs = 10.6, 14.5 respectively). This was calculated by subtracting the number of erroneous trials from the number of estimated errors for each participant. These estimates were

calculated from the guesses they made at each break and subtracted from the number of errors;

Own errors: 32/360 SD = 14; Partner's errors: 32/360, SD = 13.

4.5.1 Event Related Potentials

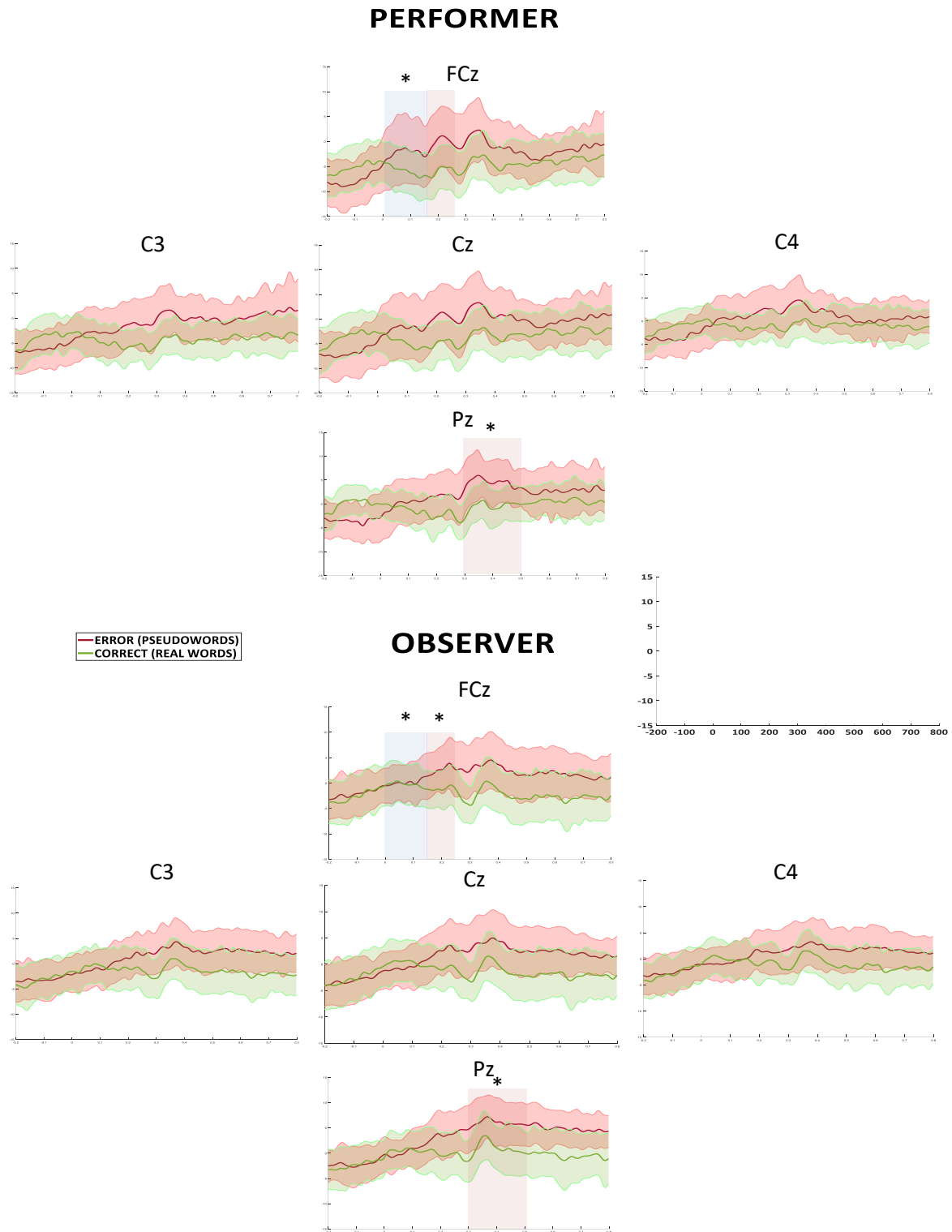


Figure 4 Scalp distribution time-locked to response times for each group; red lines for error trials in pseudowords (yes response to pseudowords), green lines for correct trials in real words (yes response to real words). The y axis: -15 to 15 μ V, negative down; the x axis shows -200 prereponse period; time0 indicates the response time. Blue box indicates the time window of interest for ERN and oERN; red box for early Pe and oPe, and for the late Pe (*) indicates the statistical significance. (Note that the baseline correction was done using a 200 ms interval *before* the Stimulus Onset, therefore the pre-response interval on the figure does not reflect the baseline.)

In both groups (Performers and Observers), the opposite effect of the standard ERN-Pe pattern were observed. In correct trials (yes to Real words), there was a large negative deflection compared to errors (yes to Pseudowords) as can be seen in Figure 4, FCz electrode, with a significant difference between conditions (Performer, 0-150 ms: $t(32) = -2.07$, $p = .046$; Observer, 250-350 ms: $t(32) = 3.28$, $p = .003$). For the analysis of early Pe in the electrode FCz, the only significant difference was present for the Observers (Performer, 150-250 ms: $t(32) = -.68$, $p = .5$; Observer, 350-450 ms: $t(32) = 3.44$, $p = .002$). This difference was in the expected direction but with a sustained positive deflection instead of the typical Pz peak. For the late Pe in the Pz electrode was significant in both groups (Performer, 300-500 ms: $t(32) = 2.45$, $p = .02$; Observer, 300-500 ms: $t(32) = 3.40$, $p = .002$).

4.6 Discussion

In this study, we aimed to detect EEG error-related activity on an Auditory Lexical Decision Task, both for performance errors (i.e. ERN, in the Performer role), and for observed errors (i.e. oERN, in the Observer role). The task was designed in a way to allow us to compare errors that were made due to a lexical deviation, which resulted in an incorrect prediction (yes response to Pseudowords) of the stimuli, to correct responses (yes response to Real words). We have manipulated the classical errors to be due to the revelation at the end of the stimuli (i.e. there is no error until the deviation of the stimulus towards being a pseudoword), so that the performance error would be due to the incorrect prediction of the word rather than being an error concerning the part of the stimulus that the subject had heard up to the time of his/her response. In addition, we wanted to see if the Pe would be present in errors on Pseudowords, since the sudden realization of the errors that are due to the deviation at the last moment would increase the saliency of the stimulus and therefore the awareness to the error. Instead, results show more negative amplitudes on FCz between 0-150 ms window after the Performers response for correct trials (on Real words), but for the Pe window error trials (on Pseudowords) do show a larger Pe. These findings are not in agreement with our expectation, as the results were the opposite of the typical ERN-Pe pattern (Holroyd & Coles 2002). For the Performers and Observers, we see a similar pattern in the ERP waveform in response to both error and correct trials, with smaller amplitudes for the Observers.

We observed a significantly more negative deflection for the correct responses compared to the errors on pseudowords, with a sustained negativity, a contrary result to the negative peak for errors in the well-established ERN time window (0-150 ms after response). A possible driving effect for this result could be the nature of the Pseudowords that only deviated from a Real word at the last moment. This deviation may have made the participants doubt every Real word until after the last syllable. Previously, Hammer et al (2013) suggested that contrary to the intuitive expectation of a larger negativity, in some cases the ERN amplitude appears to be smaller due to competing processes in error monitoring and insufficient perceptual input. While this may seem in contradiction with the previous evidence, it suggests that response-conflict is lowered when there is stronger distractor processing. In other words, ERN amplitude is modulated by the degree of response conflict in relation to error awareness. In conflict monitoring literature, ambiguity has been related to Correct Related Negativity, a negative peak larger for correct responses compared to erroneous ones (Luu et al 2000; Pailing & Segalowitz 2004; Grützmann et al 2014), which is thought to represent uncertainty in speed-choice tasks that are used to study error activity at a cognitive level and the activity of at a cognitive level. In our task, there are only small differences between Real words and Pseudowords at the very end, which may have led participants to expect a deviation at the end of each long Real word. Furthermore, instead of the ERN-Pe pattern that is observed in error monitoring paradigms, our data seem to show multiple positive peaks after the sustained negativity. Alternatively, an N400 effect overlapping with Pe might create confounding effects in the current pattern in the waveform, due to unexpected deviation on the Pseudowords (semantic incongruity; Praamstra et al 1993), however, we think this is unlikely because the correct trials show more negative amplitudes, and not the errors on Pseudowords. Therefore, we think that the results are better explained with CRN that is due to the uncertainty.

The more negative deflection in the initial time window is followed by a positive peak in both correct and error trials in the early Pe window, which was significantly more positive only for the Observers. In the error monitoring literature, the Pe has been observed in the absence of ERN and has been reported to be dependent on error awareness (Nieuwenhuis et al 2011), stimulus representations (Gibbons et al 2011), detection of an erroneous action (Panasiti et al 2016) and use

of different evidence in the detection of errors (Di Gregorio et al 2018). Di Gregorio et al suggest that while the early ERN reflects an early signal in the MFC that quickly indicates the need for behavioral adjustment, the Pe reflects the conscious evaluation of errors, two independent systems together forming a dual monitoring system. In the present study, CRN might indicate the encoding for continued ambiguity for both groups, followed by a significantly larger Pe for errors in the Observers, encoding the awareness for the errors. From the guess-rates regarding the number of errors, we can claim that mainly the errors were mostly attended to, which could explain the clear presence of Pe, although following the CRN and not the ERN. For the late parietal Pe, the mean amplitudes were significantly more positive for both groups during errors. Previously, salient and infrequent targets have been associated with stimulus-locked P300 which was thought to share characteristics with late Pe following errors (de Bruijn et al 2007; Ullsperger et al 2014b). While our analyses were response-locked, it is true that the Pseudowords were rare and salient in our paradigm; the participants have reported their attention was drawn every time there was a Pseudoword. Thus, we believe that the larger late Pe for the errors on Pseudowords marks the attention to the infrequent but salient deviation of the words.

3.6.1 Limitations

As a limitation, with the current analysis, we are not able to address the potential movement-related effects. However, we believe the response (tap finger on the touch screen button) did not confound the data, as both groups show a similar pattern in the ERP waveform, while Observer's were not required to respond (their task was to both discriminate between words and non-words without performing any response, and pay attention to the Performer's errors).

Furthermore, there is a small baseline difference that is present in the Performer's ERP signal. This is likely to be caused by the response time differences relative to the baseline period used (which was the 200 ms time interval before the *stimulus onset*). This can be addressed by matching the word length of the correct trials to the error trials in further analyses. Lastly, to keep the experiment duration to a minimum for both of the participants to be able to do the experiment in each role, there were not sufficient number of erroneous trials in each category (Real words, Obvious non-words, Pseudowords) for every participant. Therefore, we were not able to compare error/correct

trials in these categories with each other. Potentially, the question of whether stimulus related effects differ between each category (e.g. higher early and late Pe amplitudes for Pseudoword errors compared to Obvious non-words due to the effect of salience and rarity) can be addressed by mixed-models analyses, which take into account the weight of the number of trials in different experimental conditions. This approach would make the claim about the late Pe being related to errors to Pseudowords more trustable, thus allowing to interpret the late Pe as a stronger response to an incorrect prediction of stimuli.

3.6.2 Conclusions and Future Directions

In the present study, I aimed to integrate the EEG error-related brain responses during action observation (van Schie et al 2004; de Bruijn et al 2011; de Bruijn & von Rhein 2012; Pezzetta et al 2018), with EEG responses associated to lexico-semantic processing (Davidson & Indefrey 2011; Bultena et al 2017). The results suggest that the Auditory Lexical Decision task results in CRN for correct trials (on Real words) compared to errors (on Pseudowords) due to continued ambiguity for both Performers and Observers. This is followed by a significant Pe marking the error awareness only for the Observers. Finally, a late Pe is present for both groups in errors, potentially due to the salience of the rare and deviant stimuli. Further data analysis for time-frequency and source analysis in order to determine the involvement of performance monitoring processes are required to support this claim (Cohen et al 2008).

Chapter V. General Discussion

Performance monitoring of actions is crucial for survival (Kilner 2007a, 2007b). During the actions we perform, both motor control and performance monitoring processes support the execution of movements. (Kawato et al 1999; Rushworth et al 2004). Research shows that we simulate others actions through our own motor repertoires (Di Pellegrino et al 1992; Rizzolatti and Craighero, 2004; Aglioti et al 2008; Inuggi et al 2018). Through these systems, we are also able to understand other's goals and intentions; we can integrate the outcomes of their actions with one's own movements for cooperation and competition (de Bruin et al 2012). It is not only fundamental to monitor actions, but also the changing environment. Error and feedback monitoring supports learning processes (Ylinen, 2017); together with other cognitive control and memory functions, detecting and correcting errors minimizes future errors (Holroyd & Coles 2002). This thesis relied on two distinct theoretical backgrounds: performance monitoring typically studied using tasks that require discrete responses and monitoring of observation of actions that are continuous such as kinematics. The question addressed was whether performance monitoring of observed kinematics and observed discrete choices might share the same markers that are associated to performance monitoring processing. The study in Chapter II shows the CNV, normally a potential that is observed when the subject expects an imperative stimulus requiring motor response, present during the prediction of action outcomes within the domain of expertise. This study is unique because paves the way to dissociate different types of physical capability in future experiments, through expertise or injury level. Chapter III includes a commentary on an empirical research that show ERN for the prediction of own action outcomes in a partially virtual environment. In this chapter, the use of virtual reality techniques for action observation research is discussed. In the empirical study in Chapter IV, we show the CRN, a negative deflection for correct trials compared to erroneous trials, contrary to our expectation for an ERN-Pe pattern during the incorrect prediction of a word in an auditory lexical decision task. This would be relevant from an 'prediction error' point of view, as our manipulation entailed pseudowords that subjects had thought to be real, until it was too late. Their response became erroneous, not because of a performance error but because of the predictive nature of word recognition was tricked. This study investigated the observation of the task performance as well as the effects during the performance itself, and showed a similar effect between the observer condition and the perform

condition. In the current chapter, I discuss how the presented results add to the body of research on performance monitoring and address future research lines that might emanate from them.

