THE UNIVERSITY OF QUEENSLAND
AUSTRALIA

Neural processes for action observation

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A thesis submitted for the degree of Doctor of Philosophy at
The University of Queensland in 2014
Queensland Brain Institute

Abstract

Through actions we explore the world around us, we express ourselves, achieve goals and interact with others. We are thinking about actions, planning, executing, imitating, observing, and understanding them. In other words, our life is filled with *motor cognition*. Yet our knowledge of the brain processes underlying these tasks is limited. Based on extensive literature we know that action observation and production share common neural mechanisms and a common neural network. Throughout the studies in this thesis, I use this connection to explore neural processes related to motor cognition.

In the first chapter, I examine current theories on action observation and identify key concepts investigated in the later experiments. I review a wide range of literature from the fields of neural disorders and healthy participants tested on various tasks, such as visual illusions, motor expertise, and conscious and unconscious visual processing. Focusing on the bidirectional information flow between motor and perceptual areas, I examine how well the common coding theory, the direct matching hypothesis, and predictive coding models fit the current experimental results. I argue that, while predictive coding theories are best to explain the wide variety of results related to motor cognition, there are still important questions unanswered in the literature. There is a relative lack of studies investigating motor cognition in close-to-natural settings, and attentional modulation is often ignored. Furthermore, more research is needed to explore the spatial and temporal dynamics of how observed and executed actions present on the neural level.

In the first experiment, I investigate how the brain processes actions when they are not consciously attended. I recorded brain activity related to action observation under an attentionally demanding visual task. Data indicate that even when our attention is directed away from actions both the motor and perceptual systems -as part of the action observation network- show a systematic change depending on the novelty of action properties. The results of this experiment also suggest that action related information is prioritised even when attentional resources are limited. In the second experiment, I examined how attention on specific action representations, such as kinematics, goals and agency, influences brain response during the processing of actions. The results of this experiment suggest that, even though novelty-related

changes are very strong throughout in the action observation network, attention can specifically modulate neural activity to enhance the processing of task-specific information.

Finally, in the third experiment, I investigated how a common system can deal with the parallel processing of action execution and observation. I aimed to give a comprehensive picture of neural activity related to motor cognition, and thus analysed event-related magnetic field activity and power changes in theta, alpha and beta frequency bands. Data indicated that neural processes are sensitive to conflict between observed and executed actions as early as 100ms after stimulus presentation. Furthermore, theta and beta frequency bands were found to be the most sensitive to the concurrent effects of action execution and observation, while the alpha frequency range showed neural processes related more to attentional mechanisms than to motor preparation.

During these studies, I have attempted to test how the brain deals with motor cognition in everyday situations. I have described neural activation with fMRI and MEG and shown the involvement of a widespread network in motor cognition. I focused my investigation on attentional processes, and found that actions are processed even when attention is diverted away to a different demanding task. However, when actions are task-relevant and explicitly attended, task-specific areas are selectively enhanced to help discriminate effectively between sensory information. Indeed, a conflict between planned and observed actions is registered in the brain as rapidly as within 100ms. Furthermore, with a detailed description of brain oscillations and event related field changes, this thesis provides a comprehensive picture of how neuronal changes manifest on a temporal level during the early processing of an observed action. While this research clarified several important questions, further research is needed to explore one of the fundamental brain processes, motor cognition.

Declaration by author

This thesis is composed of my original work, and contains no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others to jointly-authored works that I have included in my thesis.

I have clearly stated the contribution of others to my thesis as a whole, including statistical assistance, survey design, data analysis, significant technical procedures, professional editorial advice, and any other original research work used or reported in my thesis. The content of my thesis is the result of work I have carried out since the commencement of my research higher degree candidature and does not include a substantial part of work that has been submitted to qualify for the award of any other degree or diploma in any university or other tertiary institution. I have clearly stated which parts of my thesis, if any, have been submitted to qualify for another award.

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Publications during candidature

Journal articles:

Published:

Halász, V., & Cunnington, R. (2012). Unconscious effects of action on perception. *Brain Sciences, 2*(2), 130-146.

In preparation:

Halász, V., Mattingley, J. B., & Cunnington, R., (2014). Enhanced neural activity for unattended novel actions.

Halász, V., Mattingley, J. B., & Cunnington, R., Attention and perception influence the neural processing of observed actions.

Halász, V., Woods, W., & Cunnington R., Interaction of concurrent motor plans and perceived actions on neural oscillations.

Conference papers & abstracts:

Halász, V., Mattingley, J. B., & Cunnington, R., (2013). Action processing under attentional load. *19th Annual Meeting of the Organization of Human Brain Mapping, 2013*. Seattle, USA.

Halász V., Mattingley, J.B., and Cunnington, R., (2013). Attention to action reveals neural representation for agency, kinematics, and goals. *Frontiers in Human Neuroscience. Conference Abstract: ACNS-2013 Australasian Cognitive Neuroscience Society Conference.* Melbourne, Australia.

Halász, V., Mattingley, J. B., & Cunnington, R., (2012). Action processing under attentional load. *Frontiers in Human Neuroscience. Conference Abstract: ACNS-2012 Australasian Cognitive Neuroscience Conference.* Brisbane, Australia.

Halász, V., Mattingley, J. B., & Cunnington, R., (2011). Attention to actions, goals, and agency influences neural activity during action observation. *17th Annual Meeting of the Organization of Human Brain Mapping*. Quebec, Canada.

Publications included in this thesis

Halász, V., & Cunnington, R. (2012). Unconscious effects of action on perception. *Brain Sciences, 2*(2), 130-146. - incorporated as Chapter 2.

Contributor	Statement of contribution
Author Halász, V. (Candidate)	Wrote the paper (90%)
Author Cunnington, R.	Edited paper (10%)

Halász, V., Mattingley, J. B., & Cunnington, R., (2014). Enhanced neural activity for unattended novel actions. - incorporated as Chapter 3.

Contributor	Statement of contribution
Author Halász, V. (Candidate)	Designed experiments (90%)
	Wrote the paper (90%)
Author Mattingley, J. B.	Designed experiments (5%)
	Edited paper (3%)
Author Cunnington, R.	Designed experiments (5%)
	Edited paper (7%)

Halász, V., Mattingley, J. B., & Cunnington, R., Attention and perception influence the neural processing of observed actions. - incorporated as Chapter 4.

Contributor	Statement of contribution
Author Halász, V. (Candidate)	Designed experiments (90%)
	Wrote the paper (90%)
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	Edited paper (3%)
Author Cunnington, R.	Designed experiments (5%)
	Edited paper (7%)

Halász, V., Woods, W., & Cunnington R., Interaction of concurrent motor plans and perceived actions on neural oscillations. - incorporated as Chapter 5.

Contributor	Statement of contribution
Author Halász, V. (Candidate)	Designed experiments (90%) Wrote the paper (90%) Statistical analysis (95%)
Author Woods, W.	Statistical analysis (5%)
Author Cunnington, R.	Designed experiments (10%) Edited paper (10%)

Contributions by others to the thesis

“No contributions by others.”

Statement of parts of the thesis submitted to qualify for the award of another degree

“None”

Acknowledgement

Köszönöm.

Keywords:

action observation, action, perception, attention, predictive models,
motor cognition, oscillation, fMRI, MEG

Australian and New Zealand Standard Research Classifications (ANZSRC)

ANZSRC code: 170101, Biological Psychology (Neuropsychology,
Psychopharmacology, Physiological Psychology) 60%
ANZSRC code: 170205, Neurocognitive Patterns and Neural Networks 25%
ANZSRC code: 110999 Neurosciences not elsewhere classified, 15%

Fields of Research (FoR) Classification

FoR code: 1701, Psychology, 60%
FoR code: 1109, Neurosciences, 40%

Table of Contents

List of Figures

List of Tables

List of Abbreviations

AON	action observation network
BOLD	blood-oxygenated-level dependent
EBA	extrastriate body area
EEG	electroencephalography
EPI	echo-planar imaging
ERF	event-related field
ERP	event-related potential
FBA	fusiform body area
fMRI	functional magnetic resonance imaging
FRN	feedback related negativity
FWHM	full-width-at-half-maximum
IFG	inferior frontal gyrus
IPL	inferior parietal lobule
LOC	lateral occipital cortex
MEG	magnetoencephalography
MMN	mismatch negativity
MTG	middle temporal gyrus
PMd	dorsal premotor cortex
PMv	ventral premotor cortex
RS	repetition suppression
SD	standard deviation
SMA	supplementary motor area
SSS	signal-space separation
STG	superior temporal gyrus
STS	superior temporal sulcus
TE	echo time
TR	repetition time
VPP	vertex positive potential

Ab ovo

More than 20 years ago I was watching my baby brother exploring the world. My grandmother with no more than primary school education, was never short on advices. One of her favourite pieces of advice was that my brother “needs to move because that what’s going to make him clever”. Whenever she played with my brother she always encourage him to learn new movements, even simple things such as to reach, touch, clap hands and later, to turn, crawl or step. It took me more than a decade to see the real wisdom in my grandmother’s advice. After learning about child development, neuroanatomy, perception, after thinking about the colour “red”[1], mirror neurons, and kittens in a carousel[2], I understand: we need movement to learn how to perceive[3] and we need perception to move effectively, then through action and perception our brain starts to “think”[4]. The link between perception and action is a fascinating one, and one that we still hardly understand. In this thesis I will examine this connection by looking at neural processes related to action observation.

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Chapter 1

General introduction

Perception and action are interlinked in our life, just as they are interlinked on a neural and functional level. In the present thesis I investigate this link to deepen our knowledge about how we understand others' actions. With my experiments I explore situations that we often encounter in our daily life, such as how we keep track of actions around us when we are busy with some other task or, observing an action when we also act. The main aim of my thesis is to examine how attention and context modulate the neural mechanisms behind action perception. My experiments broadly investigate motor cognition and the neural processes by which we express ourselves, achieve goals, interact with and understand others and world around us. In the following introductory chapter my aim is to shortly highlight the main theme of my thesis, to define core concepts, and to link ideas and theories across my experimental chapters.

Motor cognition and its neural network

Our brain rarely stops preparing and executing actions. The urge to act, to move, to "do" is so strong that we need a special neural mechanism to stop us acting while we are asleep. But we are also not only "acting": We are planning, intending, learning, imitating, perceiving and understanding actions. I will use the term *motor cognition* to refer collectively to these brain processes, which all rely to some extent on the motor areas of the brain (Jeannerod, 2006). It is easy to see that we need perceptual areas to imitate, memory to learn and recall actions, and higher-order cognitive areas to plan ahead. Indeed, motor cognition relies on a widespread neural network that extends from early visual areas to parietal, motor and frontal areas of the brain (Caspers et al., 2010; Grosbras et al., 2012; Hétu et al., 2013; Molenberghs et al., 2012). In this thesis, I use functional magnetic resonance imaging (fMRI) and magnetoencephalography (MEG) to map brain regions actively involved in motor cognition. My paradigms involved action observation (Chapter 3 & 4), and combined action preparation and observation (Chapter 5), thus I mostly refer to these brain regions as the *action observation network* (AON). However, many functions of motor cognition, like observation, motor imaginary, imitation or execution, all share neural sources.

Action-perception link

A core theme of my thesis is the link between *action* and *perception*. It is important to note that in my experiments I examine brain areas involved in the processing of *visual* information related to actions. Some suggest that perception is an active process by which our brain creates an internal representation of the world (Noë, 2004). In philosophy, the enactive approach to perception claims that we need physical motion or action to perceive, and in this sense they are inseparable (Noë, 2004). However, the term *perception* refers here to brain processes primarily involved in the processing of incoming sensory (visual) information.

A long line of research shows that the same areas are active when we execute an action and we observe actions (Bonini et al., 2010; Keysers & Gazzola, 2009; Kilner & Lemon, 2013; Rizzolatti & Sinigaglia, 2010). The link between perception and motor processes exists on the single cell level and is also well established with neuroimaging data (Di Pellegrino et al., 1992; Gallese et al., 1996; Mukamel et al., 2010). It is clear that sensory information guides our actions, however the reverse flow of information, from motor to perceptual areas, is less well understood. I specifically explore evidence for effects of the motor system on perception in Chapter 2, where I review action-to-perception effects in previous literature. Furthermore, I examine the effect of concurrent motor preparation on action observation with a MEG experiment (Chapter 5).

Predictive coding models

While the link between perception and action is strong, the debated question in the literature is *how* they are connected, and what neural mechanism is behind the fast and seemingly effortless execution and understanding of actions. In the Chapter 2 I examine three prominent theories of action processing: the *common coding theory*, the *direct matching hypothesis*, and the *predictive coding models* of action understanding. While my experiments do not directly test the validity of these theoretical models, I argue that predictive coding models are the best to explain a wide range of experimental effects in the current literature. In essence, predictive models claim that motor cognition is proactive, our brain constantly anticipates or predicts future sensory states based on internal or external motor information (Friston, 2009, 2010; Halász & Cunnington, 2012; Kilner et al., 2007; Kilner, 2011). The predictive models offer an elegant theory as to why and how perceptual and motor areas interact and provide an overarching framework by which to understand motor cognition as examined throughout this thesis.

Attention and context

Actions do not exist without context. Goals, intentions, skills and external forces are major factors in motor cognition. In the real life we often do not pay attention to all of the actions around us, yet still we are somehow processing may of them. In a social situation we act to complement each other's actions, or quite the contrary, we act to disrupt others in their movements. Surprisingly little research is available about how attention, one of the most important modulating factors of human perception, influences action perception. My first experiment (Chapter 3) investigates whether others' actions are still processed in the brain when our attention is directed away from those actions and how we detect novel and repeated actions even when they are not task relevant. In Chapter 4, I present results on how focused attention to action goals, kinematics or agency influences neural activity for action perception by manipulating which aspects of actions are task relevant. Finally, in the last experiment (Chapter 5) I investigate how concurrent motor plans affect the neural processing of concurrently observed actions.

Current experiments

The main focus of my thesis is to investigate neural patterns linked to action observation under different conditions of attention and task context. I present a broad overview of the existing literature and important theoretical models of action understanding in Chapter 2. I argue that the predictive coding theories are the best to model action perception. Building on core assumptions of these theories I indirectly test whether predictive loops are continuously/automatically created during action observation (Chapter 3 & 4). In Chapter 3 I set up an experiment to test whether predictive processes exist during a task that heavily loads visual resources. I use fMRI to test brain activity related to the processing of actions under high and low attentional loads to investigate the neural processes of action observation outside of attentional focus.

In Chapter 4 I examine the functional organisation of the AON and its sensitivity to top-down modulation by selective attention or task relevance. During this paradigm participants actively observe actions, however their attention is always focused on one specific aspect of the action: the moving agent, goals or action kinematics. With this experiment I examine how engagement of different parts of the AON changes depending on task context, when specifically monitoring changes in agency, kinematics or goals while observing actions.

Finally in Chapter 5 I examine how concurrent active motor plans for our own intended actions influence the neural processes during action observation. I used MEG to measure neural processing on a millisecond time-scale and to give a comprehensive overview of frequency changes linked to action observation. My data indicated that the brain rapidly matches observed and executed actions within the first 100ms. Furthermore, I describe how theta, alpha and beta frequencies change during action observation and how frequency changes modulated with concurrent motor plans.

My overall aim through this thesis is to reveal more of the neural patterns related to action observation and motor cognition, and in particular to examine the influence of attention and context on the action observation network. We need deeper understanding of how these important cognitive mechanisms operate for better theoretical models of the working brain.

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Chapter 2

Unconscious effects of action on perception

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Abstract: We spend much of our life predicting the future. This involves developing theories and making predictions about others' intentions, goals and about the consequences of the actions we are observing. Adapting our actions and behaviours to the environment is required for achieving our goals, and to do this the motor system relies on input from sensory modalities. However, recent theories suggest that the link between motor and perceptual areas is bidirectional, and that predictions based on planned or intended actions can unconsciously influence and modify our perception. In the following review we describe current theories on the link between action and perception, and examine the ways in which the motor system can unconsciously alter our perception.

Keywords: perception; action understanding; motor system; predictive coding

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This chapter has been published as:

Halász, V., & Cunnington, R. (2012). Unconscious effects of action on perception. *Brain Sciences, 2*(2), 130-146. doi:10.3390/brainsci2020130.

2.1. Introduction

Our actions and behaviours are continuously adjusted to correspond with changes in the environment and in social settings. To do this, the brain needs to rapidly and efficiently process incoming sensory information and match with predictions based on our current actions or intentions. Perception and action are therefore closely linked, and regulating the brain processes underlying perception helps us to achieve our goals in a constantly changing environment. Recent theories posit that information flows not just from perception to action, but also from action to perception, such that predictions based on our own actions or intentions can unconsciously influence our perception of others' actions.

Our aim in this review is to explore how information from the motor system of the brain can unconsciously influence perception. Of course, perceptual guidance is crucial for our everyday actions, and there is extant literature on how sensory information links to the motor system for guiding our behaviour. However, very recent research has also begun to examine the inverse relationship—specifically, how actions can unconsciously influence perception. Mixed results are reported whereby actions can sometimes facilitate or attenuate our perception. Here we describe current theories on the link between voluntary action and perception, and examine the different ways that perception can be modulated by the motor system. We conclude by arguing that predictive models of action perception can best explain how our motor system unconsciously influences our perception.

There are three main theories that are used to explain how actions represented in the motor system link with perception—the *common coding theory*, the *direct matching hypothesis*, and *predictive models* of action understanding. These theories largely describe how we understand and perceive others' actions, but can also describe how motor plans or intentions can influence perception.

These theories are all based on the fact that neural circuitry involved in action observation and perception overlaps extensively with those areas that important for executing our own actions. For example, during action observation, neuroimaging studies have demonstrated automatic activation of motor and premotor areas in the brain (Buccino et al., 2001; Gazzola & Keyers, 2009), while neurophysiological measurements show covert corticospinal motor pathway excitation (Fadiga et al., 2005). Additionally, the link between action and perception also exists on a single-cell level. A subset of premotor and parietal neurons discharge when monkeys both execute certain actions and when they observe the same actions executed by others (Rizzolatti & Craighero, 2004; Gallese et al., 1996). These neurons are called *mirror neurons*, while the phenomenon that observed actions elicits similar neural activity as executed actions can be collectively called *action mirroring*.

In reviewing these theories, an important distinction is whether they propose mechanisms for action understanding that are predominantly *postdictive* or *predictive*. Postdictive theories postulate that observers rely on motor memories or associations based on previous experiences in order to understand the observed actions. In other words, these theories suggest that the main task during action-observation is to decode sensory information to extract meaning after it is received in the brain, as if the system would ask the question: "What has just happened?" In contrast, predictive theories claim that, during action observation, our brain unconsciously makes predictions of the near future, already setting-up sensory processes for what we are most likely to perceive in the following instants, answering the question: "What will happen next?".