5.1 Action observation and expertise

Action observation literature is largely based on the humans' capacity for action understanding through simulation (Rizzolatti & Craighero 2004; Keysers and Perret, 2004; Avenanti et al 2012; Cross et al 2008; Kourtis et al 2013). Expertise has been shown to modulate this capacity (Aglioti et al 2008; Sebanz and Shiffrar 2009; Fujii et al. 2014; Amoruso et al 2014). For example, it has been shown that experts can both anticipate the successful basket throws and detect fake passes from kinematics. The neural mechanisms of the expert advantage are still not clear. It has been proposed that N400 (contribution of semantic integration process to motor expertise; Amoruso et al 2014), Pe (error recognition in piano finger sequences; Panasiti et al 2016), CRN (Wang & Tu 2017) have been involved in supporting action expertise. In other words, the nature of the predictive processes behind the contribution of expert knowledge in action outcome prediction is still an open question that deserves to be studied. In Chapter II, I investigated the mechanisms of expert knowledge using EEG. I had the following predictions: during the observation of domain-specific actions, specifically when the action is observed for advancing in a game (therefore the inflow of visual input is being used to predict the next event) there would be a difference between the successful and unsuccessful shots. The unsuccessful throws might be related to error related components, or a marker of violation in action semantics. Results showed that the prediction of the outcome of a basketball free throw elicits different activation depending on expertise, observable in the ERP waveform, as CNV. Crucially, in this paradigm, it was possible for the subjects to focus on outcome prediction based on specific body kinematics: the participants had to guess the outcome of the observed action before it was completed (the trajectory of the ball and the outcome of the throw was occluded). The choice of using wheelchair basketball players made it possible to study expertise, with a potential to investigate the extent of influence of body ability in action observation in the future. Wheelchair basketball presents a rare possibility for research in action observation because there is a points system that classify the players by their physical ability (i.e. how much of their upper body the players can move; point 1 the least, point 4.5 the most). It is possible to compare

the neural differences that might be caused by the actual capability of a player (due to physical limitations) between the high and low limitations. This would of course require a sensitive control of the injury type (only spinal cord injury) as well as stimuli that targets each point class. Expertise effects on the neuromarkers that are related to performance monitoring might still be observed for action outcome prediction with a more sensitive experimental manipulation that uses first- instead of third-person perspective stimuli, as it can result in larger amplitudes in ERPs (Pavone et al 2016). Results from Chapter II suggests the domain specific action observation based on movement kinematics (in this case the free throw of a basketball) elicits an observed CNV, with significantly more negative amplitude in expert wheelchair basketball players compared to naïve observers. I would however interpret the results with caution due to the neural signature of the effect. On the one hand, we could interpret the effect modulation as CNV, which would suggest that action processing is involved in action observation (Kilner et al 2012); on the other hand, we could interpret the effect modulation as Readiness Potential (RP), if the 1.5 interval from the video offset to the response given was not sufficient for the response related confounds. RP is a negative potential observed from about 1–2 s prior to the onset of an action (responses such as a button press) which doesn't necessarily involve the action preparation but action precision (Libet et al 1993; Wen et al 2018).

The idea that neutrally observing an action is similar to making an action is not new. It is now established that the AON is activated by sheer observation of actions of other humans (Rizzolatti & Craighero 2004; Keysers and Perret, 2004; Avenanti et al 2012; Cross et al 2008; Kourtis et al 2013). Experts observe and understand actions within their domain of expertise based on priors formed due to both long-term motor and visual familiarity (Karlinsky et al 2017). This is supported by an EEG study which has shown stronger beta desynchronization (associated to action simulation) for the observation of crawling in infants compared to the observation of walking (van Elk et al 2008), which is due to the infants' experience with crawling rather than walking. Furthermore, fMRI evidence by Calvo-Merino et al (2004, 2006) have shown increased neural activity in premotor and parietal cortices of both ballet dancers and capoeira martial artists when they observed ballet and capoeira specific choreographed movements, but only in their own domain of training. Therefore, it is argued that the observed actions are integrated by one's own motor repertoire. Enhanced AON activity is

also reported in other motor activities such as archery (Kim et al 2011) or basketball (Abreu et al 2012). A priori expectations (formed by experiences) have a critical role in perception and action observation (Kilner 2007b). It can be argued that expertise modifies those expectations in a way that is traceable with various techniques. fMRI evidence suggests that high-level of cognitive expertise (e.g. in mathematics) is reflected in activation in smaller number of regions compared to a broader distribution of activation for low level of expertise (Jeon & Frederici 2016). Similarly, visual expertise (e.g. in ornithology and mineralogy) leads to domain specific changes in visual cortex, as well as domain-general changes in the frontal lobe (Martens et al 2018). Expertise then would update to the priors, thus modulate the comparison between the priors and the sensory inflow of observed actions in a more permanent way. EEG findings complement this view in both observation (Babiloni et al 2010) and anticipation (Amoruso et al 2014; Denis et al 2017) of domain specific actions. Tango dancers exhibit greater P300 responses (a positive going deflection approximately 300 ms following an event that is related to attention) compared to novices, for incongruent tango moves rather than congruent moves (Amoruso et al 2014). Likewise, alpha desynchronization was found to be lower in elite karate athletes, interpreted to reflect a neural efficiency (Babiloni et al 2010). These concepts are in line with previous evidence of the influence of expertise on motor simulation (Gallese et al, 1996), and can be re-interpreted in the predictive coding framework (Neal & Kilner 2010). Together with our results that show a more negative late CNV activity in observation of a basketball free throw during the prediction of action outcomes (in which the comparison with the actual outcome was prevented) in experts compared to naive subjects, it can be speculated that the comparison process between the priors (what the movement kinematics should be for the basket shot to be successful) and the inflow of visual input (the actual continuous movement kinematics that is observed) is affected by long-term expertise. It might be useful to use control groups comprised of non-athlete wheelchair users, as well as non-wheelchair user basketball players. Such a control would strengthen the claim of expertise modulation is the cause of the CNV effect in action outcome prediction (due to motor simulation), instead of empathy. In order to control for the any possible confounds caused by empathy (that the players might feel towards other wheelchair basketball players), another useful control would be to expose the players to stimuli created using other sports

such as wheelchair rugby, softball, or tennis. It would also be fruitful to modulate the interest of the control group, thus the effects of attention in action observation (Weng & Tu 2017). These effects cannot be ruled out completely, and require further attention.

Here, we discussed the present prediction-related activity modulated by expertise in action observation is reflected in CNV. While we can't draw concluding inferences based on the above-mentioned limitations, we can't exclude the scenario that the motor simulation of observed kinematics is modulated by expertise. Building on the previous evidence that expert observation of action leads to distinct AON activation, here we suggest that expertise is reflected by the ERP waveform during the prediction of domain specific action outcome. In other words, the motor simulation of observed kinematics is modulated by expertise (Calvo-Merino et al 2006; Aglioti et al 2008; Kim et al 2011; Abreu et al 2012; Amoruso et al 2014).

5.2 Performance monitoring and language comprehension

Both studies presented in this thesis were focused on the performance monitoring system in observation of others' movements and decisions. In daily life, we observe and can understand when others misunderstand verbal cues, sometimes when they themselves have not yet noticed. The study in Chapter IV aimed to highlight the shared nature of performance monitoring during the observation of own and others' errors that occur due to incorrect prediction of words. The rationale has stemmed from research in error monitoring in action observation, together with recent research that has supported that error related markers exist also in language errors (Sebastian-Gallés et al 2006).

Results revealed opposite patterns to the ERN-Pe pattern that was expected, where correct responses elicited a peak with more negative amplitude compared to erroneous responses. This is interesting because it may be due to the uncertainty created by our manipulation: pseudowords were rare but salient, which created expectancy in any long words that were real to be not a word. Negative peaks for correct responses - Correct Related Negativity - have been previously linked to response uncertainty in conflict monitoring literature (CRN; Luu et al 2000; Pailing & Segalowitz, 2004; Grützmann et al 2014). Furthermore, CRN has been shown to be larger for faster responses (Valt &

Stürmer 2017). In our design, the presence of pseudowords was to prevent subjects from forming a strategy. This might have created enough uncertainty the CRN, and the larger negative peak for the correct responses was present. It should be noted that this pattern was echoed in the observers' ERP waveform. The role of medial frontal cortex and ACC in performance monitoring and action observation is well established in the literature (van Noordt & Segalowitz 2012). Medial frontal negativities represent more than one response to the above-mentioned processes, as part of dynamic coordination of neural networks, and are modulated by individual differences (Cohen 2011a) and social contexts (Boksem et al 2011). Mid-frontal region has been indicated as a center for conflict monitoring and reward, both in the frontal and posterior occipital cortices (Holroyd and Krigolson, 2006). The dissociations that are found between these negativities due to various task requirements or group differences suggest that there may be both partly different sources for these, and partly different roles (van Noordt & Segalowitz 2012). Our task presents the opportunity to examine these differences with regards to stimuli as well as social context.

This study indicated that error monitoring does not result in the well-established ERN-Pe pattern in the ERP waveform like in the typical Flanker type speeded choice tasks. Instead, the processing of auditory (word) stimuli might be sensitive to conflict and uncertainty. Similar to other error observation tasks, the latency smaller amplitudes of the ERPs suggest that the conflict monitoring system might be reflected in observers for more than error observation.

5.3 Experimental Scenarios

The commentary that is presented in Chapter III draws special attention to the importance of designing experiments that will allow to address questions about performance monitoring while in keeping with the most recent models of how the brain functions, especially for being able to discriminate between observation and execution of own actions. It highlights the role that tasks using Virtual Reality (VR) environments increasingly play (Tieri et al 2018). As well as the high-level of control over the environment such as time sensitivity, it also presents the opportunity to create scenarios where individuals can observe movement in first person perspective (Slater et al 2010). In many users, VR can elicit a distinct feeling of embodiment, which can allow researchers to address otherwise impossible questions (e.g. otherwise painful stimuli in real life). While this

phenomenon permits addressing questions regarding own and others' performance monitoring markers, it also brings forth another stream of research concerning human-computer interactions. In this era, not only 2D technologies are a central part of daily life, but augmented and virtual realities are rapidly making their way into being crucial to many areas of life (starting from the gaming industry, reaching towards education and clinical applications). Thus, it is necessary to research the neural responses to performance monitoring in such environments in comparison to 2D scenarios (Zhang et al 2017).

5.4 Limits and Future Directions

The results of the studies presented in this thesis bear new questions for investigating neural correlates of performance monitoring in observation, using various settings. In Chapter II (Study with the wheelchair basketball) there were a limited number of participants due to the availability of teams. In order to have strong claims for the extents of the modulation that comes from expertise, it is important to reproduce results. Relatively small sample size of the players and it did not allow us to address another fundamental question about the effects of movement capacity, not just modulated by expertise but also modulated by injury. The next interesting step would be to increase the sample size of expert wheelchair basketball players to allow clusters to form based on injury level, time since injury as well as expertise. It also requires testing individuals with motor handicap who are not expert wheelchair basketball players, as disability (or different motor capability) might have a fundamental influence over perception. Furthermore, creating a more realistic and sensitive experimental paradigm might help obtain a stronger signal, such as in comparison of first- and third-person perspectives in a basket free-throw created in virtual reality, as discussed in Chapter II. Research on performance monitoring permits creating more informed scenarios regarding becoming experts. EEG provides extremely rich data which can be analysed in a number of ways. In the future, it would be informative to apply source analyses to investigate the cortical responses in performance monitoring with regards to expertise, especially at different stages of acquiring expertise. This has connotations for learning processes, for becoming an expert -may it be mastering a language, or a basketball shot) involves utilizing all resources of learning. With special focus on the temporal neural dynamics (Fahrenfort et al 2018) of performance and error monitoring,

we are aiming to address the role of brain markers of performance monitoring in two fundamental stages of learning, namely the building up of perceptual structures from sensory input, as well as forming of concepts. This, in combination with observation literature sets a suitable ground to investigate learning through observation.

Appendix: Additional Studies

**A. Motor errors in Parkinson's Disease: neural correlates of actions observed in
immersive virtual environments: preliminary EEG data**

Abstract

Even simple daily actions, such as grasping a glass, can become challenging in patients with Parkinson's Disease (PD). In addition to the motor execution deficits, PD patients seem to show a deficient functioning of the performance monitoring system (Farooqui et al 2011). Previous studies on error monitoring in people with PD showed contrasting results; a few studies found the typical error-related signatures (i.e. error-related negativity, ERN; positivity error, Pe; midfrontal theta oscillations) comparable to the ones shown by healthy elderly, while others showed a general decreased cortical response to erroneous actions. In particular, the evidence on the effects of the dopaminergic medication on the brain response to errors is still unclear (Holroyd et al 2002; Stemmer et al 2007; Willemsen et al 2008; Singh et al 2018).

In the present work, by combining EEG and immersive virtual reality (CAVE system), we investigated the mechanisms underlying the performance monitoring system in PD patients during the observation of reach-to-grasp a glass actions performed by an avatar in first person perspective. The preliminary sample included 8 PD tested twice, at a 2-weeks interval. Each patient was tested in two different states namely soon after assuming dopaminergic medication ('Dopa-ON') and 12-hour after assuming the medication (overnight washout; 'Dopa-OFF'). The order of the medication state was counterbalanced across patients. Ten healthy elderly controls were also tested.

Preliminary results replicate and expand our previous findings in young participants (Pavone et al 2016; Spinelli et al 2017; Pezzetta et al 2018) by showing that also healthy elderly exhibit an increased theta power activity (4-8 Hz) during the observation of erroneous actions. Interestingly, the same pattern was not found in the PD group, regardless of whether they were in Dopa -ON or -OFF state. We also found a significant difference between correct and erroneous actions in the beta range (12-30 Hz), with greater beta power in the erroneous actions, in elderly controls and Dopa-OFF participants. No such result was found in Dopa-ON participants, suggesting a link between the dopaminergic intake and the beta response to actions. Concerning the time-domain analysis, we did not find an ERN, but all three groups showed the typical Positivity Error in response to the erroneous actions. However, in both Dopa-ON and -OFF groups the cortical potential showed lower amplitude

compared to the healthy elderly. Although preliminary, these data can help to better understand the neural dynamics of action monitoring in Parkinson's Disease.

Introduction

Parkinson's Disease is a progressive disease characterized by the degeneration of the dopaminergic neurons in the substantia nigra pars compacta, which have an impact in the fronto-striato-thalamo-circuits of the basal ganglia and the frontal areas (Chaudhuri et al 2009). The alteration of the functionality of those circuits influence the motor abilities, which results in the typical motor features associated with the PD, namely: rest tremor, bradykinesia (i.e. extreme slowness of movements and reflexes), rigidity, abnormalities in gait and balance. Generally, the motor symptoms occur already in the early stages of the disease and often begin on one side of the body, but eventually affect both sides. Clinical and neuropsychological studies demonstrated that as the disease progresses, motor deficits are frequently associated to cognitive impairment (i.e. executive dysfunctions; Cools 2006; Costa et al 2009; Farooqui et al 2011). The general treatment of the PD is based on the administration of dopamine at different doses to reduce the symptoms. However, it is recognized that the relation between dopamine medication and performance is individual-specific and that it follows an inverted U-shaped function, thus implying that too little and too much dopamine can impair performance (Frank 2005; Cools & D'Esposito 2011; Fallon et al 2012). Nevertheless, these are only partial results, and nowadays the consequences on the effects of the dopaminergic medication on the cognitive functioning in PD - such as performance monitoring - are not yet completely understood (Cools & D'Esposito, 2011; Seer et al 2016).