2.1.1. Common Coding Theory

The earliest theoretical framework on the connection between perception and action is the *ideomotor theory* (Shin et al., 2011). It suggests that actions and internal images of actions are closely linked, and that actions are represented by their sensory consequences (James, 1890). Building upon these basic ideas two widely cited theories have been proposed, first the *common coding theory* (Prinz, 1997) and later the *theory of event coding* (Hommel et al., 2001). According to these theories, fundamentally the same areas of the brain are involved in perceiving and planning an event. For example, if we are about to have a cup of coffee, or maybe just smelling the coffee, the same areas of the brain become commonly active, as the motor acts and their associated sensory states are commonly coded in the brain (Figure 2.1). The common coding theory does not strictly define how information flows within this network. It is neither predictive nor postdictive for the same reason: while one thinking about "coffee" neural activity of past memories related to coffee drinking or future imagined events are equally likely to be activated. This indistinct nature makes the common coding theory flexible enough to explain several phenomena related to perception-action and action-perception connections. However, it is not exactly clear on how and why different codes become active or "remain silent" in any given situation; therefore it is hard to assess the validity of this theory scientifically.

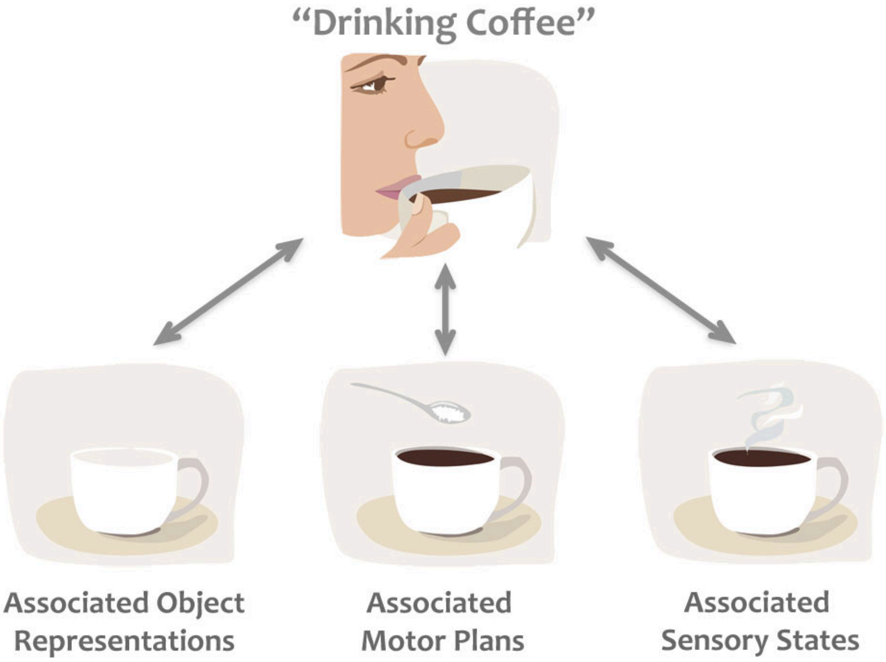

Figure 2.1. Example of the common coding theory. Thinking about "drinking coffee" activates associated codes, which frequently occur together, such as objects (e.g., coffee cup, coffee beans), motor plans (e.g., the way we like to hold our cup), and sensory states (e.g., the colour, smell, taste of coffee), biasing subsequent processing of any of these associated states.

2.1.2. Direct Matching Hypothesis

One of the most popular theories that explain the function of action mirroring is the *direct-matching hypothesis* (Rizzolatti et al., 2001). This theory claims that "an action is understood when its observation causes the motor system of the observer to 'resonate'" (Rizzolatti et al., 2001, p. 661). According to the direct-matching theory, action mirroring is a process of simulation that leads to understanding the goals of observed actions by automatically mapping those observed actions into the observer's own motor system (Rizzolatti & Sinigaglia, 2010). This is claimed to be a bottom-up or stimulus-driven process, whereby low-level representation of the observed movement kinematics triggers higher-level activation of the brain where goals and intentions are coded (Csibra, 2007). The direct matching hypothesis suggests a feed-forward flow of information whereby the visual information related to actions in occipito-temporal brain areas flows into the posterior parietal lobe and the premotor cortex (both of which contain mirror neurons) and leads to motor representation of the observed action for understanding of the action goals (Rizzolatti & Craighero, 2004). This classic view of the direct matching hypothesis is fundamentally postdictive; it suggests that observers project backwards in time to recover associated goals or intentions that they experienced previously while executing the same actions (Wilson & Knoblich, 2005). For example, while observing somebody picking up a cup, our brain matches the observed action with equivalent motor plans and identifies the goal of the action (e.g., "drinking" or "transporting a cup") by activating the associated goals or intentions we have had previously when performing the same action ourselves (Figure 2.2). However, recent studies using single cell recordings also report mirror neurons that show activation related to action sequences that are about to happen (Fogassi et al., 2005; Bonini et al., 2011). These findings suggest that mirror neurons may support a more complex, predictive type mechanism for action understanding compared to the essentially postdictive process described by the classic direct matching hypothesis.

Figure 2.2. Example of the direct matching hypothesis. While observing a motor act we automatically map the kinematics of the observed action onto our own motor plans. By retrieving the goals and intentions (in this example "drinking") behind those motor plans, based on our own prior experience, we understand others' actions or goals.

2.1.3. Predictive Models

A set of theories are essentially predictive in nature, and claim that action mirroring is used to predict actions, goals or sensory states that are about to occur, thereby readying our sensory systems for processing of the expected incoming sensory information (Csibra, 2007; Wilson & Knoblich, 2005; Kilner et al., 2007; Miall & Wolpert, 1996). While predictive models can also be described computationally from physical systems (Stepp & Turvey, 2010; Dubois, 2003), in the present review we focus specifically on predictions of future states from internal models. These theories predominantly rely on the concept of internal *forward models* by which *emulators*, or mental simulations, provide a mechanism to estimate anticipated internal neural representations of external actions or events by real-time simulation of the consequences of those events (Wilson & Knoblich, 2005; Miall & Wolpert, 1996). For example, the *predictive coding* model of Kilner and colleagues (2007) suggests that several forward and backward loops exist between the levels of a hierarchically organised system, and anatomical connections between these areas are reciprocal. The forward models suggest that, during action observation, we are constantly making predictions about the acting agent's goals, intentions or next moves. These predictions then are fed-forward to influence the way sensory brain areas process information. For example, when we observe someone holding a coffee cup, the brain predicts the most likely outcome of the action, e.g., that the person takes a sip (Figure 2.3). However, if the person's face suddenly changes and expresses negative emotions, the predicted outcome rapidly changes and the brain recomputes the next most likely outcome, e.g., perhaps to anticipate a comment from the drinker about the drink being too hot or having a bad taste. This type of prediction enables us to process expected sensory information or detect unexpected outcomes quickly and efficiently, and thereby to adapt our own behaviour to the environment or social settings.

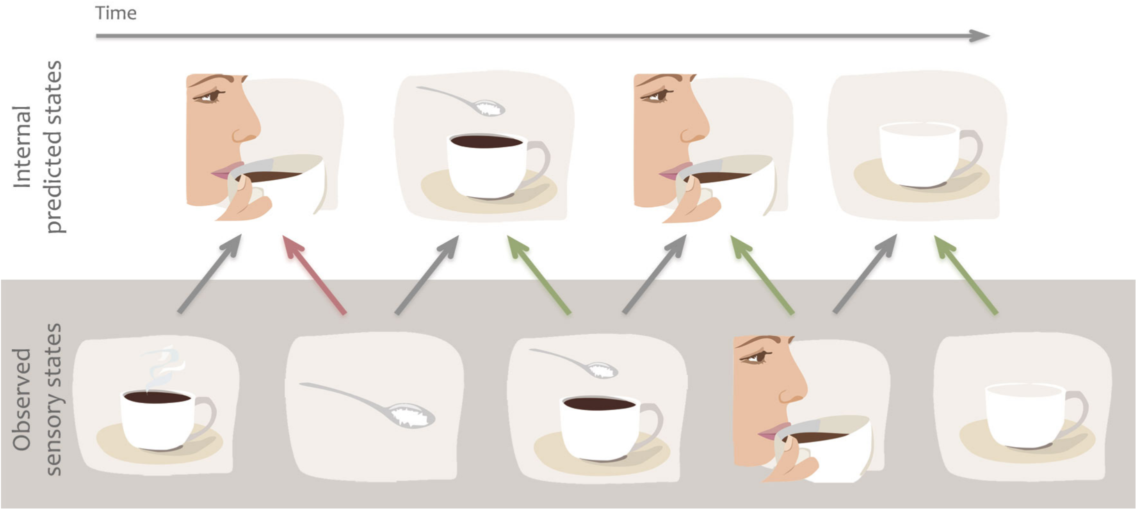

Figure 2.3. Example of predictive coding or forward models. We are constantly making predictions about the future state of our sensory system based on previous associations. Predictions are also quickly updated based on incoming sensory information to minimize prediction error. For example we predict that our friend will take sip from her coffee but when her hand grabs the sugar bowl we quickly alter our prediction.

In summary, there are three main types of the theories on how actions and perception are linked. The common coding theory is the most widely used theory to explain how the motor system can influence perception. However, this theory does not define clearly the mechanism underlying how and why different representations become active during action observation. In contrast, the direct matching hypothesis describes a feed-forward nature of information flow during action observation, whereby low-level aspects of an action are matched to higher-level action representations and goals in order to understand others' actions. This theory maintains that goals and intentions are extracted from observed actions in a mostly postdictive way. In contrast, predictive theories propose that the brain predicts the most likely future events, based on predictions about others' goals and intentions. Forward models then translate these predictions of intentions to anticipated sensory representations that can influence the way we perceive the observed actions.

2.2. Actions influencing perception

The notion that information from the motor system can influence perception is in complete contrast with traditional views of brain organisation, in which sensory systems are considered the input end and motor systems the output end of the brain. These effects of actions on perception can be divided into two categories, one dealing with how long-term changes in the motor system with skill learning or motor dysfunction can effect perception, and the other focusing on real-time effects whereby our immediate motor plans or intentions can alter perception.