Few studies found the typical error-related signatures (i.e. error-related negativity, ERN; positivity error, Pe; midfrontal theta oscillations) comparable to the ones showed by healthy elderly, while others showed a general decreased cortical response to errors and conflicting events (Holroyd, Praamstra et al 2002; Verleger et al 2013; Singh et al 2018; Stemmer et al 2007; Willemsen et al 2008; Singh et al 2018). The evidence on the effects of the dopaminergic medication on the brain response to errors is still unclear; confounds derived from the fact that PD is a pathology characterized by heterogeneous deficits, and

each patient responds to the therapy differently. Further, some studies tested the patients in both medication states, (Dopa-ON and Dopa-OFF; Stemmer et al 2007, Willemsen et al 2008) and some others only tested one category of patients (either patients in Dopa-ON or in Dopa-OFF; Holroyd et al 2002). Studies that compared the patients according to their medication state showed that, in some cases, the brain response to errors was indeed modulated by the dopamine (Volpato et al 2016), while in other cases the cortical response was unaffected by the dopaminergic treatment (Singh et al 2018).

All the aforementioned studies on error-monitoring in Parkinson's Disease were based on speed-response choice tasks, with various degree of difficulty of the task itself (i.e. go/no go, Holroyd 2002; Eriksen Flanker task, Stemmer 2007; Modified Flanker task, Willemsen et al 2008; reinforcement learning task, Volpato et al 2016; modified Simon task, Singh et al 2018). However, it would be relevant to understand how Parkinson's patients react to errors in very simple tasks, in which they have only to observe the correctness of actions. Also, all those studies provided only time domain analyses, but current literature suggests how extracting also time-frequency information can provide a clearer picture of the brain activity (Cohen, 2009). To date, only one study - Singh and colleagues (2018) - investigated the time-frequency response during a cognitive control task in PD patients. As already known, mid-frontal theta band activity is a crucial correlate for cognitive control (Cavanagh & Frank 2014; Cohen 2014b) and response to executive demands, and it is diminished in PD during a variety of tasks such as the interval timing task, in which participants estimate an interval of several seconds as instructed by a cue. These 4-8 Hz theta rhythms are modulated by cortical dopamine and can be abnormal in patients with PD. Humans and rodents with dysfunctional dopamine showed impaired performance in a timing task and had attenuated delta and theta activity (Parker et al 2015). The topographic distribution of ERPs over midfrontal cortex showed a typical central distribution. However, as Parker et al. (2015) specifies, it is likely that those oscillations are not unique to the timing tasks, but are rather a cortical response elicited by alerting and orienting responses, as a need for cognitive control (Cavanagh & Frank, 2014). It is still unclear if mid-frontal theta activity is attenuated also during tasks that require error detection in PD patients. Additional

work is also needed to dissect whether there are relative effects of the dopaminergic treatment in the theta response to errors (Seer et al 2016).

In this study we used the paradigm developed in our laboratory (Pavone et al 2016; Spinelli et al 2017; Pezzetta et al 2018) to investigate the error mechanisms in response to simple observed actions. The same patients visited the lab twice, in both dopaminergic treatment states (Dopa-ON and Dopa-OFF); an aged-matched group of healthy participants were also tested. The current analyses are done on a preliminary set of data.

Methods and Materials

Participants

Eight patients with Parkinson Disease (PD) took part in the experiment (3 females, 5 males; mean \pm SD: Age: 72.25 ± 9.84 ; Years of Education: 10.13 ± 3.23). All participant had normal or corrected-to-normal visual acuity (one patient had reduced visual acuity with the left-eye). Patients that were diagnosed with idiopathic PD were included in the study (United Kingdom Parkinson's Disease Society brain bank criteria; Huges et al 1992). The inclusion criteria were: i) absence of dementia (Mini Mental State Examination, MMSE > 26); ii) absence of other neurological and psychiatric diseases; iii) stable anti-Parkinsonian therapy; iv) sickness duration of less than 10 years. In addition, a group of 10 healthy control subjects (HC) was included in the study, comparable to the group of patients by age and level of education (6 females, 4 males. Mean \pm SD: Age: 72.71 ± 8.82 ; Years of Education: 14.43 ± 2.53). They were included according to the following inclusion criteria: i) absence of neurological and/or psychiatric diseases in anamnesis; ii) absence of subjective cognitive disorders; iii) not taking medications with psychotropic action iv) MMSE = 30.

To determine patients' cognitive profile and to exclude a diagnosis of dementia, neuropsychological batteries were administered during a first visit in the laboratory, while patients were under their dopaminergic treatment (i.e. Dopa-ON). Patients that met our criteria of inclusion were then contacted to take part to the experiment.

The PD group visited the laboratory twice, seven days apart: once in-within one hour from the medication intake (Dopa-ON) and once after a 12-hour overnight washout from their individual prescriptions of dopaminergic medication used to treat PD (Dopa-OFF). The medication sessions

were counterbalanced in the experiment. One control subject was excluded from the analyses because he was not matching our inclusion criteria. A final sample of 8 PD Dopa-ON, 8 PD Dopa-OFF (within participants, each of the 8 Parkinson was tested twice) and 9 Healthy participants were included in the analyses. The present results included in this Chapter have to be considered as preliminary; the aim is to test 20 subjects per group, that given the large effect investigated (η^2 partial square ~ 0.45 for theta power) largely satisfy the requested sample size.

Apparatus, Stimuli, and Procedure

Similar to the Procedure described in the studies of Chapters 2 and 3 of the present work, participants sat in a cave automatic virtual environment (CAVE) with projectors directed to four walls of a room-sized cube (3m X 3 m X 2.5 m; Cruz-Neira et al. 1993). The virtual scenario consisted of a basic room with a table. At the center of the table, a yellow parallelepipedon was located with a blue glass on top of it. Participants observed one avatar in first-person perspective (1PP; see Figure 1) seated on a chair in front of a table with its arms resting on the table. The glass was placed in the avatar's peripersonal space at a distance of ~ 50 cm (Costantini et al. 2011). The avatar and the scenarios were created by means of Autodesk Maya 2011 and 3D Studio Max 2011, respectively. The kinematics of the avatar were implemented by HALCA library (Gillies and Spanlang 2010), and the experiment was performed in an immersive three-dimensional (3D) virtual environment with a real-size avatar drawn on a 1:1 scale and rendered in XVR 2.1 (Huang et al. 2013; Tecchia et al. 2014). Participants wore Nvidia stereo glasses in which 3D virtual images were alternately displayed on both eyes with a refresh rate of 60 Hz. Moreover, these stereo glasses were interfaced with an Optitrack system and constantly tracked the head position during the experiment.

Experimental Procedure

Before the beginning of the experiment, participants underwent a familiarization phase with the experimental setup, as well as a calibration phase within the virtual environment, which consisted of adapting the size of the virtual body to the real one. The participants were engaged in 3 minutes eyes-open resting state in which they were asked to be relaxed and observe the scenario in front of them, followed by 3 extra minutes of resting state after the end of the task (the analyses on these

sessions are not reported in the thesis). After this phase, a brief practice session (8 trials, 4 correct and 4 erroneous) occurred. Each participant was informed that the goal of the avatar's movements was to reach and grasp the glass on the table and that the action might or might not be successful. The total number of trials per participant was 110, 70 of which were correct and 40 of which were incorrect (similarly to Pavone et al 2016). The total duration of our experiment was approx. ~20 min. At the onset of each trial, a sound signaled the beginning of the action. During the trial, participants observed the movement of the avatar's right arm in 1PP. The total duration of the movement was of 1050 ms; the kinematics of the movement were identical for the 70% of the action in both conditions and diverged in the last 30% of the movement, leading to either a successful or unsuccessful grasp (Pavone et al 2016; Spinelli et al. 2017). The deviation from the to-be grasped object was identical in all the erroneous trials (Figure 1). The sequence of correct and incorrect trials was randomized. After the end of the action, the avatar's arm rested for 1000 ms (\pm 50 ms) before a black screen appeared. During the intertrial interval (ITI), three different situations could occur: 1) in 10 trials (4 incorrect, 6 correct), participants had to answer a catch question ("Did the arm take the glass?" (yes/no answer); 2) in 65 trials, an empty black screen was presented; and 3) in 35 trials (12 incorrect, 23 correct), participants had to provide ratings concerning the sense of embodiment. When the first and third cases occurred, the black screen lasted until a vocal response was given, whereas when the second case occurred, the experimenter pressed a key to start the next trial, producing a variable ITI (mean duration: ~4,000 ms, range 2000-6000ms). To measure their sense of embodiment, participants were asked to verbally rate the embodiment questions on a visual analog scale (VAS) from 0 to 100. The question was about their sense of ownership ("To what extent did you feel the arm was yours?"; 0 = no ownership to 100 = maximal ownership; Slater et al. 2010; Fusaro et al 2016; Tieri et al 2015a, 2015b). A total of 208 embodiment ratings were collected for each group of Parkinson patient, and 315 embodiment ratings for the healthy group.

Statistical analyses were performed using R software (R Core Team 2014). ERPs and time-frequency statistical analyses were performed using the erpR package (Arcara and Petrova, 2014). As data were normally distributed, analyses were performed using repeated-measures ANOVA, and

Greenhouse-Geisser correction for nonsphericity was applied when appropriate. All ANOVAs were performed using the ez package (Lawrence, 2013). Practice trials were excluded from the analyses.

EEG recording and processing

The EEG recording procedure was identical to the steps written in Chapter 2. The only difference was in the EEG caps which included two additional parietal electrodes as compared to the settings in the previous chapters. For easy of reference, we will briefly explain the EEG recording and preprocessing also here. EEG signals were recorded using a Neuroscan SynAmps RT amplifier system and 62 scalp electrodes embedded in a fabric cap (Electro-Cap International), arranged according to the international 10–10 system¹. Horizontal electro-oculogram was recorded bipolarly from electrodes placed on the outer canthi of each eye. EEG signal was recorded continuously in alternating current mode with a bandpass filter (0.05–200 Hz) and sampling rates of 1.000 Hz. Impedances were kept under 5 k. All electrodes were physically referenced to an electrode placed on the right earlobe and re-referenced offline to the common average across all electrodes.

Offline, raw data were band-pass filtered with a 0.1-100 Hz filter (finite impulse response filter, transition 40–42 Hz, stopband attenuation 60 dB). Independent component analysis (ICA; Jung et al. 2000) was performed on the continuous EEG signal and components that were clearly related to blinks, ocular artifacts, sweat were removed (on average, 3.4 ICA components). For ERP analyses, an additional bandpass filter (0.3–30 Hz) was applied on the continuous raw signal. EEG signal was then downsampled to 500 Hz and epoched in wide windows of 3-s length, from -1.5 to +1.5 s to avoid edge artifacts induced by the following wavelet convolution. Epochs were time-locked (0ms) to the end of the avatar's arm-path deviation (Pavone et al 2016). All epochs were DC offset corrected to the previous 200 ms preceding the end of the movement. Each epoch was then visually inspected for artifacts to manually remove residual eye blinks or epochs exceeding -100/+100 μ V amplitude. Bad channels were not interpolated, and they were excluded from the analyses. Analyses were performed using the Brainstorm toolbox for Matlab (free open source for MEG/EEG analysis,

¹ The EEG was recorded from the following channels: Fp1, Fpz, Fp2, AF3, AF4, F7, F5, F3, F1, Fz, F2, F4, F6, F8, FC5, FC3, FC1, FCz, FC2, FC4, FC6, T7, C5, C3, C1, Cz, C2, C4, C6, T8, TP7, CP5, CP3, CP1, CPz, CP2, CP4, CP6, TP8, P7, P5, P3, P1, Pz, P2, P4, P6, P8, PO1, PO2, PO7, PO3, AF7, POz, AF8, PO4, PO8, O1, Oz, O2, FT7, and FT8.

<https://neuroimage.usc.edu/brainstorm/>; Tadel et al. 2011) and customized Matlab routines (Cohen 2014a).

EEG analyses

For the time-domain, analyses focused on the oPe. The oPe is a P300-like component peaking at the Pz electrode likely associated with the conscious recognition of errors, either committed (Vidal et al 2000; Pavone et al 2009) or observed in others (de Bruijn et al 2007). All ERPs analyses were based on mean amplitude (Luck 2005). We performed a time-point cluster-based permutation analyses with 1000 repetitions for each run ($p < 0.05$) and MonteCarlo correction in an extended time window from 0 (end of avatar's action) to 600ms. For the time-frequency analysis, we used a complex Morlet transformation to compute time-frequency decomposition. A mother wavelet with central frequency of 1 Hz and 3 s of time resolution (full width half maximum, FWHM) was designed as in Brainstorm software (Tadel et al. 2011). The other wavelets were computed from this mother wavelet and ranged from 1 to 80 Hz, with 0.5-Hz linear frequency steps. To normalize each signal and frequency bin separately with respect to a baseline, we computed the relative power change (in %) over the time-frequency decomposition as

$$F = \frac{S(t, f) - S_{\text{base}}(t, f)}{S_{\text{base}}(t, f)} * 100$$

where $S(t, f)$ is the signal spectrum at a certain given interval of time (t) and frequency (f), and $S_{\text{base}}(t, f)$ represents the signal power of the reference signal used as baseline. To avoid edge effects, the power activity from -700 to -500 ms, a window in which the avatar's movement was identical in erroneous and correct conditions, was used as the baseline interval. Positive and negative values index a decrease or an increase in synchrony of the recorded neuronal population (Pfurtscheller and Lopes da Silva 1999) with respect to a given reference interval, where equal neural activity is expected between conditions. In our case, a relative power increase/decrease represents a modulation of power compared with the mean power activity during the baseline. As in Pavone et al.

(2016), the main analyses were computed on FCz and Pz electrodes, focusing on oPe in the time-domain (200-600ms) and the mid-frontal theta activity in the time-frequency domain (0-600ms). For the time-frequency domain analyses, after computing the Morlet convolution on the Frequencies 1-80 Hz, we squeezed the frequency of interest on the following: delta (2-4 Hz), theta (4–8 Hz), alpha (8 –12 Hz), and beta (13–30 Hz) bands. Similarly to the ERP analyses, in the time-frequency, separately for each frequency band, we performed a time-point cluster-based permutation analyses with 1000 repetitions for each run ($p < 0.05$) and Montecarlo correction from 0 (end of avatar's action) to 600ms. Both for time and time-frequency domain, with positive and negative cluster we refer to the grouping of neighboring significant effects in time, space (and frequencies) with the same sign (positive or negative).

For each group within analyses are performed. Then the differential outcome (obtained by subtracting the correct from the erroneous conditions) was compared within patients in condition Dopa-OFF and Dopa-ON, to investigate a direct effect of the dopaminergic treatment on the error monitoring. The same was done also between the PD groups (PD Dopa-ON and PD Dopa-OFF) and the healthy participants, to investigate differences between the error monitoring system in healthy and pathological populations (similarly to Singh et al 2018). Embodiment ratings are analyzed.

Results

Cluster-based permutation

Event-related potentials – oPe

Cluster-based statistics found significant clusters differentiating erroneous compared to correct actions for the three groups, but with different extension in time. In the HC a positive cluster ($p = 0.01$) was found starting from 240 to 570 ms, with greatest spatial extent of the cluster reached at 332ms. In the PD Dopa-ON a positive cluster ($p = 0.001$) was found in the range 300 to 600 ms, with largest spatial extent at 518ms. Finally, in the PD Dopa-OFF a cluster was found ($p = 0.002$) in the range 374-600 ms and largest spatial extent at 482ms. The topographical scalp maps (Figure 1C) show the clusters in the averaged window 0-600ms. Direct cluster-comparisons between groups did not show significant differences.

Delta (2-4Hz)

Cluster-based statistics found significant clusters for the three groups, with different extension in time. In all cases the clusters showed greater delta activity for erroneous compared to correct actions. In the HC a positive cluster was found from about 0 to 600 ms ($p = .005$), and it was located over the posterior regions, reaching the largest spatial extent at about 318ms. Another middle-central positive cluster was found in the PD Dopa-ON ($p = 0.04$), from 0 to 600ms, and largest spatial extent at 600ms. A middle-central cluster was found also in the PD Dopa-OFF ($p=.04$) lasting from 0 to 600ms and showing a maximal activity at 352ms. No difference between groups was found at a cluster level.

Alpha (8-12 Hz)

No significant activity was found between erroneous and correct actions in the three groups.

Theta (4-8Hz)

Cluster-based statistics found a significant, positive cluster ($p=.02$), only for the HC, which was present from about 80 to 560 ms and was spread over the central and posterior regions, reaching the largest spatial extent at about 298ms (Figure 2C). The cluster in the HC showed greater theta activity for erroneous than for correct actions. The PD showed no significant cluster in neither PD-Dopa ON nor Dopa-OFF conditions.

A significant contrast was found between HC and PD-Dopa OFF (in which the mean values obtained by correct minus erroneous actions – respectively for each group - were compared). More specifically a comparison between independent groups found a positive cluster for HC compared to PD Dopa-OFF ($p = .03$) in the theta-band, from 100 to 480ms at a mid-frontal cluster, reaching the largest spatial extent at 250 ms (Figure 2C).

Beta (12-30Hz)

Cluster-based statistics found a positive cluster ($p=.04$), for the HC, which was present for a short window from 0 to 190 ms and was located over the central regions with a slightly contralateral distribution compared to the observed arm (Figure 2D). The PD Dopa-ON showed no significant cluster. The PD Dopa-OFF showed a positive cluster ($p = .002$), with a greater activity in the

erroneous than correct actions from 240 to 600 ms, with largest spatial extent at about 570ms and an activity mainly located on the central electrodes (Figure 2D).

The independent-samples t-tests between groups compared the difference value obtained by correct minus erroneous trials and was performed between these groups: HC vs. PD Dopa-ON; HC vs. PD Dopa-OFF. The analysis revealed positive clusters for the contrast HC vs PD Dopa-OFF ($p=0.04$), accounted for by the fact that PD Dopa-OFF exhibited increased beta power in the time range 430-600 ms at the fronto-central electrodes (Figure 2D).

Analyses on a-priori chosen electrode

In the time-domain, the oPe and its topographical distribution can be seen in Figure 1. Traditional analyses on electrode Pz showed that while the HC group reached a significant difference between erroneous and correct actions ($t(8) = -3.81$, $p=0.005$, $M_{ERR}=10.93\ \mu V$; $M_{CORR}=7.91\ \mu V$), the same was not showed by the two PD groups (PD Dopa-ON: [$t(7) = -2.26$, $p=0.06$, $M_{ERR}=6.14\ \mu V$; $M_{CORR}=3.53\ \mu V$; PD Dopa-OFF ($t(7) = -2.13$, $p=0.07$, $M_{ERR}=4.83\ \mu V$; $M_{CORR}=2.75\ \mu V$). The fact that oPe is not significant at the single electrode level (Pz) but it is significant at a cluster-level, is accounted by the fact that the cluster found in the Parkinson's groups (when erroneous and correct actions were compared), showed a greater activity in the central rather than parietal electrodes. Thus, the analysis at a cluster-level might have captured more information, as a more frontal rather than parietal activity for the oPe.

In the time-frequency domain, traditional theta frequency band analyses (4-8Hz) on electrode FCz comparing erroneous versus correct actions found that in the HC there was a significant difference between action type (HC: [$t(8) = -2.60$, $p=0.03$, $M_{ERR}=-3.54$; $M_{CORR}=-16.04$), that was not found in the PD groups (PD Dopa-ON [$t(7) = -1.00$, $p=0.35$, $M_{ERR}=-8.20$; $M_{CORR}=-14.11$), PD Dopa-OFF [$t(7) = 0.004$, $p=0.99$, $M_{ERR}=-22.44$; $M_{CORR}=-22.40$), thus confirming the findings on a cluster-level. Thus theta activity for erroneous trials is significant only for the control group (HC) both at a cluster level and by analyzing the typical electrode of reference, FCz.

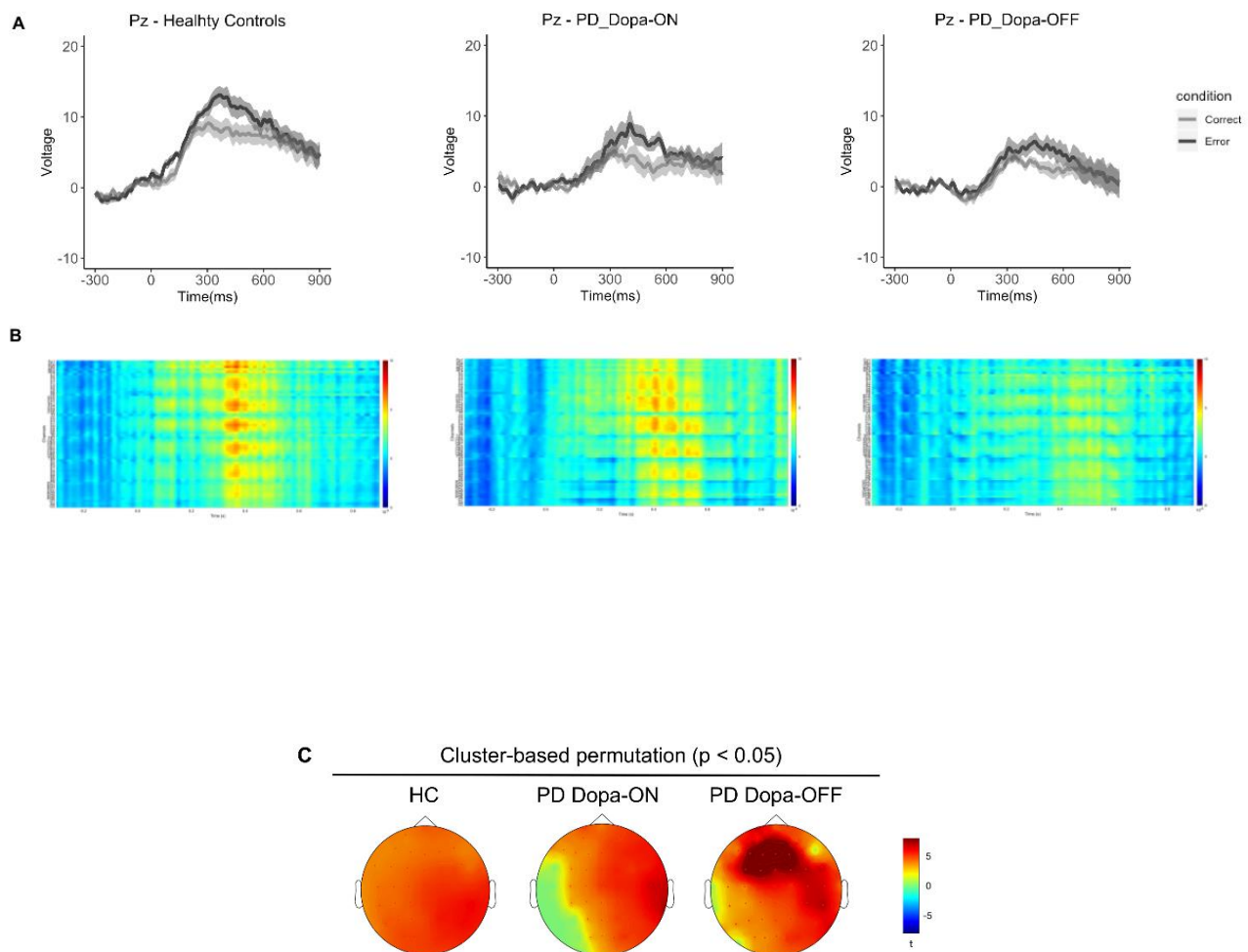


Figure 1. Electrophysiological results in the time domain for each group **A.** Grand average waveforms of oPe at electrode Pz. The end of avatar's movement is set at 0ms. Light colors denote the standard error around the mean. **B.** Graphical representation of voltage distribution across channels. The values are the result of the erroneous-minus correct action (y-axis: channels, x-axis: time in ms). **C.** Cluster-based permutation (dependent sample t-test with cluster-correction $p < 0.05$) for erroneous versus correct actions in the three groups. The maps represent the time-point in which the cluster was found with largest spatial extent.

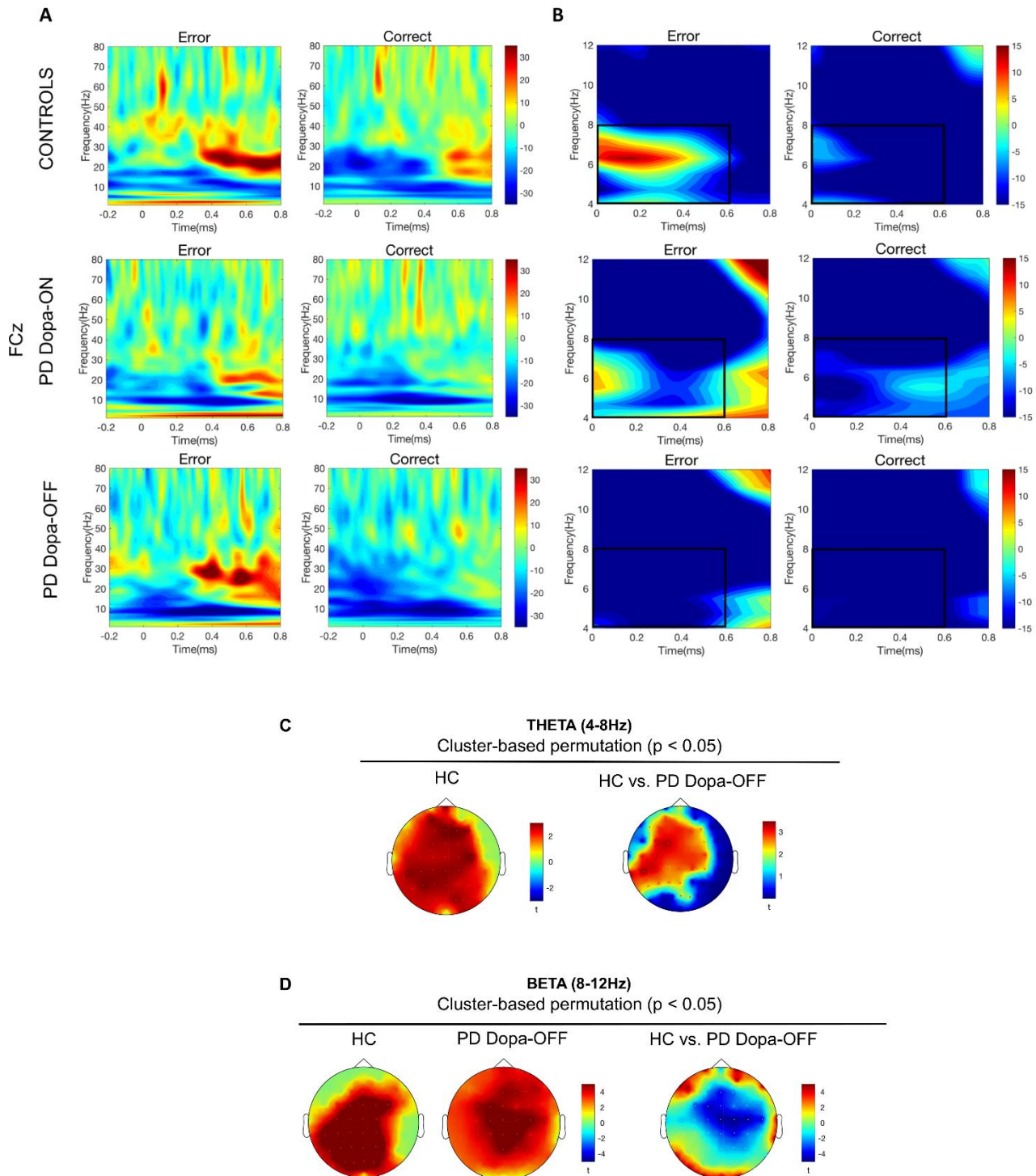


Figure 2. Time-frequency representation of Relative Power change (in %) with respect to the baseline for erroneous and correct conditions. The end of avatar's limb-path deviation is set at 0ms. **A.** Erroneous and correct plots at electrode FCz in the three groups, with all frequencies 1-80Hz displayed **B.** Erroneous and correct plots at electrode FCz in the zoomed range of interest, only frequencies from 4 to 12 Hz are displayed. The black rectangles highlight the a priori chosen window of interest between 0-600ms and 4-8 Hz, that indicate the values that have been submitted to

statistical analyses. **C.** Cluster-based permutation ($p < 0.05$) for erroneous versus correct actions in theta. Only the HC showed a significant cluster. Independent Cluster comparison ($p < 0.05$) found a positive cluster only when HC and PD Dopa-OFF were compared, with the HC showing greater theta activity in the fronto-central electrodes. Only significant cluster are displayed in the figure **D.** Cluster-based permutation ($p < 0.05$) for erroneous versus correct actions in beta. HC and PD-OFF showed a significant cluster. In the PD Dopa-ON no cluster was found. Independent Cluster comparison ($p < 0.05$) found a positive cluster when HC and PD Dopa-OFF were compared, with the HC showing less beta activity in the fronto-central electrodes. Only significant cluster are displayed in the figure. The maps represent the time-point in which the cluster was found with largest spatial extent.

Embodiment

Preliminary application of the Shapiro-Wilk test showed that embodiment ratings were normally distributed therefore parametric analyses for within- and between-groups were used. In order to explore the link between sense of embodiment and electro-cortical indices of error processing, Spearman correlations between Embodiment ratings and error signatures (Theta and oPe) were conducted across subjects. Paired sample t-test for each group showed no significant difference in the avatar's grasp accuracy (correct vs. erroneous) in terms of sense of Embodiment (Healthy Control: $t(8) = -0.33$, $p = 0.74$; PD-Dopa ON = $t(7) = 0.05$, $p = 0.96$; PD-Dopa OFF: $t(7) = 0.21$, $p = 0.83$). Also, in this preliminary sample, we did not find a correlation between the sense of Embodiment and neurophysiological signatures (oPe, theta).