2.2.1. Effects of long-term changes in the motor system on perception

2.2.1.1. Motor disorders

A crucial set of evidence regarding the effect of the motor system on perception comes from patient studies, in which dysfunction of the motor system also impairs action recognition. For example, stroke patients with a motor deficit affecting their contralesional upper limb not only show impairment in action recognition, but that impairment is significantly stronger when it corresponds to their hemiplegic arm (Serino et al., 2010). Similarly, paraplegic patients with severe spinal injury are significantly impaired in detecting and discriminating the direction of biological motion in point-light walkers (animation sequences of human motion represented by the movement of the joints) compared with healthy individuals (Arrighi et al., 2011). Deficits in motor planning have also been shown to impair the ability to discriminate the gestures of others (Pazzaglia et al., 2008). Apraxic patients, who have impairment in performing complex movements following stroke, show a strong group-level correlation between motor impairment and the ability to recognise and perceive movements (Negri et al., 2007); however, the authors point out that, at an individual level, intact motor production is not always necessary for action or object recognition (Negri et al., 2007). Patients with motor impairment due to cerebellar lesions also show impairment in understanding the sequence of observed actions (Leggio et al., 2008; Cattaneo et al., 2011a), suggesting that the cerebellum is heavily involved in sequencing executed and observed motor acts and probably also predicting the sensory consequences of both observed and executed actions (for a review see Leggio et al., 2011). Finally, people with developmental disorders involving impaired movement performance also typically show impairment in biological motion perception (Atkinson & Braddick, 2011; Bhat et al., 2011; Kaiser & Pelphrey, 2012; Virji-Babul et al., 2010). These studies show that damage to the motor system impairs movement perception, implying that the perception of action relies on functioning of the motor system of the brain.

2.2.1.2. Motor expertise

Changes to the motor system with skill learning also affect perception. Whilst the term "expert eye" is often used colloquially, perceptual expertise is not hidden in the eyes, nor is it necessarily in our visual system. Several studies have shown how learning new motor skills or motor expertise changes the way we perceive observed actions (Calvo-Merino et al., 2006; Cross et al., 2006; Engel et al., 2008). An fMRI study measured brain activity in expert female and male dancers while they observed gender specific movements, such that visual exposure was equal for both types of movements but motor familiarity was gender specific for the participants (Calvo-Merino et al., 2006). Enhanced brain activity was found in shared action observation/execution areas of the brain while participants watched actions from their own motor repertoire. In a similar study, brain activity was correlated with the amount of physical practice in novel dance movements (Cross et al., 2006). Furthermore, imitating artificial object movements also led to increased brain activity in perceptual areas (Engel et al., 2008). The authors of these studies argued that, according to forward models, the specific motor knowledge of experts resulted in a quantitatively increased processing of observed actions, leading to a more precise prediction on how other's actions unfold in time and space.

Indeed, studies have shown increased accuracy in discrimination tasks in motor experts. For example, active basketball players predicted the success of free shots more quickly and accurately compared to individuals with similar visual but less motor experience (sport journalists or coaches) (Aglioti et al., 2008). Likewise, recognition of a gait pattern presented by point-light displays was higher after blindfolded training, with visual accuracy showing a strong correlation with the accuracy with which participants executed the learned movements (Casile & Giese, 2006). These results indicate that increased visual accuracy does not originate from visual familiarity with the action, but from the expertise of the motor system.

Similar results have also been reported on accuracy in relation to sinusoidal movements (Hecht et al., 2001), atypical movements novel for the motor system (Beets et al., 2010a), or on dart throwing (Knoblich & Flach, 2001). In the latter case, participants watched videos showing darts being thrown and were required to predict where the dart would land. Participants were significantly better at predicting their own throwing than other's throws. Similarly, accuracy to identify point-light movements was highest when participants observed their own action, less precise but still above chance when friends executed the actions, but fell below chance level for strangers (Loula et al., 2005). Changes to the motor system with skill learning or familiarity therefore appear to result in changes to perceptual abilities, supporting a critical role for the motor system in action perception.

Long-term motor practice not only increases visual accuracy but can also affect other perceptual systems. In an experiment by Repp and Knoblich (2009), participants showed altered auditory processes as a consequence of concurrently performed actions. Participants heard ambiguous tone-pairs that could equally be perceived as rising or falling tones. Interestingly, when they made concurrent key-presses from left to right, in the direction of rising tones on a normal keyboard, they were more likely to perceive the sounds as a rising tone. Vice-versa, when they made right-to-left key-presses they more often reported hearing the tones as decreasing. Both pianists and non-pianists showed this effect, but it was significantly stronger for pianists. These results clearly show that the actions performed have an influence on how concurrent sensory stimuli are perceived, and importantly that extensive motor practise or skill can have an additive effect on this association between the motor system and perception.

2.2.2. Effects of planned, intended, or executed actions on perception

2.2.2.1. Facilitatory effects

While studies of motor skill learning show long-term facilitatory effects of the motor system on perception, concurrently planned or executed actions can also immediately influence action perception. In line with results in the previous section, several studies have reported enhanced perceptual performance for stimuli that are congruent with concurrently planned or executed actions (Craighero et al., 2002; Lindemann & Bekkering, 2009; Wykowska et al., 2009). For example, in an experiment conducted by Lindemann and Bekkering (2009), participants were prepared to turn an object clockwise or counterclockwise when presented with a "Go" signal that was also turning either congruently or incongruently with the planned action. Participants were faster to respond to the rotating visual cue and turn the object in the congruent condition than in the incongruent condition. The authors interpreted this result according to the common coding theory, whereby preparing to execute the action would have also prepared the visual system for perceiving the consequences of that intended action, hence resulting in faster detection times for congruent stimuli. Other studies have similarly reported faster reaction times when the prepared action and visual stimulus were congruent, and have been interpreted as a facilitatory effect of the action on perception (Craighero et al., 2002; Wykowska et al., 2009). These types of studies, however, are open for alternative interpretation, as it is possible that the presented stimulus affected action execution, particularly when it was incongruent, and not that the prepared action facilitated the processing of the visual stimulus.

2.2.2.2. Twisted illusions

A clever way to measure changes in perception is to use ambiguous sensory stimuli and perceptual illusions, as did Repp and Knoblich (2009) with ambiguous tones. In a study by Wohlschläger (2000), the actions performed by participants determined how they perceived the direction of motion of an ambiguously rotating sphere. In their study, participants watched a rotating sphere that could equally be perceived as turning clockwise or anti-clockwise. When participants concurrently turned a knob either clock-wise or anti-clock-wise, they were more likely to perceive the sphere to be rotating in the same direction as their action; that is, their planned actions were shown to prime the perceived direction of the visual stimulus. Moreover, their study also showed that the priming effect was present when the goal of the planned action shared a common dimension with the visual display and that a strict correspondence between the actual hand movement and the visual motion display was not necessary for the effect to be observed. The effect of actions on perception can rely on higher order action representations, such as action goals, and a strict matching between the perceived stimulus and low-level kinematics is not crucial for the modulation effect. This study is one of the few that take into account the hierarchical organisation of the motor system, and addresses the possible effects of this hierarchy on the action-perception link.

Interestingly, only actions that are dependent on the currently perceived stimulus influence the perception of that stimulus (Beets et al., 2010b). In a recent study, participants were asked to report the direction of an ambiguously turning stimulus again, but either by turning a manipulandum or making key presses. When indicating the perceived direction by rotating the manipulandum, incongruency between the perceived and reported direction destabilized the percept, while congruency stabilized it. However, this effect disappeared when participants reported the perceived direction by key presses, even if they were concurrently performing a predefined (congruent or incongruent) turning movement on the manipulandum (Beets et al., 2010b).

Another experiment involving visual illusions showed how motor plans can reduce visual illusory effects. The Ebbinghaus illusion (Figure 2.4) is a classic visual illusion in which the central circle surrounded by small circles appears considerably larger than the circle surrounded by large circles. Vishton et al. (2007) showed that if participants were asked to grasp or touch the circle they perceived larger, rather than verbally reporting which was the larger central circle, the magnitude of the illusion was significantly decreased. This suggests that motor plans can partially correct for deceived perception in visual illusions. In summary, the above experiments on visual illusions indicate that the motor system can unconsciously alter sensory ambiguity to be in line with concurrent motor plans.

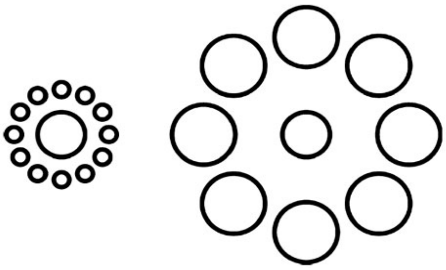

Figure 2.4. The Ebbinghaus illusion. This illusion leads to the misperception of the size of the central circle; however the effect decreases significantly if there is a grasping or pointing action directed to the central circle.

2.2.2.3. Action-affected blindness

In striking contrast to the above results, other studies report an attenuating or inhibitory effect on the processing of visual stimuli that are congruent with actions. Müsseler and Hommel first described an apparent blindness to response-compatible visual stimuli, calling it action-affected blindness (Müsseler & Hommel, 1997). This effect later was replicated by several studies, all using a very similar method (Müsseler et al., 2000; Nishimura & Yokosawa, 2010; Stevanovski et al., 2002, 2003, 2006). Participants plan left or right keypresses, but, just before they execute the action, an arrow is presented very briefly and they must report whether the arrow is pointing left or right. The perception of this arrow is impaired if it is pointing in the same direction as the planned action. The interpretation of this effect by the common coding theory suggests that, since planned and perceived actions share a common encoding, the planned action establishes the code associated with its execution and sensory consequences. Subsequently, when the congruent visual stimulus appears, this code is already represented and is less accessible for perception, and thus the perception of the congruent stimulus is impaired (Müsseler et al., 2000).

With an interesting twist on the original experiment, Stevanovski and colleagues revealed that this blindness effect does not rely on low-level congruency between the presented stimuli, but on higher-level representations (Stevanovski et al., 2002). In their experiment, participants were instructed that arrowhead symbols (i.e., "<"or ">") were actually headlights, so that the direction in which they were pointing was reversed compared to the original experiment. The blindness effect was still present, but now in the reversed direction. Thus, this experiment indicates that the action-blindness effect is not due to low-level similarity, but depends on how we interpret the stimulus in a given context.

Motor plans have also been shown to cause longer-lasting inhibitory effects on action perception. Cattaneo and colleagues (2011b) showed that, after a training session of simple pulling or pushing movements, participants were more prone to perceive movement of an ambiguous stimulus in the opposite direction compared to that trained in the motor task. The authors explained these results by postulating that mirror neurons, linking actions to perception, showed an adaptation effect as the consequence of motor training. This effect then was carried over for the visual perception task, resulting in decreased sensitivity in those neurons that equally encode executed and observed actions. In summary, the above studies suggest that motor plans can decrease the sensitivity of visual perception for stimuli that are congruent with the current or recently executed motor plan.

2.2.2.4. When similar repels and different attracts

Most of us probably spent time as a child trying to push together the like poles of bar magnets, contrasting with the strength of the attracting force between north and south poles. The same effects are hypothesised to occur in perception and concurrently executed actions: similar repels and different attracts. When there is congruency between the motor plan and the sensory information, the latter gets “repelled”, or in other terms does not reach consciousness. On the other hand, if there is a mismatch between the motor plan and the sensory information we are quicker and more precise to perceive that information as it would attract our attention.

For example, Zwickel and colleagues asked participants to make hand movements in a certain direction while simultaneously reporting the direction of the motion of an independent stimulus (Zwickel et al., 2007). Motion deviations of this independent stimulus were detected faster when their direction became incongruent with the executed hand movement. Similar effects have been reported for visual discrimination of hand movements (Miall et al., 2006), judging weights (Hamilton et al., 2004), or judging gait speed (Jacobs & Shiffrar, 2005). Zwickel and colleagues interpreted these results based on the common coding theory, and argued that people are more sensitive to perceive stimuli that deviate from the anticipated effects of their actions (Zwickel et al., 2007). When an observed stimulus matches the expected sensory consequences of the planned action, consciously perceiving it is less important because it does not carry any additional information in assisting the effective execution of the action. However, when the observed stimulus contradicts the expected sensory outcomes of the action, rapid perception of that stimulus can be crucial for modifying our action to better fit the environment to achieve our goals.

The above argument can also explain the results of Bortoletto and colleagues who showed that motor plans can influence early visual processing of an observed action (Bortoletto et al., 2011). The authors measured visual event-related potentials related to the perception of hand actions while participants were planning either congruent or incongruent hand actions (Bortoletto et al., 2011). Two components of early visual processing, namely N170 and Vertex Positive Potential were significantly higher to observed actions when those actions were incongruent with the planned actions. This result indicates that even early visual processing of observed actions—that is out of conscious perception—can be modified by motor plans.

A curious case that fits this section is related to an everyday experience with which we should be all familiar: why we cannot tickle ourselves. A touch feels ticklish when it is somewhat unpredictable; when we are concentrating on a very obvious movement we might not feel the tickle at all. Of course when we decide to move, our brain has a very precise prediction of what we are going to do and by predicting the sensory consequences of those movements we become less sensitive to perceive them. Blakemore and colleagues tested this theory by inducing delays and variation to participants' movements when they were intending to tickle themselves (Blakemore et al., 2000). When the sensory stimulus and the planned action were more consistent, the less ticklish the touch felt; however, the more inconsistent they were, the more ticklish the touch became. In conclusion, a complex two-fold interaction between perception and action exists. Motor plans can reduce the sensitivity for perception of congruent sensory information, but can also enhance the perception of a stimulus that is incongruent with concurrent actions.

2.2.2.5. Dynamic systems, complex interactions

Having previously highlighted the key findings related to action modulated perception it is important to stress the complexity of the brain processes underlying these phenomena. While experimental studies usually reduce tasks to a single motor plan and a sensory stimulus, in the real world there is dynamic, continuous interplay between action and perception. At present there is a relative lack of research investigating more real-life interactions between action and perception. One such study by Bhalla and Proffitt (1999) showed that hills appear steeper to people who are wearing a heavy backpack, fatigued or perceive their physical fitness as relatively low. Based on forward models the effect can be explained as follows: the motor plan forms the base of a predicted sensory state; this prediction is influenced by the relative heaviness of the backpack in a way that the predicted execution of the motor plan seems more tiring; this prediction in turn can influence the perceived steepness of the hill in correlation with the predicted difficulty of the task. Similarly, objects look closer when a tool is held and the intention is to touch the object with the tool than when the tool is not held or there is no intention to touch the object (Witt & Proffitt, 2008). These examples demonstrate how brain processes during action execution and observation comprise a complex dynamic system in which there is a constant process to interpret, suppress or enhance sensory information based on our motor plans and goals. Information during action observation and action execution flows to and from the sensory areas of the brain and intricate interactions and modulatory factors, relating to our action goals and intentions, influence what we perceive about the world.

2.3. The case for predictive models

There is ample evidence in the recent literature suggesting that the motor system not only receives information from the sensory areas of the brain, but also influences sensory processing and thereby unconsciously modulates our perception. The effect that actions can have on perception can be divided into two types: effects of long term motor expertise on subsequent perception, and immediate effects of either planned or executed actions on perception of concurrently observed stimuli. While studies of motor expertise show long-term facilitatory effects of the motor system on perception, planned or executed actions have been reported to either facilitate or attenuate visual perception of the concurrent stimulus. In the following we will review how the key theories on action observation relate to this modulatory effect and we will argue that predictive or forward models can best explain the complex interactions between motor and perceptual systems.

The common coding theory proposes that repeatedly paired actions and sensory outcomes may strengthen common codes or representations and lead to facilitation of perceptual performance during associated actions. Simultaneous activation of perceived sensory information and anticipatory effects of actions, however, can also lead to interference effects, thereby resulting in decreased perceptual performance. This decrement is suggested to arise because the commonly-coded action representations are already occupied from action planning and less sensitive to new sensory or perceptual information. The common coding theory, however, is only a theoretical framework and does not define clearly *why* concurrently performed actions sometime facilitate or attenuate perception. The direct matching hypothesis, on the other hand, proposes that low-level visual information about observed actions are mapped to the observer's motor system where, through action mirroring, the goal of the action or intention of the actor is decoded. This theory is essentially postdictive in nature, emphasising information flow only from visual to higher cognitive areas, making it difficult to explain how actions may have a feed-forward effect on perception.

In contrast, we argue that predictive or forward models are the best candidates to explain the variety of effects that the motor system can have on perception. These theories propose that planned actions or predictions of observed actions lead to anticipated sensory representations of the outcomes of the action (Csibra, 2007; Wilson & Knoblich, 2005; Kilner et al., 2007; Miall & Wolpert, 1996). Forward models explicitly propose information flow from motor to visual areas and can therefore explain how and why perception may be modulated by motor plans or intentions.

According to predictive models, whenever we are preparing for an action or watching others move our brain makes predictions about what we are going to see, hear, and feel in the following instants. We are also automatically and unconsciously making predictions about what are other people's goals and intentions based on their actions. There is a constant information flow between higher-level cognitive areas of the brain, the motor system, and the sensory system that enables us to predict anticipated actions and expected sensory consequences of those actions. When we gain expertise in some motor acts we become more efficient at predicting the sensory consequences of those actions (Aglioti et al., 2008; Casile & Giese, 2006; Knoblich & Flach, 2001). Similarly, our predictions of other's actions are more precise the more familiar we are with the acting person (Loula et al., 2005).

The picture becomes more complex, however, if we focus on the immediate effects of planned or executed actions on perception. When we act, or prepare to act, a sensory prediction based on our motor plan is generated and used to match or compare with incoming sensory information during perception. If this external sensory information is ambiguous it is affected by the sensory prediction based on our actions. This logic can explain how an ambiguous tone pair is perceived as rising or falling depending on whether our actions involve moving left to right or right to left (Repp & Knoblich, 2009), or create the illusion of a stimulus turning clockwise when our own hand actions involve turning clockwise at the same time (Aglioti et al., 2008; Wohlschläger, 2000).

There are also times when there is incongruency between what we perceive and what our motor system predicts. For example, in the case of the Ebbinghaus illusion (Figure 2.4) what we see is different from what our motor system predicts. When we move towards an object, we automatically and unconsciously adjust our fingers to take up a position that allows the best manipulation of the object (Jeannerod et al., 1995). This prediction based on our action can then weaken the perceptual bias of the visual illusion. Crucially, this effect only exists when we are planning to act upon the object, as passive observation does not involve any activation of motor plans (Bub & Masson, 2006).

When motor plans and the perceived stimulus overlap, experiments often report action-blindness effects (Müsseler & Hommel, 1997; Müsseler et al., 2000; Nishimura & Yokosawa, 2010; Stevanovski et al., 2002, 2003, 2006) that is, the relative blindness or missed perception of a stimulus that is congruent with the action-plan. Under limited resources, the system should filter out unnecessary information and focus on detecting stimuli that do not match predictions and therefore may require modification of actions. A stimulus that fits the predictions of the ongoing motor plan requires no special attention, and is thus less likely to reach consciousness in comparison to a stimulus that differs from the predicted sensory states.