Discussion

In the present study, we investigated the temporal dynamics of correct and erroneous action observation in Parkinson patients, in two different experimental conditions: i) once right after their dopaminergic treatment (PD Dopa-ON) and ii) once after a night of dopaminergic withdrawal (PD Dopa-OFF); a control groups of healthy individuals (HC) was also tested. Participants' EEG was acquired during the observation of correct and incorrect reach-to-grasps presented through immersive virtual reality.

Results in the time-domain revealed that observation of erroneous actions produced an oPe in all the three groups (detailed information about clusters latency in the *Results section – Cluster-based permutation Event-related potentials – oPe*), but with a different latency as revealed by

cluster-analyses. Time-frequency analyses showed that error-related mid-frontal theta power was not present in PD patients, regardless of whether they were in Dopa -ON or -OFF state. Differently, the control group of HC participants showed the typical error-related theta increase that has already been observed in young healthy samples (Pavone et al 2016; Spinelli et al 2017; Pezzetta et al. 2018). A greater beta activity was found in PD patients only when in Dopa-OFF and not -ON condition, suggesting a relation between beta oscillations and dopamine. Compared to most of existing studies, that mainly investigated the integrity of the error-monitoring system in the time-domain, we showed how complementary and additive information is present in the frequency domain. These preliminary data suggest that patients with dopaminergic loss have an altered monitoring system from a neurophysiological point of view, compared to healthy controls.

From visual inspection of the ERP graphs across the experimental groups, we did not observe an error-related negativity (oERN). Similar to the Study on apraxic patients in Chapter 3, oERN suppression can be explained in terms of an age-dependent effect (e.g., Gehring & Knight 2000; Nieuwenhuis et al 2001), or in view of the novel evidence that errors can elicit error-positivity in absence of an ERN (Di Gregorio et al 2018; Tan et al 2019). The fact that the stimuli used in this task are continuous actions rather than all-or-none events (as are usually in speed response tasks – e.g. Flanker task) might also contribute to make more difficult to observe time-locked potentials as the oERN compared to other strong deflections (e.g. oPe). All the three groups (HC, Dopa-ON and Dopa-OFF) showed a significant positive cluster in the time-domain when erroneous and correct actions were compared, which suggests that an oPe is elicited in the erroneous actions in both HC and Parkinson patients. However, the three groups showed a different topography and latency of the oPe, as revealed by the cluster's latencies. Moreover, since extensive literature points to the parietal regions of the scalp as the ones in which the oPe can be largely seen, we also performed traditional a-priori analyses on the electrode Pz. Interestingly, when Pz was considered, only the HC group showed a significant difference, whereas the Parkinson' patients, neither in Dopa-ON nor Dopa-OFF, showed a statistically significant distinction between conditions. The different result between the traditional analyses (single electrode) and the cluster-based ones is accounted by the fact that the electrodes found in the cluster are mostly located in the central - rather than parietal –

areas. This activity might be associated with the early oPe, that is the positivity related to the low-level detection of an error. The early oPe is a component that share similar features with the P3a, an event-related potential associated with the orientation of attention (Overbeek et al 2005). The late oPe on the other side has been instead associated with the P3b and linked with the awareness of the event and the updating of the recently acquired information.

Interestingly, Luu and colleagues (2004), found that in a filtered signal, most of the energy of the Pe was not concentrated in the theta band, but rather in the slower delta band. We thus performed also the analyses on the delta frequency range (2-4Hz) and we found that the cluster-based permutation showed that all the three groups evidenced a significant cluster when erroneous and correct action were compared, but only the HC showing a parietal distribution. The results of the delta activity are thus quite in line with the ones found in the time domain (oPe) for the electrode Pz, which shows a significant difference between erroneous and correct trials only in the HC group. The Parkinson's groups – regardless dopaminergic treatment - show no significant difference in such a posterior electrode; however when analyses were performed at a cluster level, also the groups with Parkinson patients showed a cluster – more anterior than posterior - suggesting that both oPe (in the time-domain) and delta activity (in the time-frequency domain) might involve mostly the anterior regions of the scalp, in the Parkinson patients.

However, these analyses rely only on evidence collected at the scalp-electrode level, further analyses on the source level might shed light on the cortical areas involved in the processes, in the three groups. As for what concerns the theta activity, only the HC group showed the typical theta increase when observing erroneous actions, whereas both PD group, in either medication conditions, did not. Reduced theta activity was previously found in timing and novelty response tasks (Cavanagh, Kumar, Mueller, Richardson, Mueen, 2018; Chen et al 2016; Kim et al 2017; Parker et al 2015). Only recently this has been extended to cognitive control (Singh et al 2018). In this study Singh and colleagues tested 16 PD twice (Dopa-ON and Dopa-OFF) in a modified speed-response Simon task, and they found no theta activity after erroneous events in both groups, regardless dopaminergic medication. Several studies confirmed that mid-frontal theta signals are a mechanism

of cognitive control, which engage the involvement of medial frontal cortex as well as other connected areas (Cohen, 2011a; Cavanagh & Frank, 2014; Cavanagh & Shackman, 2015; Holroyd & Coles, 2002). Parkinson patients' accuracy in answering the questions in the catch trials ("Did the arm take the glass") revealed that PD were able to understand whether an error or a correct action occurred. In fact, patients typically made zero or one mistakes within the entire session (only one PD in Dopa-OFF committed several errors when in -OFF, but not when he was in -ON). Despite behavioral accuracy, the fact that there is a lack of theta response in the Parkinson' patients suggests that the mechanism is alternated as compared to that of the healthy aged-matched controls, even when the PD are under dopaminergic treatment. An interesting result here is the fact that Parkinson patients on one side did not show an increased theta power to the occurrence of errors, but on the other side it was still possible to observe an oPe, despite with a more central than parietal scalp distribution. This might be in line with the recent results of di Gregorio and colleagues (2016), in which that found a dissociation between the early response of the monitoring system (usually the ERN/theta) and the Pe response, suggesting a complex and hierarchical architecture of the monitoring processes.

Concerning the alpha activity, we were surprised not to find a difference between erroneous and correct actions in the three groups, especially in the healthy old participants, as was the case in previous studies with a similar paradigm (Pavone et al 2016; Pezzetta et al 2018); however, the modulation of some frequencies seems particularly age-dependent; for example, Babiloni et al (2006) suggest that the occipital delta and posterior cortical alpha rhythms decrease in magnitude during physiological aging, with both linear and nonlinear trends. The fact that other studies on healthy young participants with a similar paradigm (Pavone et al 2016; Pezzetta et al 2018) found a modulation in the alpha band, while experiments on aging and pathological populations did not, might follow that idea.

In addition to the absent theta response, PD Dopa-OFF showed an atypical long beta synchronization after the erroneous actions that was not present in the PD Dopa-ON patients and that was present only as a brief contralateral beta rebound in the HC. This enhanced beta activity

that we found in the PD Dopa-OFF deserves further discussion. Previous evidence in literature has showed that the passive observation of a movement is characterized by beta suppression. The beta increase in synchrony – or beta rebound - that follows the end of movement is believed to reflect the active inhibition or general deactivation of the motor system (Pfurtscheller, Neuper, Brunner, & Da Silva, 2005; Jurkiewicz, Gaetz, Bostan, Cheyne, 2006). Local field recordings on the subthalamic nucleus identified excessive neural oscillations in the β -band in PD patients as well as a general increased rhythmic activity associated with pathophysiological aspects (Oswal, Brown, Litvak, 2013). Also, Engel and Fries (2010) suggested that the pathological enhancement of beta-band activity is likely to result in an abnormal persistence of the status quo and a deterioration of flexible cognitive control. However, when the dopamine depletion is compensated by the dopaminergic treatment, the beta activity might be restored to a functional activity (Doyle et al 2005). In our study, the fact that the increased beta activity was found in the erroneous but not in the correct actions, is in line with some prior findings on healthy adults (Koelewijn et al 2008). Koelewijn and colleagues (2008) showed beta rebound was stronger for the observation of incorrect than correct actions, suggesting a potential role of the beta activity in the evaluation of action significance. The over-response that we observe during the dopaminergic withdrawal, goes along with the findings linking the Parkinson's Disease to a pathological beta response. Still these interpretation needs to be supported by further investigations. In particular, collecting data on additional and larger samples will help clarify the modulation of these oscillations in response to action monitoring.

In the embodiment ratings, we were surprised not to find a difference between erroneous and correct actions in the groups, as was the case in previous studies with a similar paradigm (Pavone et al 2016); however it might be the case that aging people had a different sensitivity to explicitly refer their sense of embodiment on the observed action; also, in previous studies (Pezzetta et al 2018), we observed that the sense of Agency correlate with the brain responses to actions. In this case, for a matter of time, since the task could not last more than 25 minutes (to be able to test the PD Dopa-ON in their maximum peak of medication), we decided to include only the sense of Ownership question.

One limitation of the current study is the fact that PD were tested twice, whereas HC were seen once time. However, as also previous works (Singh et al 2018), we can reasonably exclude a learning effect, since the task is of simple action-observation and it is not related to the acquisition of task-specific abilities. Further, it is important to underline that our sample size is considerably low as in the current sample we tested only 8 PD and 9 control participants. Thus, the results should be considered only preliminary, as should the related interpretations. An objective of the present study is in fact to reach a full sample of 20 PD Dopa-ON, 20 PD Dopa-OFF and 20 matched HC. Previous error monitoring studies on Parkinson patients had a low number of participants (generally 10-15, always < 20; Seer et al 2016) or tested the patients only in one of the two therapeutic conditions (Dopa-ON/OFF), making difficult direct comparisons across studies. Furthermore, since the Parkinson's Disease is an heterogenous pathology, characterized by different levels of gravity and impairment, it is important to enlarge the sample in order to achieve more firm information.

Conclusions

Some of the most debilitating aspects of PD include motor and cognitive disturbances. While it is widely appreciated that cell death in PD somehow contributes to deficits in higher cognitive functioning, the mechanisms underlying these deficits remain somehow unclear. In this investigation, we tested PD patients during dopaminergic treatment and after night withdrawal, to test the integrity of the monitoring system, by focusing on the modulation of error-related signatures. The findings reported here, despite preliminary, suggest the deficient theta may be a promising candidate correlate for studying cognitive dysfunction in Parkinson's Disease.

B. Theta tACS over the frontal midline modulates behavioural adjustment during human-avatar motor interactions

Abstract

When engaging in joint actions, we need to continuously monitor our partner's movements and to predict their possible outcomes. Recent findings from our research group showed that motor interactions requiring moment-to-moment adaptation to the partner's actions elicit brain activity related to performance monitoring (i.e. enhancement of midfrontal Theta synchronisation). Importantly, this activity seems not associated to any explicit feedback concerning the interactive performance, but rather a response to observed violations to ones' expectation of the partner behaviour; in this sense it seems to mediate the process of adapting to a partner behavioural change. In the present study we explored the causal role of midfrontal Theta on behavioural adjustment during motor interactions by means of transcranial alternating current stimulation (tACS). Participants received Theta or Beta (between-subject) tACS at their individual frequency and Sham stimulation over the frontal midline (FCz) and parietal sites while coordinating their movements with those of a virtual partner to synchronously touch one of two different targets. Importantly, there were two experimental conditions that differed in the degree to which participants needed to adjust their movements to virtual partner's unexpected motor change. Results showed that, compared to Beta tACS, Theta tACS improved synchronisation in all conditions and increased movement times after the virtual partner's motor change (making individuals' behaviour more synchronized with that of the partner), but only in the condition in which participants were asked to compensate that motor change.

Introduction

During motor interactions, in both cooperative and competitive settings, the ability to coordinate our actions with those of our conspecifics requires the continuous monitoring of own and other's movements. This monitoring activity seems to be dependent on individuals' ability to predict the actions of the observed partner behaviour, namely the anticipation of the consequences of observed actions (Aglioti et al 2008; Abreu et al 2012), which is likely implemented through sensorimotor simulation processes that occur in the fronto-parietal mirror neurons system (Di Pellegrino et al 1992; Rizzolatti and Craighero, 2004). Expectations about the unfolding of others' actions in a pure observational context are generated on the base of previous experience, knowledge about biological motion and intention understanding (Urgesi et al 2010). Violations of our expectation of the fate of observed actions elicits error-related brain signatures. Error and conflict monitoring are two interrelated cognitive functions that contribute to improve adaptive behaviour during environmental and social demands. Mounting evidence from EEG and MEG studies revealed that the electrical correlates of error processing are characterized by specific neurophysiological signals, namely the Error Related Negativity (ERN, Gehring et al 1993) and the positivity error (Pe, Falkenstein et al 2000; Van Elk et al 2012), likely generated in the anterior cingulate cortex (ACC, Ishii et al 1999). These signatures are maximally distributed over the frontocentral and parietal (for Pe) areas of the cortex, sharing a common spectral signature in theta band (4-8 Hz), a frequency that correlates with the increment of need for control.

Studies have reported that observing a motor error from a first-person (Pavone et al 2016; Spinelli et al 2018; Pezzetta et al 2018) and third person (van Schie et al 2004; De Bruijn & von Rhein, 2012; Pavone et al 2016) perspective elicits the ERN, a phenomenon called observational ERN (oERN, Miltner et al 2004; van Schie et al 2004). Conversely, the enhancement in Theta power seems to be specific for one's own rather than for other's errors Pavone et al 2016. At a behavioural level, observing an error in third-person perspective also induces a slowing in reaction times in the subsequent trial when participants are asked to grasp and move an object (Ceccarini and Castiello, 2018). This phenomenon is named post error slowing (PES) and is thought to reflect the

implementation of adaptive adjustment to avoid further errors (Rabbitt, 1966; Notebaert et al 2009; Danielmeier and Ullsperger, 2011). These findings suggest that the detection of committed and observed errors might rely on similar neural processes.

During motor interactions, action prediction also relies on knowledge about the interaction rules and shared goals (Sacheli et al 2015). For a shared goal to be fulfilled, each part of a dyad needs to achieve its individual sub-goal while monitoring the other part's actions (Sebanz et al 2006; Sacheli et al 2012; 2018). When one of the two partners fails to comply with the interaction rules, the success of the joint action is jeopardized. Unexpected movements or changes in the context of motor interactions can therefore be considered as “errors”, since they not only create a mismatch between expected and observed outcome, but also hinder the fulfilment of a shared goal. Indeed, error-related brain signatures are also elicited during motor interactions after observing a sudden change in partner's movement. In two recent studies, participants were asked to coordinate their reach-to-grasp (Moreau et al 2019) and reach-to-press (Moreau et al in preparation) movements with those of a virtual avatar to perform either complementary or imitative movements. In both studies, in 30% of the trials the virtual avatar suddenly changed its initial movement before reaching the target (i.e. from grasping the lower part of a bottle-shaped object (through a power grip) to grasping its upper part (through a precision grip) in the first study and from reaching and pressing a target button with the index to pressing it with the middle finger in the second one. The avatar's motor change required participants to promptly update their own motor plan in order to fulfil the common goal (i.e. performing an imitative or complementary movement). EEG results showed the presence of error-related brain activity both in the time domain (i.e. ERN) and in the frequency domain (i.e. increase in midline frontal Theta power) which was time-locked to the avatar's movement change (not to the corresponding change in the individual action). Interestingly, these brain signatures were absent in a control condition that was perceptually identical but did not require participants to adapt to the avatar's change because in this case they knew in advance which target they had to grasp or press.