The above logic can also explain the repellent effect of actions on concurrently perceived stimuli. The predicted sensory state, based on the motor plan, can influence or alter the perceived sensory information, resulting in a relative insensitivity for congruent stimuli (Zwickel et al., 2007;

Miall et al., 2006; Hamilton et al., 2004; Jacobs & Shiffrar, 2005; Blakemore et al., 2000). However, sensory information that is incongruent with the predicted state is processed rapidly (Bortoletto et al., 2011) as it is most likely to carry information important to modify our motor plans. Table 2.1 illustrates how the relationship between sensory information and concurrent motor plans may manifest in unconscious effects on perception.

Whatever theory is used to interpret effects of actions on perception, there is one common aspect that seems to be central and future studies might like to address: that is, congruency between the perceptual stimulus and the action. The action observation network is thought to be organised in a similar hierarchical manner to the motor system. Actions are formed by a sequence of steps, and these steps are organised hierarchically (Jeannerod, 1994; or for a review see Grafton & Hamilton, 2007). At the top of the hierarchy is an overarching goal, which needs to be achieved by completing sub-actions. These sub-actions are built from co-ordinated motor movements that, in turn, are built from individual muscle activations. It is hypothesized that the action observation network has a similar hierarchical organization in which different aspects of actions (e.g., goals, kinematics) are represented at different neural levels (Hamilton & Grafton, 2007). To date, however, it has remained unclear how congruency between the motor and perceptual system interacts to facilitate or attenuate perception of the stimulus. Most researchers fail to define the specific dimensions along which congruency may be varied, and so it is still unclear which level of action representation leads to effects of the motor system on perception. Furthermore, future studies should investigate the temporal and spatial dynamics of the modulating effects of actions on perception. The timing of the perceived stimulus compared to the action (*i.e.*, whether it appears during the planning phase of the action or during execution) should be an important determining factor of how motor and visual systems interact in the brain.

Table 2.1. Relationship between sensory information and concurrent motor plans and their consequent perceptual effects.

Sensory Information Compared to Motor Plan	Reported Perceptual Effect
Same	sensory information does not reach consciousness “action-blindness effect”
Similar	slow detection of stimuli, somewhat biased towards motor plan
Ambiguous	perception biased towards the direction of the motor plan
Different	quick detection of stimuli, no bias towards motor plans

More studies are needed to clarify how action and perception are linked in clinical populations. As described above there is a strong correlation between motor deficits and perceptual sensitivity in some clinical groups, but symptoms can be highly variable between individuals. Better understanding of how information flows between motor and perceptual areas would help to develop specific treatments for stroke patients or patients with severe motor disorders, such as cerebral palsy. Furthermore, it is still unclear in the developmental disorders literature whether an initial motor deficit leads to decreased perceptual sensitivity or the correlation is the result of complex interaction within the action-perception network (for an interesting paper on this issue see Pavlova et al., 2003).

2.4. Conclusion

In this review we have highlighted some of the existing literature on how our visual perception is unconsciously influenced by plans for action encoded in the motor system and reviewed the main theories applied to describe the action-perception link. Predictive theories, suggesting the existence of internal forward models and emulators, could best explain how information from the motor system can modulate perception. These theories claim that, during action observation and execution, we are constantly making predictions about the future and representing expected states in our sensory system. These predictions then modulate the way our brain processes the incoming sensory information to influence what we perceive. In this sense, action-modulated perception sheds light upon one of the core but silent mechanism of our brain: how we predict the future and how those predictions influence what we perceive and understand of the world around us.

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Chapter 3

Enhanced neural activity for unattended novel actions

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Abstract: The processing of actions for understanding others' goals and intentions is an important but seemingly automatic function. Even when attention is engaged elsewhere, we keep track of others' movements and unexpected changes in actions quickly grab our attention. Recent theories suggest that our brain does not just passively processes the motions around us, but also predicts the future states of our environment based on those actions. Here we used functional magnetic resonance imaging to investigate the effect of attention and prediction on neural processes of action observation. Specifically, we examined neural responses to novel and repeated actions when they were not the main focus of attention. Participants performed an attentionally demanding visual task under conditions of high and low perceptual load, while videos of object-directed hand actions were simultaneously presented in a repetition suppression paradigm. Repeated versus novel presentation of the agent, goal, or kinematics of the action resulted in attenuation of brain activity in bilateral inferior frontal, premotor, and inferior parietal brain regions. This widespread repetition suppression, for all action representations, was significantly greater when attentional resources for processing actions were most limited, that is, during high-load compared with low-load conditions. Crucially, this increased repetition suppression effect arose because neural responses to novel actions were enhanced under conditions of high load. Our data suggest that the processing of novel action properties compared to repeated ones are prioritised, particularly when attentional resources are limited. We suggest that this may serve as a mechanism to facilitate perception of novel or changed actions when those actions occur outside the focus of attention.

Keywords: action observation; attention; fMRI; predictive coding; action perception; repetition suppression

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3.1.Introduction

Understanding others' actions is a crucial skill in life. We are quick to make predictions about the goals and intentions behind actions, while not always being consciously aware of the underlying processes leading to these predictions. In an everyday situation, such as chopping ingredients for dinner, we keep track of what others are doing around us despite the attentionally demanding task of handling the knife. Although our attention may seem fully focussed on the task at hand, it is also clear that our brain processes a vast amount of information outside of our focus of attention. From time to time our attention is grabbed by salient events that can signal threat, danger, or simply something that we do not expect. Attention and expectation or prediction are key forces that shape action processing, however little is known about how they interact on a neuronal level during action observation. Our main aim here was to investigate how observed actions are processed when they are outside of our attentional focus. Furthermore, we examined predictive mechanisms by manipulating the novelty of action properties to investigate how attention and prediction interact during action observation.

The perception and understanding of observed actions and the processing of biological motion have been considered a fundamental function of our brain because of their importance in our everyday life. Actions, especially when they are novel or unexpected, can convey crucial information for our successful navigation in the world and in our day-to-day interactions with others. Because of its apparent effortlessness, the processing of biological motion is often considered automatic, that is independent of attentional modulation (Blake & Schiffrar, 2007; for a recent review on attention and biological motion processing see Thompson & Parasurman, 2012).

The discovery of *mirror neuron*s has led to theories regarding direct and automatic neural processing of action-related sensory information. Mirror neurons are cells that discharge during execution and observation of the same motor act (Di Pellegrino et al., 1992; Gallese et al., 1996). As these neurons represent a clear connection between action-related visual information and motor knowledge, they are hypothesised to be engaged automatically and necessarily for action understanding (Rizzolatti & Sinigaglia, 2010). The observation of even the simplest movements involves the recruitment of a network of brain areas that are collectively known as the *action observation network* that includes regions of the lateral occipital cortex (LOC), the superior temporal sulcus (STS), the middle and superior temporal gyri (MTG, STG), the inferior parietal lobule (IPL), inferior frontal gyrus (IFG), and the dorsal and ventral premotor cortex (PMd, PMv) (Grafton & Tipper, 2012; Grosbras et al., 2012; Molenberghs et al., 2012a). Specific regions of the action observation network, consisting of the IPL, IFG, and PMv, have been commonly referred to as the *mirror neuron system,* based on mainly indirect measures suggesting the existence of mirror neurons in those areas (Chong et al., 2008; Kilner et al., 2009; Kilner & Lemon, 2013; Gazzola & Keysers, 2009).

More recently, studies have questioned the assumption that the mirror system is engaged automatically to process observed actions. According to *dual process theories*, automatic processing requires very little if any attentional capacity, while consciously controlled processing relies heavily on attentional resources (Styles, 2006). Given that attentional resources have limited capacity (Lavie, 1995; Tombu & Jolicœur, 2003), a very effective way to examine automaticity of neural processing is to load cognitive or attentional resources with a demanding secondary task and thereby limit the available attentional resources that could "spill over" to process observed actions.

While some fMRI studies have shown no change in action processing under attentional load and argued for the automaticity of action processing (Hamilton & Grafton, 2007; Jastorff et al., 2010), there is growing literature describing attentional modulation of action processing (Chong et al., 2008; Molenberghs et al., 2012b; Pavlova et al., 2006; Safford et al., 2010; Thornton et al., 2002). For example, Chong et al. (2008) showed that neural responses to observed actions in the IPL and STS were unaffected by attentional load, but activation of the IFG decreased significantly under high load when attentional resources for processing observed actions were most limited. Overall, previous studies suggest that the effect of attention on neural responses to observed actions are not consistent across the whole action observation network, but reliance on attention for action processing differs in different brain regions, possibly underling different aspects of action perception.

Additional to these effects of attention, it has recently been proposed that anticipatory or predictive mechanisms are also crucial processes in the brain that underlie action perception (Friston, 2005, 2010). Predictive theories of action understanding claim that during action observation we constantly make predictions about the possible goals and intentions behind the action, as well as its sensory consequences (Csibra, 2007; Friston, 2010; Halász & Cunnington, 2012; Kilner et al., 2007; Kilner, 2011; Wilson & Knoblich, 2005). When sensory events meet our predictions the brain allocates limited resources for processing them, to maintain an efficient energy state. However, when there is a mismatch or conflict between the predicted and observed states, the new and unexpected information leads to enhanced neural processing (prediction error) that helps us to adapt our internal model to the changed circumstances. In our example of chopping ingredients, predictive theories would suggest that we rapidly become aware of unexpected actions of others, even when our attention is focused strongly on our own task at hand, because we are implicitly making predictions about others' actions and rapidly detect violations of those predictions for enhanced processing.