Theories on error-related midfrontal theta activity posit that these brain oscillations may act as a nonspecific “alarm” signal that may be used to implement behavioural adjustment by synchronizing

the simultaneous employment of the frontal (Hanslmayr et al 2008), motor (Nigbur et al 2012) and sensory (Van Driel et al 2012) areas. Indeed, a Theta phase synchrony between the MFC and frontal sites has been repeatedly observed in various tasks eliciting the need for cognitive control (Cavanagh, 2015). Several studies have related midfrontal Theta power to PES, although with mixed results (Valadez and Simons, 2017; Van Driel et al 2015; Fusco et al 2018). Less clear is the relationship between midfrontal Theta and task performance. Since the implementation of cognitive control should serve the need of optimising behaviour, it should be expected that an increase in Theta power would produce an improvement in performance.

The present study aimed at investigating the causal role of midfrontal theta oscillation on behavioural adjustment to observed errors in a motor interaction context by means of Transcranial Alternating Current Stimulation tACS. To this end, we used a modified version of the task from Moreau and colleagues (in preparation) and asked participants to coordinate with a virtual partner to touch one of two targets. Importantly, in 30% of the trials the virtual partner would suddenly change its movement, therefore requiring participants to operate a motor correction. TACS is a non-invasive brain stimulation technique that can be used to target cortical oscillations by taking advantage of alternating current. A low intensity electric flow is delivered on the scalp through rubber-conductive electrodes. The oscillation frequency of the electric current can be set to mimic endogenous brain oscillations. Previous studies have shown that tACS is a viable tool to entrain endogenous rhythmic activity in a frequency-dependent manner (Helfrich et al 2014; Neuling et al 2013) and modulate behaviour (Feurra et al 2013; Vosskhul et al 2015). At the neurophysiological level, tACS enhances the power of existing brain oscillations, therefore acting as an “excitatory” neuromodulation. For the present study, we hypothesised that Theta (but not Beta) tACS would boost endogenous error-related Theta activity following an observed movement correction and facilitate behavioural adaptation (i.e. better synchrony performance in trials with a motor correction).

Methods

Participants

Forty-four (44) healthy participants without any declared neurological or psychiatric issues were recruited from Sapienza University. Suitability to receive non-invasive brain stimulation was

assessed by a standardized questionnaire (Antal et al 2017). All participants had normal or corrected-to-normal vision and were naïve as to the purpose of the experiment. Four subjects were excluded from the study because they reported: i) motion sickness induced by Immersive Virtual Reality (1 subject), ii) discomfort induced by tACS (2 subjects) or iii) anomalies in the resting-state EEG Alpha peak shape (1 subject). Our final sample comprised 40 right-handed subjects that were randomly assigned to receive either Theta (N=20 (10 Female) age = 25.4 ± 3.9) or Beta (N= 20 (8 Female) age = 23.3 ± 3.3) fronto-parietal tACS. Our sample size was determined from previous studies that employed tACS with a similar design (Van Driel et al 2015 (20 subjects); Onoda et al 2017 (15 subjects per group); Zaehle et al 2010 (20 subjects per group)). All participants gave written informed consent to participate in the study. The experimental procedure was approved by the Fondazione Santa Lucia (Rome) Ethics Committee and was performed in accordance with the 2013 Declaration of Helsinki.

Procedure

At their arrival at the laboratory, participants went through the EEG resting-state recording session (see details below) where they were asked to sit in a quiet room and stay still with their eyes closed for 5 minutes. Then, participants had a small break (around 20 minutes), during which we extracted the individual-frequency information (see Figure 1).

Prior to the stimulation session, subjects' scalp was measured to determine FCz and Pz positions according to the International 10-10 EEG layout. The areas of interest were cleaned with a cotton swab soaked in ethyl alcohol in order to reduce the skin's conductance and marked with a marker. The two tACS electrodes were then fitted through an EEG-cap over the head of the participants, with the side toward the skin coated with electro-conductive gel. The stimulation sessions started with a training phase so that participants could familiarize with the tACS-induced physical sensations (i.e. itching, heat). During this phase, participants received 15 seconds (5 ramp-up, 5 stimulation, 5 ramp-down) of tACS at 13 Hz and were asked to report physical sensation or discomfort. If no irregularities were reported, participants were asked to wear the Oculus Rift Head Mounted Display (HMD, www.oculus.com) where they would observe a virtual body in 1PP and the experimental scenario (see below). Participants underwent Calibration, Familiarization and Training

phases in the virtual scenario before starting the experiment. In the Calibration phase, the perspective point-of-view of each participant was adjusted to match the virtual body with individual positioning in order to obtain the best spatial-match between the participant's real and virtual body. In the Familiarization phase, participants were invited to look both at the virtual body and at the environment, and to verbally describe what they were seeing (~30 sec) (Tieri et al. 2015b). During the Training phase, which was provided at the beginning of each of the two first blocks, participants completed 10 trials of the IVR Motor Interaction Task. The experimental phase consisted of two sessions (Theta/Beta tACS and Sham, order counterbalanced), each of which comprised two blocks (Interactive and Cued, order counterbalanced – see next section for a description of the tasks). At the end of each Session, participants completed the Embodiment Questionnaire, adapted from previous studies (Botvinick & Cohen, 1998; Tieri *et al* 2015a; Tieri *et al* 2017) and a standardized questionnaire measuring tES-induced physical sensations (Fertonani et al 2015).

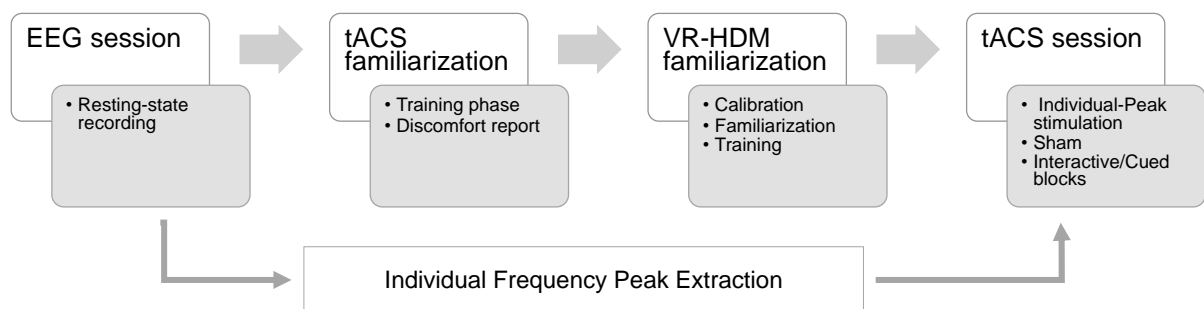


Figure 1 – Timeline of the experimental procedure.

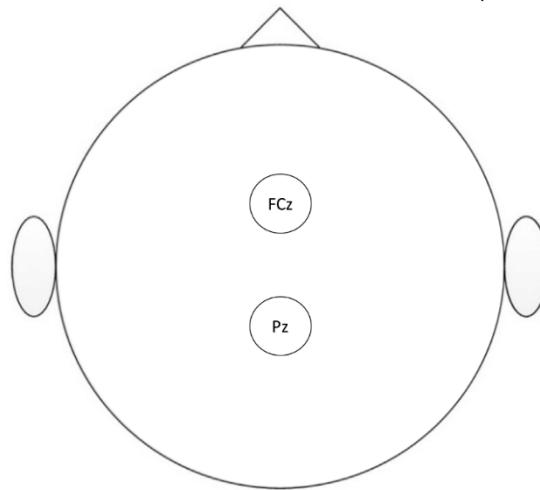
Electroencephalography (EEG) Protocol

EEG signals were recorded via Neuroscan SynAmps RT amplifier system, from an elastic headband (Electro-Cap International) EEG arranged according to the International 10-10 EEG System with 58 scalp electrodes (Compumedics, Ltd). EEG was recorded using following channels: Fp1, Fpz, Fp2, AF3, AF4, F7, F5, F3, F1, Fz, F2, F4, F6, F8, FC5, FC3, FC1, FCz, FC2, FC4, FC6, T7, C5, C3, C1, Cz, C2, C4, C6, T8, TP7, CP5, CP3, CP1, CPz, CP2, CP4, CP6, TP8, P7, P5, P3, P1, Pz, P2, P4, P6, P8, PO7, PO3, PO1, POz, PO2, PO4, PO8, O1, Oz, O2. The amplifier hardware band-pass filter was 0.01–200 Hz and the sampling rate was 1000 Hz. Impedances were lowered below 5 kΩ using electrogel. Reference electrodes were applied to the left (digital reference) and

right (physical reference) earlobes, and all electrodes were re-referenced offline to the average of both.

Transcranial Alternating Current Stimulation (tACS) protocol

Electrical stimulation was delivered via two circular sponge-based rubber electrodes (Sponstim, 25 cm², Neuroelectronics, Barcelona, Spain) soaked in saline water (NaCl) and connected to a rechargeable battery-operated stimulator system (Starstim/Enobio, Neuroelectronics, Barcelona, Spain) which in turn was controlled via Bluetooth by a dedicated software (Neuroelectronics Instrument Controller – NIC, Neuroelectronics, Barcelona, Spain). Electrodes were placed over the midline at FCz and Pz (International 10-20 System) beneath an EEG cap. Participants received sinusoidal alternating current (AC) of 1500 mA at their individual Theta (mean Hz = 5.5 ± 0.65) or Beta (mean



Hz = 17.6 ± 2.54) frequency while engaged in the IVR-based Motor Interaction task. Impedance was kept below 5K Ω . Stimulation/task blocks lasted approximately from 9' to 9'30". During each block, the current was ramped up for 5 seconds before starting the task and ramped down for 5 seconds after the task was completed. In half of the blocks, participants received sham stimulation which included 5 seconds of ramp up, 20 seconds of AC and 5 seconds of ramp down.

Figure 2 tACS electrodes placement

Experimental stimuli

The virtual scenario and avatars were designed by means of 3DS Max 2017 (Autodesk, Inc.) and IClone 7 (Reallusion, Inc.), respectively, and implemented in Unity 5 game software environment. The scenario was presented by means of the Oculus Rift Head Mounted Display (HMD; www.oculus.com) having 110° field-of-view (diagonal FOV) with a resolution of 2160 x 1200. The

virtual scene consisted of a real-size room (1:1 scale), two virtual avatars sitting on opposite sides of a table and a virtual grey panel placed between the avatars that blocked their reciprocal view except for their hands, arms and lower part of the trunk. In front of both avatars, at the centre of the table, appeared the 3D model of two buttons, coloured purple and yellow and a LED light that could either turn red or green. Participants observed the virtual body from a first-person perspective (1PP) through HMD. A right Oculus Touch controller (www.oculus.com) was used in order to allow the participants to control the movement of the right arm of their avatar in real time, observed in 1PP. In particular, participants could i) move the avatar's hand forward in space by using the analogic stick of the Oculus touch controller with right thumb and ii) animate the right index or middle finger by pressing the Oculus touch controller's up and down trigger button, respectively. During the experiment, the virtual scenario was rendered in both HMD and a computer screen, such that the experimenter could observe and assist the participants.

IVR Motor Interaction task

The IVR Motor Interaction Task (Figure 3) comprised two conditions (blocks) that differed for the instruction received and for the type of interaction required. In the Interactive block, participants were asked to reach and press one of the two buttons as synchronous as possible with the virtual partner while performing either an imitative ('Same') or a complementary ('Opposite') movement with respect to the virtual partner's (e.g. if the instruction received is 'Opposite' and the virtual partner raises the index finger to press the purple button, the participant will need to raise the middle finger to press the yellow button). In the Cued block, participants still had to synchronize their reach-to-press movements with those of the virtual partner but were in this case instructed to press either the 'Purple' (index) or 'Yellow' (middle finger) buttons, regardless of which action the avatar was performing. In the Interactive condition participants needed to predict and monitor the action of the virtual partner in order to perform their own action, while action prediction and monitoring was not needed during the Cued condition, where participants already knew what action to perform. It is important to note that in the Interactive condition, Correction trials require participants to adapt their own behaviour to the observed change (i.e. change their own finger) in order to fulfil the request (e.g.

to perform a complementary movement). In the Cued condition, instead, participants observed the avatar changing its initial behaviour but were not required to change and adapt their own behaviour.

Each trial started with an acoustic 'go' signal ("beep") delivered by the Oculus headphones. Both avatars started with their hands closed and placed in the centre of table's midline. After the go signal ("beep") was delivered the participant and the virtual partner started moving (virtual-partner total movement time lasting 3170 ms). 1056 ms after it started moving (33% of the whole movement time), the avatar would raise a finger in order to press the associated button (index finger for purple button and middle finger for yellow button, see Fig 3). Participants were required to control his/her avatar's right hand with the Oculus touch controller to reach and press one of the two buttons as synchronously as possible with the virtual partner. With the analogic stick of the controller, participants could move their avatar's arm forward and regulate its velocity (i.e. velocity was proportional to the force applied by their thumb) and, by pressing the index and middle trigger button of the controller, they could raise either the virtual index or the virtual middle finger of their avatar. Depending on the Asynchrony (i.e. absolute time difference between the two pressing times) the LED light could turn either green ('win' trial) or red ('fail' trial). A staircase procedure was adopted to make the task more challenging: after each 'win' trial the minimum time difference to turn the light green was reduced by 50 ms (e.g. from 200 ms to 150 ms), while in the case of 'fail' trials, the time window was increased by 50 ms (e.g. from 200 to 250 ms). The trial ended 2 seconds after the LED visual feedback. Importantly, in 30% of the trials the virtual partner changed its initial behaviour 2113 ms after starting its movement (66% of the total movement time), namely from using the middle to the index finger to press the button (Correction trials). The avatar's total movement time (i.e. the time from start to touch) lasted approximately 3.2 seconds and did not vary through the task or in different conditions. Each of the two tasks (i.e. Cued and Interactive) comprised 68 trials, of which 20 were Corrections (10 Opposite, 10 Same) and 48 were NoCorrection (24 Opposite, 24 Same).