An experimental paradigm that allows us to examine predictive mechanisms and their role in action processing is a technique known as fMRI *repetition suppression.* Repetition suppression is based on the principle that repeated exposure to the same stimulus results in a reduced fMRI BOLD signal in brain regions that are sensitive to that specific stimulus (Grill-Spector et al., 2006; Krekelberg et al., 2006). Traditionally, repetition suppression has been assumed to reflect neural fatigue, whereby neurons that have just fired in response to a stimulus fire less when that same stimulus is repeated. More recent studies, however, suggest that repetition suppression partially arises from predictive mechanisms (Friston, 2005, 2010; Friston et al., 2006, 2011; Kovács et al., 2012; Larsson & Smith, 2012; Summerfield et al., 2008). Predictive coding theories suggest that anticipatory mechanisms during action observation operate to predict and represent future states in both motor and perceptual areas (Halász & Cunnington, 2012; Kilner et al., 2007). When an unexpected or novel stimulus occurs, rather than a repeated one, this triggers a “prediction error” and consequently enhances neural processing (Friston, 2005, 2010). Based on this logic, the relative expectation of a given stimulus should determine the magnitude of repetition suppression; indeed, this effect has been reported in several recent experiments (Andics et al., 2013; Kovács et al., 2012; Larsson & Smith, 2012; Summerfield et al., 2008).

For predictive models of action perception, it is important to consider what constitutes novel or unexpected actions and the precision with which predictions of future states arising from observed actions can be formed. In general, through predictive processes, we learn and constantly update a model of the world in which the rules and regularities of our environment are quickly acquired, allowing us to flexibly interact with the world in an adaptive manner (Fiser et al., 2010; Engel et al., 2001). The precision of predictions of future states therefore depends very strongly on context and prior learning (Friston, 2005; Hohwy, 2012; Kok et al., 2013; den Ouden et al., 2012). In the present paradigm, novel and repeated actions were presented randomly and thus there was no regularity with which to form predictions of future actions. In general, in our prior life experience of observing others’ actions, we do not expect action properties such as agency or goals to change from one instant to the next, as our external world is relatively stable over short timescales (Koster-Hale & Saxe, 2013; Wacogne et al., 2012). Furthermore, in the action sequence used in this study, with many possible and equally likely alternatives for a “changed” action, no precise sensory prediction of a novel action could be formed. In this sense, novel actions can be considered “unexpected” as predictive processes cannot represent expected future sensory states for novel actions in this paradigm.

In the present experiment we aimed to examine repetition suppression to observed actions as a marker of implicit predictive processes during action observation. Specifically, we aimed to assess repetition suppression to observed actions that are not attended. Previous studies have not examined repetition suppression to *unattended* stimuli; however, detection of novel stimuli outside the focus of attention is well-described in the phenomenon of *mismatch negativity*. Mismatch negativity (MMN) is an enhanced neural signal that arises in response to a novel or deviant stimulus even when not attended. MMN is a component typically measured with electroencephalography that is thought to reflect an automatic, pre-attentive change detection mechanism (Näätänen, 1990). While most commonly examined in response to auditory stimuli, MMN has also been shown in sensory modalities of vision (Czigler et al., 2002; Czigler, 2007; Kimura et al., 2011; Kimura, 2012; Pazo-Alvarez et al., 2003), somatosensation (Akatsuka et al., 2007; Kekoni et al., 1997; Restuccia et al., 2007), and olfaction (Krauel et al., 1999; Pause & Krauel, 2000). Current theories of the mechanisms underlying MMN emphasise its reliance on cortical predictive processes (Garrido et al., 2009a, 2009b; Wacongne et al., 2012). In the context of action observation and repetition suppression, based on predictive processes involved in MMN, we might expect novel compared with repeated actions to elicit greater neural responses even when unattended.

Previous studies of action observation have examined repetition suppression, but rarely to unattended actions and never in the context of predictive processes for action understanding (e.g. Halász & Cunnington, 2012; Kilner et al., 2007). Most studies have used repetition suppression as a tool to separate different aspects of action representation such as goals, kinematics, and agency (Hamilton & Grafton, 2007, 2008; Kable & Chatterjee, 2006; Majdandžić et al., 2009; Ramsey & Hamilton, 2010a, 2010b; Wiggett & Downing 2011). Only a few studies have controlled or manipulated attention during repetition suppression. For example, in the study of Hamilton and Grafton (2008), participants attended to one specific aspect of the action (e.g., the action goal) while repetition suppression was examined to the unattended aspects of the action (e.g., the action kinematics). The authors reported no effect of attention on repetition suppression and concluded that repetition suppression "... is unrelated to visual attention or cognitive factors, but is an obligatory part of processing action information" (Hamilton & Grafton, 2008, p.396). In a similar study, Majdandžić and colleagues (2009) showed that repetition suppression during action observation is modulated by attention. In their experiment, participants attended to the outcomes and kinematics of observed actions by reporting if the actor violated pre-set rules regarding either aspect. They found repetition suppression for these two attended aspects of actions but not for a third unattended factor of movement trajectory, suggesting that certain aspects of action might require attentional focus to be processed.

More broadly, studies focusing purely on the visual system have supported the idea that attention can modulate repetition suppression (Eger et al., 2004; Murray & Wojciulik, 2004). In particular, Eger et al. (2004) showed no repetition suppression for unattended objects, whereas Murray and Wojciulik (2004) reported that the magnitude of repetition suppression depended on the degree to which stimuli were attended. Overall, the literature is mixed on whether repetition suppression is dependent on or modulated by attention, and suggests that stimulus complexity and salience might be important factors during the processing of novel and repeated visual stimuli.

Importantly, attention and predictions modulate neural activity quite differently and little is known about how they interact at the neuronal level (Summerfield & Egner, 2009). It is well known that attention facilitates behavioural performance and heightens neural responses in those sensory regions relevant to the attended stimuli (Chelazzi et al, 1993, 1998; Kastner et al., 1999; Spitzer et al., 1988; Yeshurun & Carrasco, 1998; Treue & Martínez Trujillo, 1999). Predictive mechanism appear to have an opposite effect whereby neural responses are suppressed to expected sensory stimuli and increased to unexpected or novel stimuli (Grill-Spector et al., 2006; Summerfield et al., 2008; den Ouden et al., 2010; Todorovic et al., 2011; Todorovic & de Lange, 2012). In many experimental paradigms, attention related effects and expectation related effects are conflated, and there are few studies that control these factors to explore how they shape neural responses (Summerfield & Egner, 2009). One exception is the study of Kok and colleagues (2012) whom orthogonally manipulated attention and prediction in an fMRI experiment focusing on early sensory visual areas. Their results indicated that there is a strong interaction between attention and prediction, whereby attention can reverse the attenuating effect of prediction on expected stimuli to improve the precision of perceptual inference (Kok et al., 2012). How factors of attention and prediction interact for action understanding, particularly in the context of relatively common repetition suppression effects in fMRI, is not known.

In the present study we use a repetition suppression paradigm to examine neural responses to novel compared with repeated presentations of action goals, kinematics, or agency. We follow closely the paradigm of previous studies of repetition suppression (Hamilton & Grfton, 2007, 2008; Ramsey & Hamilton, 2010a, 2010b), which allow us to independently manipulate the aspects of observed actions that are repeated or novel. As a secondary aim, this also allows us to examine whether attentional load differentially affects the neural processing of the specific action features of goals, agency, and kinematics. Crucially, participants also performed an attentionally demanding perceptual discrimination task in the periphery, under conditions of high and low attentional load, to limit the attentional resources that could be directed to the non task-relevant action videos. We therefore specifically examined effects of attention on neural responses to novel and repeated action properties in order to examine the role of attention in predictive processes for repetition suppression. Based on recent predictive coding theories of action perception (Halász & Cunnington, 2012; Kilner et al., 2007), and implicit predictive mechanisms suggested to underlie mismatch negativity (Garrido et al., 2009a, 2009b; Wacongne et al., 2012), we might expect enhanced neural responses to novel action properties even when those actions are unattended.

3.2. Materials and methods

3.2.1. Participants

Twenty healthy, young volunteers took part in the study, ranging in age from 18 to 40 years. Three participants' data were discarded, one because of scanner failure, and two because of excessive head movement during the scans, leaving a final dataset of 17 participants (M = 24.8, SD = 5.9 years; 6 males). All participants were right handed, had normal or corrected to normal visual acuity, and no history of mental or neurological diseases. Participants gave informed consent and received $20 as a reimbursement. Approval for this study was granted by The University of Queensland Medical Research Ethics Committee.

3.2.2. Stimuli and procedure

Sets of video-clips depicting simple, object-directed hand actions were presented in a pseudo-random order (Figure 3.2). In order to measure repetition suppression, video-clips were arranged such that each video depicted an action in which the goal, the movement kinematics, or the actor/agency were either novel or repeated relative to the immediately preceding video. Participants concurrently monitored two streams of crosses presented on either side of the video clips and detected target crosses in both high-load and low-load versions of the attentional load task (Figure 3.3). Experimental data was collected in the same session as for the experiment described in Chapter 4, but task order was counter-balanced between participants.

3.2.2.1. Video clips and one-back repetition suppression paradigm

Video-clips were created depicting either a male or female hand (agency), acting either to open or to close a book or a pencil case (goals), and moving with either fast or slow speed (kinematics) (see Figure 3.1). The actors wore a black tight-sleeved shirt so that only their hands below the wrist were visible. Every video-clip was edited so that it showed only the right hand and forearm reaching into the frame and then either opening or closing the book or pencil case. Importantly, the goals of both opening and closing the object were shown with similar kinematics of actual hand movement and grasp, thereby allowing the independent manipulation of goals and kinematics. We carefully matched the actions filmed in the video-clips so that all actions were as similar as possible between actors and goals.