From the IVR Motor Interaction Task we extracted the following behavioural parameters: Asynchrony (absolute difference between the virtual partner's and subject's pressing times), Movement Times (time between subject's movement start and button press), Last Press Time (time of the last effector selection, note that in Correction trials the effector is selected twice, once before

and once after the correction) and Reaction Times (time between the 'go' signal and subject's movement start), see Table 1.

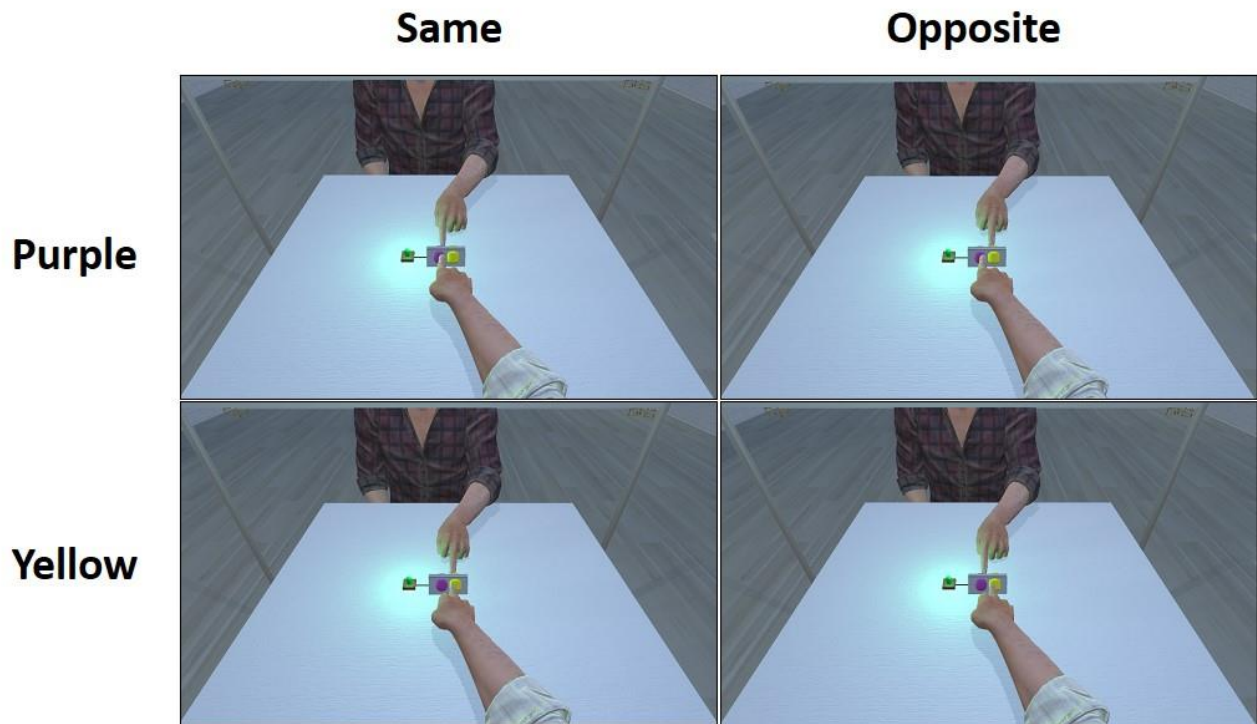


Fig 3– Motor Interaction Task. Participants were required to synchronise their reach-to-touch movements with those of the virtual partner to perform either an imitative (Same) or complementary (Opposite) in the Interactive Blocks or to touch either the Purple or the Yellow button in the Cued Blocks.

Embodiment ratings

After each experimental session, a black panel with a horizontal green line (VAS scale, 60 cm length, left and right extremity marked as “0” and “100” respectively) was presented in the virtual scenario. In order to assess the degree to which participants experienced the illusory Feeling of Ownership (FO) and Agency (A) over the virtual right hand, a 6-item questionnaire (Table 2) was used. The questionnaire consisted of two blocks, each with three items concerning the FO (Q1–2 experimental, Q3 control) and Agency (Q4–5 experimental, Q6 control), respectively. Participants

were asked to move a vertical bar along the horizontal VAS line by using the analogic stick of the right Oculus touch controller in order to answer the items reported in Table 1.

Behavioural variables	Experimental design
<ul style="list-style-type: none"> Asynchrony (absolute difference between 1PP and 3PP touch time) Movement Time (time from Start to Stop) Motor Preparation Time (Time from 'go' signal to Start) Last Press Time (time of last effector selection) 	<ul style="list-style-type: none"> Group (<i>Theta, Beta</i>) Stimulation (<i>Real, Sham</i>) Task (<i>Interactive, Cued</i>) Trial (<i>NoCorrection, Correction</i>) Movement (<i>Same, Opposite</i>)

Table 1. List of behavioural variables and within/between subjects design.

Index	Item
<i>e-FO</i>	Q1 I felt as if I were looking at my own hand
<i>e-FO</i>	Q2 I felt as if the Virtual Hand were my hand
<i>c-FO</i>	Q3 It felt as if I had more than one right hand
<i>e-A</i>	Q4 It felt as if the movements of the Virtual Hand were my own movements
<i>e-A</i>	Q5 I felt as if I could have caused a/the movement of the Virtual Hand
<i>c-A</i>	Q6 I felt as if the Virtual Hand were controlling me

Table 2. Embodiment Questionnaire. Items Q1, Q2, Q4 and Q5 measure Feeling of Ownership (e-FO) and Agency (e-A), items Q3 and Q6 are control items.

Resting EEG Data Analysis

The EEG data analysis was performed using the FieldTrip toolbox for EEG/MEG (Oostenveld et al, 2011; Donders Institute for Brain, Cognition and Behaviour, Radboud University, the Netherlands. See <http://fieldtriptoolbox.org>). In order to extract the individual peak frequencies, we segmented the five-minute resting state recordings into epochs of 4 seconds (Pahor & Jaušovec 2014). Independent Component Analysis was computed to identify and remove eye movements and muscular artifacts (ICA; Jung et al 2000). An average of ~ 0.94 components ($SD = 0.75$) per subject was removed and ~ 69.53 artifact-free epochs ($SD = 4.17$) per participant was kept. Data were band-pass filtered at 1-70Hz and a Fast Fourier Transformation (FFT) with 0.25 Hz resolution was performed to derive estimates of absolute spectral power (Pahor & Jaušovec 2014). We first identified the individual Alpha peak frequency (IAF) ($M_{IAF} = 10.64$, $SD_{IAF} = 0.66$). Following Methods from Klimesch (1999), individual Theta frequency (ITF) was extracted by choosing the highest peak between IAF - 4.0 Hz - IAF - 6.0 Hz range ($M_{ITF} = 5.5$, $SD_{ITF} = .65$). For individual Beta frequency (IBF), the peak between 12.5 Hz and 22.5 Hz was chosen ($M_{ITF} = 17.5$, $SD_{ITF} = 2.54$). The calculated peaks were rounded-up to 0.5 Hz, and were visually inspected and confirmed, or changed when necessary (Klimesch 1999; van Driel et al 2015)

Data handling

Behavioural measures (Asynchrony, Movement Times, Motor Preparation Times, Last Press Times)

As a first step, for each behavioural variable we removed trials in which participants i) failed to follow the instructions (i.e. Same or Opposite for the Interactive Block and Purple or Yellow for the Cued) or ii) failed to touch the target. From this new dataset, we removed trials that fell more than 2.5 standard deviations below or over the individual mean in the corresponding condition. Analysis on raw data showed that the two groups (Theta and Beta) were significantly different between each other in many behavioural variables. In order to deal with between-subjects variability, we decided to perform data analysis on sham-corrected values. Then, for each participant values from each trial

in the Real Stimulation condition were standardized by subtracting the corresponding average Sham Stimulation value in the same condition. For example, each trial in the Interactive Correction Opposite Real Stimulation condition was standardized by subtracting the mean value in the Interactive Correction Opposite Sham Stimulation condition.

Statistical analyses

Data from the Embodiment Questionnaire and behavioural measures (Asynchrony, Start – to Stop, Motor Preparation Times and Last Press Times) were analysed with Multilevel Linear Mixed Models using the software R and the packages lme4 (version 1.1 -21, Bates et al 2015). For each model, the random part was selected using the principal component analysis (PCA) method (Bates et al 2015). We kept all random factors that explained at least 1% of variance. Statistical significance of fixed effects was determined using type III Anova test with the *mixed* function from *afex* package. Post-hoc comparisons were performed with the ‘Estimated Marginal Means’ R package (version 1.3.3, Lenth, 2017) via the *emmeans* and *emtrends* functions, respectively, and Tukey correction for multiple comparisons.

For Asynchrony and Movement Times we ran LMM with Asynchrony values as our dependent continuous variable, *Frequency* (Theta, Beta), *Block* (Interactive, Cued), *Trial* (Correction, NoCorrection), *Movement* (Same, Opposite) and their respective interactions as our fixed effects, and *Participant:Block* (i.e., random intercept for each level of Block) as our random part.

For Motor Preparation Times we collapsed the Correction and NoCorrection trials, since at the moment in which participants start moving they still do not know whether there will be a correction or not. Therefore our model included *Frequency* (Theta, Beta), *Block* (Interactive, Cued), *Movement* (Same, Opposite) and their respective interactions as our fixed effects and *Participant:Block* (i.e., random intercept for each level of Block) as our as our random part.

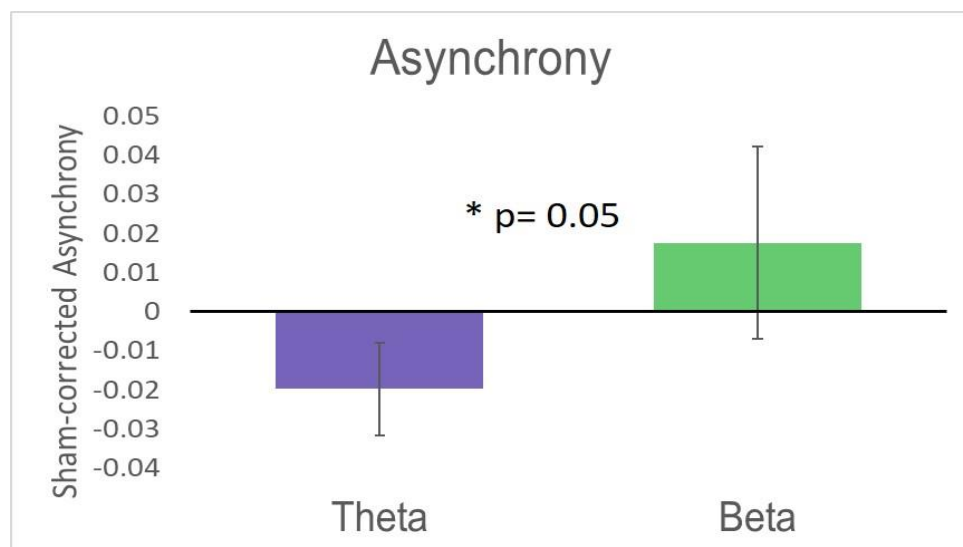
Since in the Cued block participants were not required to correct their movement and therefore Last Press Times were not informative, we decided to run LMM on Last Press Times only for the Interactive blocks. Moreover, we coded trials from the Interactive block as follows: NoCorrection (i.e. trials in which the avatar did not change its movement), Correction (i.e. trials in

which the avatar changed its movement and the participant adapted) and FakeCorrection (i.e. trials in which the avatar changed its movement but the participant did not adapt). Our model for Last Press Times in the Interactive block included *Frequency* (Theta, Beta), *Trial* (Correction, NoCorrection, FakeCorrection), *Movement* (Same, Opposite) and their respective interactions as our fixed effects and *Participant:Trial* (i.e., random intercept for each level of Block) as our random part. tACS-induced physical sensations were analysed with non-parametric statistics. Embodiment ratings were analysed with LMM including Group (ThetaGroup, BetaGroup), Stimulation (Real, Sham) and Item (Experimental, Control) as fixed effects and Participant (i.e., random intercept) as our random part.

Results

Asynchrony

Type III ANOVA on sham-corrected Asynchrony values with Block (Cued, Interactive), Trial (Correction, NoCorrection) and Movement (Opposite, Same) as within-subjects and Frequency



(Beta, Theta) as between-subject factor revealed a significant main effect of Frequency ($F = 3.81$, $p = 0.05$). Indeed, Asynchrony values in the Theta group were smaller than in the Beta group (Theta $M(SD) = -0.04 (0.17)$, Beta $M(SD) = 0.02(0.23)$), see Figure 4. It should be noted that, given the standardisation over the sham condition, negative Asynchrony values indicate a better performance (i.e. smaller asynchrony) compared to baseline performance. Also, there was a significant interaction between *Frequency*, *Block*, *Trial* and *Movement* ($F = 8.52$, $p < 0.01$). Tukey-corrected post hoc test did not show any significant difference between conditions of this interaction (all $ps > 0.1$).

Figure 4. Main effect of Frequency for Asynchrony. Theta tACS reduced (and Beta tACS increased) Asynchrony across all conditions. Error bars indicate standard error (SE).

Movement Time (Time from Start to button press)

Type III ANOVA on sham-corrected Movement Times values with Block (Cued, Interactive), Trial (Correction, NoCorrection) and Movement (Opposite, Same) as within-subjects and Frequency (Beta, Theta) as between-subject factor, revealed a main effect of Frequency ($F = 6.28$, $p = 0.01$), indicating that Movement Time values in the Theta group were significantly longer than in the Beta group and a 3-way interaction between *Frequency*, *Block* and *Trial* ($F = 7.60$, $p = 0.006$). Tukey-corrected post hoc tests showed that only in the Interactive block the contrast between Beta and Theta was significant for Correction trials (estimate = - 0.18, SE = 0.04, z-ratio = - 3.69, $p = 0.001$). Namely, Movement Times during Correction trials were increased by Theta tACS and decreased by Beta tACS (see Figure 5). None of the Frequency contrast in the Cued block reached or approached significance. The ANOVA also revealed a significant main effect of Movement ($F = 8.72$, $p = 0.003$), indicating that Movement times were longer for Opposite than for Same trials and a 3-way interaction between *Block*, *Trial* and *Movement* ($F = 13$, $p = 0.0003$), which we further analysed with post hoc tests. Results showed that Movement Time values in the Interactive block when performing Opposite_Correction trials were higher than in Same_Correction trials (estimate = 0.02, SE = 0.02, z-ratio = 2.465, $p = 0.06$), while no difference was seen between Opposite_NoCorrection and Same_NoCorrection (estimate = 0.01, SE = 0.01, z-ratio = 0.10, $p = 0.99$). This means that in the Interactive block participants' reach-to-press movements were longer for Opposite than for Same trials only when the avatar changed its movement. Conversely, in the Cued block there was a significant difference between Opposite_NoCorrection and Same_NoCorrection (estimate = 0.07, SE = 0.01, z-ratio = 4.17, $p < 0.0001$) but not between Opposite_Correction and Same_Correction (estimate = -0.01, SE = 0.02, z-ratio = -0.63, $p = 0.92$), meaning that in the Cued block participants'

reach-to-press movements were longer for Opposite than for Same trials only when the avatar did not change its movement.

Figure 5 Frequency * Block * Trial Interaction for Movement Times. Theta tACS increased (and Beta tACS reduced) Movement Times during Correction trials in the Interactive Block.

Motor Preparation Times (Time from 'Go' signal to Start)

Type III ANOVA on sham-corrected values with Block (Cued, Interactive), Trial (Correction, NoCorrection) and Movement (Opposite, Same) as within-subjects and Frequency (Beta, Theta) as between-subject factor, revealed a significant Frequency * Block interaction ($F = 4.53$, $p = 0.04$). Post hoc analysis showed a marginally significant difference between Theta and Beta group in the Interactive Block (estimate = 0.07, SE = 0.03, z-ratio = 1.85, $p = 0.06$), suggesting that Theta tACS tended to reduce the Motor Preparation time only in the Interactive block, see Figure 6.

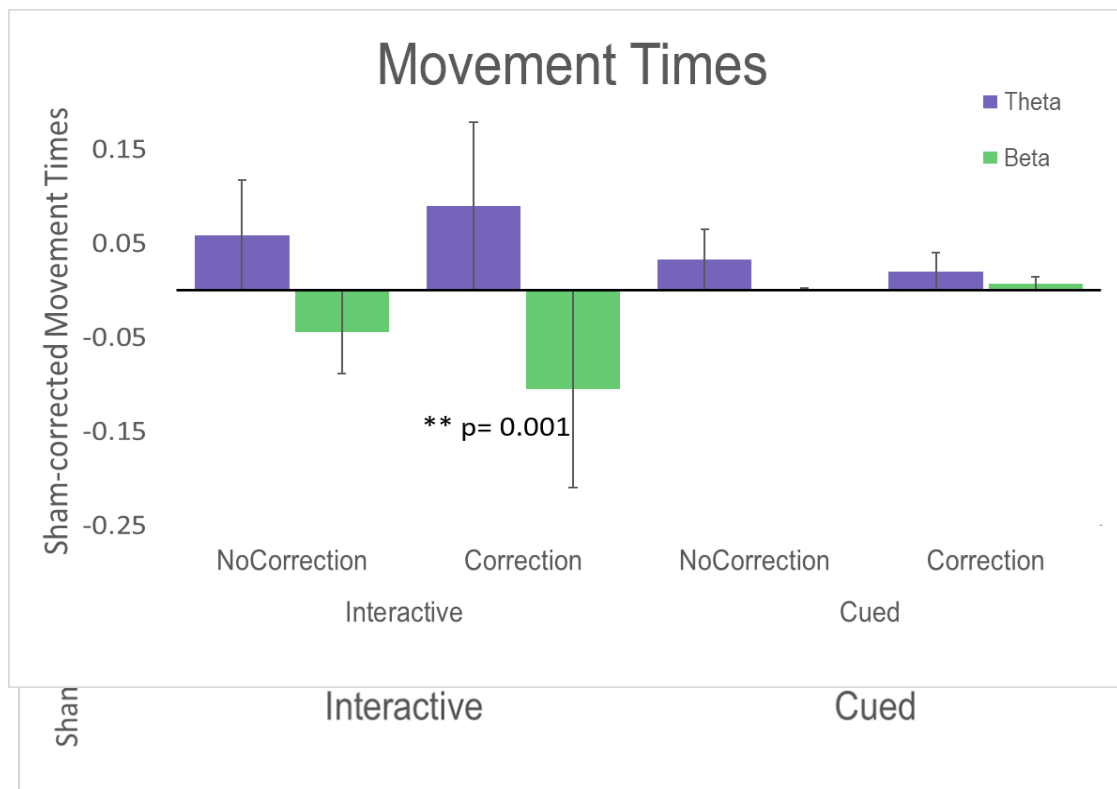


Figure 6. Frequency x Block interaction for Motor Preparation Times. Theta tACS reduced (and Beta tACS increased) Motor Preparation Times in the Interactive Block.

Last Press Times (Interactive Block)

Type III ANOVA on sham-corrected values with Block (Cued, Interactive), TypeTrial (Correction, NoCorrection, FakeCorrection) and Movement (Opposite, Same) as within-subjects and Frequency (Beta, Theta) as between-subject factor, revealed no significant main effect or interaction (all $F_s < 0.0$, all $p_s > .99$) suggesting that tACS didn't have any effect on this variable.

Correlational analyses

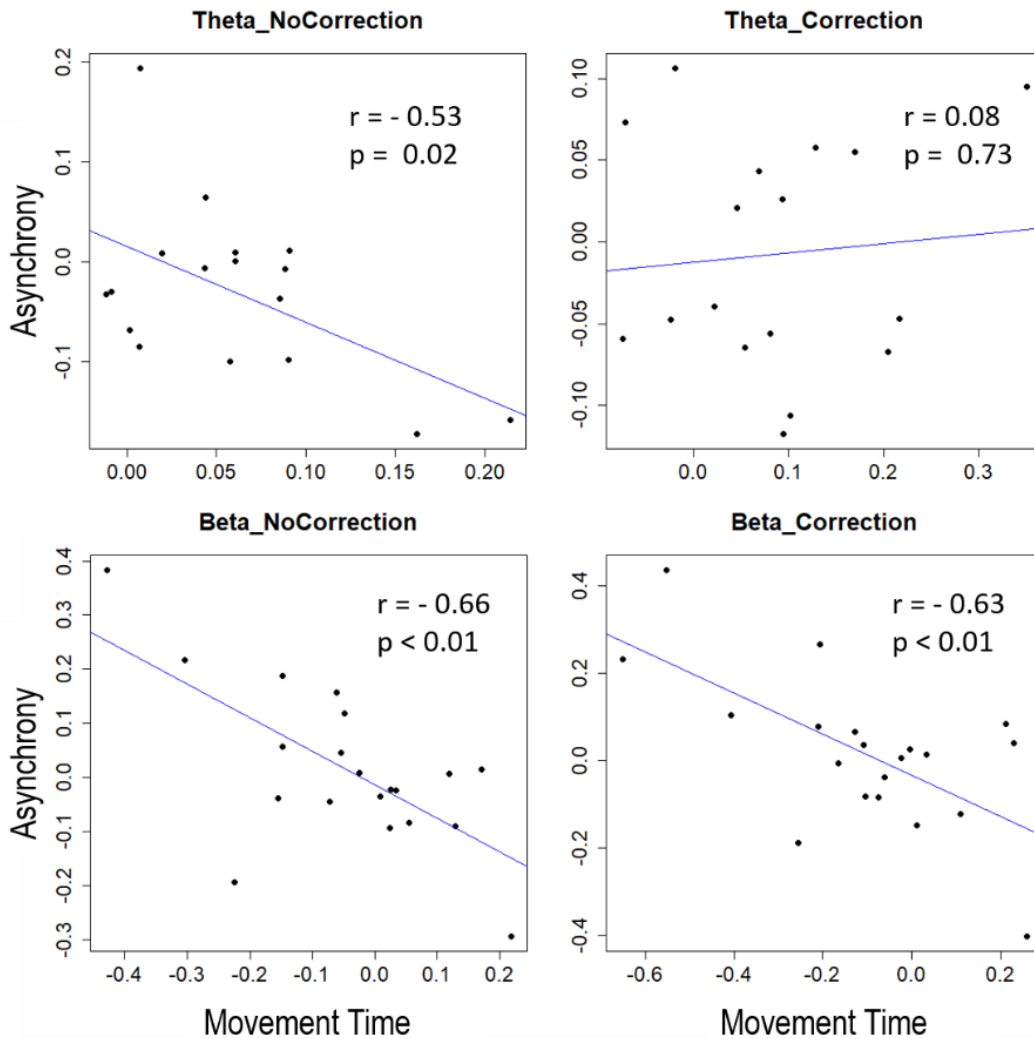


Figure 7. Correlations between Asynchrony and Movement Times in the Interactive Blocks.

Our results indicate that Theta tACS had the effect of reducing Asynchrony across all conditions and increasing Movement Times in Correction trials. Also, although not significant, an increase in Movement Times was found in NoCorrection trials during the Interactive Task (see Fig 7). We reasoned that longer Movement Times might have allowed participants to be more synchronous with the virtual partner in touching the targets. Indeed, we found that (across all conditions) the average participants' Movement Time was $2.65 (\pm 0.35)$, while the virtual partners was $3.18 (\pm 0.01)$. This means that, on average, participants touched the target earlier than the virtual partner. In this vein, increasing Movement Times should allow participants to touch the target more in synchronous with the virtual partner. To test this hypothesis, we ran correlation analysis between Asynchrony and Movement Times during the Interactive Block. We focused on the

Interactive condition as the one in which a significant effect of tACS on Movement Times was found. Results showed a significant negative correlation between the two variables in all conditions (see Figure 6) except for Theta_Correction. Specifically, Asynchrony and Movement Times were correlated in Theta_NoCorrection ($r = -0.53$, $p = 0.02$), Beta_NoCorrection ($r = -0.66$, $p < 0.01$) and Beta_Correction ($r = -0.63$, $p < 0.01$) but not in Theta_Correction ($r = 0.08$, $p = 0.73$).

Discussion

Motor and behavioural adjustment following observed errors in social contexts have been mainly investigated in turn-taking speeded reaction time (Schuch and Tipper, 2007, De Bruijn et al 2008) or grasping tasks (Ceccarini and Castiello, 2008). However, rather than “observing, then doing”, the most part of everyday motor interactions require agents to “observe *while* doing”, therefore involving a moment-by-moment integration of observed and executed movement. From this perspective, the most part of “joint errors” (i.e. errors occurring in the context of a joint action and influencing its success) can, and need to, be corrected online. Considering the classical example of two people moving a table together, if one of them accidentally loose his grip, the other will need to quickly implement a motor adjustment to compensate the other’s failure and ensure the fulfilment of the joint action. Previous studies from our research group have shown that unexpected motor changes during motor interactions elicit error-related midfrontal Theta activity (Moreau et al 2019, Moreau et al in prep.), a neural marker of error and conflict detection. In the present study, we used a sham-controlled mixed design to test the hypothesis that boosting midfrontal Theta with tACS would modulate adaptive motor adjustments after the observation of a virtual partner’s unexpected change.

Our results showed that Theta and Beta tACS had both general and condition-specific effects on performance in the motor interaction task. Participants’ ability to synchronise their reach-to-press movements with those of the virtual partner was improved during Theta, compared to Beta, tACS, irrespective of the experimental condition. Synchronisation in motor interaction tasks requires the continuous monitoring of both the observed and the executed movements. Endogenous midfrontal Theta activity has been related to sustained attention during cognitive tasks (Sasaki et al 1996; Onton et al 2005) and meditation (Aftanas et al 201, Tang et al 2009). Since Theta tACS was

delivered continuously, this improvement in synchrony performance might reflect an increased engagement of attentional systems. In this vein, Theta tACS might have helped participants to focus their attention on the motor task and to better control their own movements.

We also found an increase in movement time during Theta, compared to Beta tACS that was specific for Correction trials in the Interactive task, namely when participants observed a motor change in the virtual partner *and* needed to implement a motor correction. Midfrontal Theta activity has been related to both error detection (Cavanagh et al 2009) and conflict resolution (Botvinick et al 2007; Nigbur et al 2011), two processes sharing the need of increased cognitive control. More in general, midfrontal Theta is elicited whenever a habitual response needs to be overcome (Cavanagh et al 2013). In our task, when the virtual partner was correcting its movement, participants needed to inhibit their ongoing motor plan (e.g. pressing the button with the index finger) and to reprogram a different action (e.g. pressing the button with the middle finger). Motor inhibition involves movement slowing or stopping and has been associated with a brain network consisting of the lateral inferior frontal cortex (IFC), the presupplementary motor area (pre-SMA) and the subthalamic nucleus (STN) (Aron et al 2007). Activity in this network has been associated with the implementation of PES (Danielmeier and Ullsperger, 2011). Interestingly, the STN is directly interconnected with the ACC (Orieux et al 2002), where information about errors and conflict are processed and where Theta oscillations are putatively generated (Luu et al 2004).

From this perspective, the Theta-tACS-induced increase in movement times during correction trials might reflect an enhanced activation of the performance monitoring system which in turn modulated the implementation of PES. Since in our task participants were not asked to be as fast as possible but, rather, as synchronous as possible, we did not expect to observe any slowing in reaction times in the following trial. Instead, we found an increase in movement times *during* the trial that could possibly reflect a phenomenon of motor inhibition (and movement slowing) induced by a response conflict. Interestingly, movement times during correction trials seemed to be reduced by Beta tACS. This result is particularly surprising, considering that increased EEG Beta power has been related to motor inhibition (Kuhn et al 2004), movement slowing (Pogosyan et al 2009) and

PES (Marco-Pallares et al 2008). However, since our participants were exerting a continuous force over the Touch controller button and since the velocity of the Avatar 1PP movements was directly related to the exerted force, it is possible that Beta tACS, rather than affecting motor control *per se*, has influenced the strength of the button press. Indeed, one study found that unexpected somatosensory and auditory events delivered while participants were performing an isometric task triggered an increase in force power that was paralleled by an enhancement in Beta EEG power recorded over the central electrodes (Novembre et al 2019).

Correlation analyses showed that movement times were correlated to synchrony. Namely, those participants who took more time to move their virtual arm to the target were also better at synchronising their reach-to-press movements with those of the virtual partner. The fact that, on average, participants' movement times were shorter than the virtual partner's ones might explain why their synchrony performance benefited from an increase in movement time. However, this was not true for correction trials in the Theta group, possibly because the increase in movement time elicited by Theta tACS was so large.

Limits

There are potential limitations in this study that should be taken account in the interpretation of the results. First, the time between the real and sham stimulation session might have been too short to cancel tACS aftereffects for those participants that received real tACS in the first session. This could explain why the two groups were showing differences in various kinematic parameters not only during real tACS but also (although to a lesser extent) during sham. There is still no consensus on the actual duration of tACS aftereffects, which seem highly dependent on the stimulation parameters (Veniero et al 2015). However, the possibility that tACS effects might last after stimulation, especially for what concerns plasticity (Vossen et al 2015) should be considered. Another potential limitation of our study is the absence of EEG recording during or after the stimulation, which prevents us to claim that we were, indeed, enhancing midfrontal Theta power. Future research should consider the potential benefits of concurrent EEG/MEG recording during Theta tACS stimulation.

Conclusion

In the present study we have addressed the causal role of midfrontal Theta oscillations in online motor adjustment to a “joint error”. To our knowledge, this is the first study investigating the causal role of the performance monitoring system in dyadic motor interactions. We showed that Theta tACS improved synchrony performance in all conditions and increased movement times when a motor correction was required. These results hint to a potential beneficial effect of combining tACS with motor interaction tasks for the treatment of motor impairments (e.g. Apraxia or Parkinson disease).

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