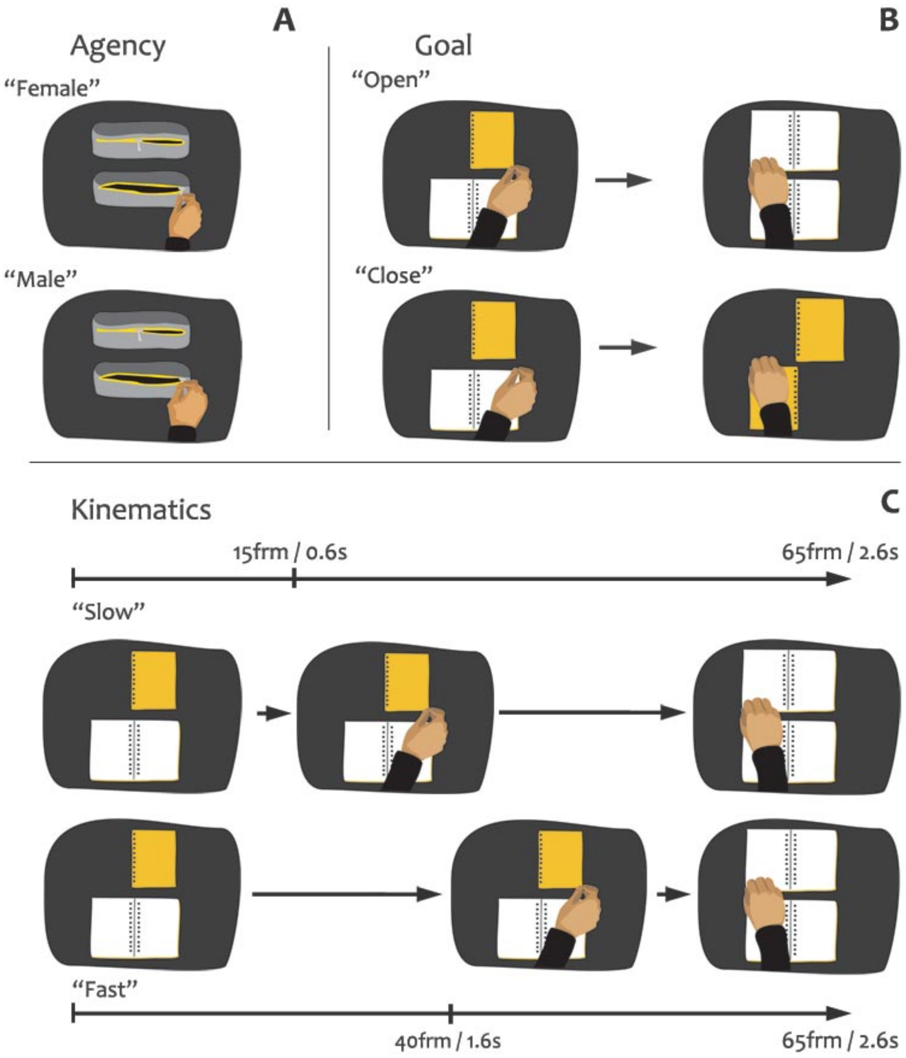

Figure 3.1. Schematic of the three repetition suppression conditions. **A|** Agency, showing "female" and "male" hands; **B|** Goals, showing "open" and "close" actions; **C|** kinematics showing "slow" and "fast" movements when interacting with the objects.

For agency, two hand-actors were selected, one male and one female. They were specifically chosen so that, even when only their hands were visible in the clips, they could be clearly identified as male or female, allowing participants to recognise the different agency between the clips. We specifically kept these two actors constant throughout the practice trials and experiment paradigm to build a sense of real agency for recognition of the hands rather than having participants focus on low-level visual differences between hands. For goals, actions depicted either opening or closing of the book or pencil-case object. For all clips, two examples of the same object were shown: in the case of books, one open and one closed; in the case of pencil cases, one closing to the left and one closing to the right. This manipulation prevented participants from judging the nature of the action (opening or closing) purely based on the objects shown prior to the actions. Video clips then depicted the hand reaching in to either open or close one of the objects. The position of the open/closed objects, whether they were at the top or at the bottom of the screen, and the object that the action was directed toward were counterbalanced throughout. For movement kinematics, two distinct profiles of movement speed throughout the reach and object interaction were created by video-editing software (Adobe PremierePro). In half of the videos, the hand approached slowly toward the object then acted quickly upon it. In the other half of videos, after a quick approach the hand acted slowly upon the object. These two levels of movement kinematics were named "fast" and "slow", referring only to the part of the movement when the hand manipulated the object.

All videos were edited so that they consisted of exactly 65 frames (2.6 seconds) from the point when the hand first appeared in the video until the movement on the object was completed. In the "fast" condition, the action on the object lasted for 25 frames (1 second), whereas in the "slow" condition the action lasted for 50 frames (2 seconds) (See part (c) of Figure 3.1). The aspect ratio of the video clips was 640x480 pixels. Altogether, 32 videos were created as follows: 2 objects (book, pencil case) x 2 actors (female, male) x 2 goals (open, close) x 2 types of kinematics (slow, fast) x 2 object-positions (top, bottom).

A one-back repetition suppression paradigm was used (Hamilton & Grafton, 2008), as shown in Figure 3.2. Every video-clip was defined as either novel or repeated for agency, kinematics, or goals compared with the immediately preceding stimulus. For example, if the first clip depicted the female hand opening a book and the second depicted the female hand closing a book, the second stimulus would be coded as repeated agency (for the female hand repeated) but novel goal (for “closing” after previously viewing “opening” goal). In this way every video clip was both a prime for the following video clip and a target in the repetition suppression analysis.

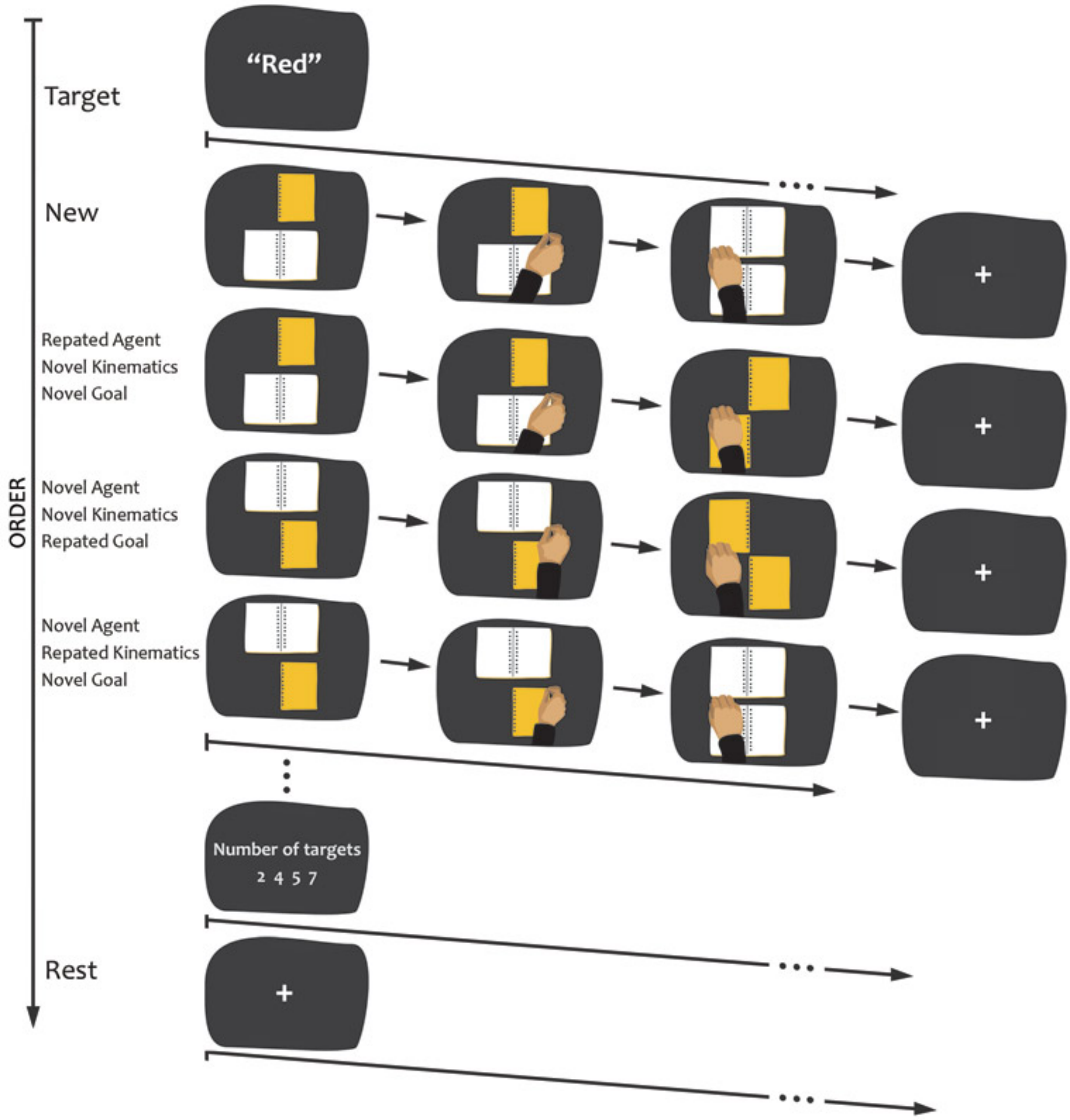

Figure 3.2. Experiment time course in a block of the repetition suppression paradigm. Every block started with the presentation of the word indicating the target cross for the attentional task, followed by a series of video clips. Video-clips were defined as either novel or repeated for agency, kinematics, or goals compared with the immediately preceding stimulus. Following the series of video clips, participants were prompted to indicate the number of target crosses detected in the attentional task.

Between 13 and 16 video clips were shown consecutively within a block, with a 400 ms blank screen between clips (39 to 48 s duration). Each fMRI run contained 10 blocks, with 15 s rest between blocks. Videos were shown in a pseudo-random order based on the one-back repetition suppression paradigm in which each of the videos was defined as novel or repeated relative to the previous video clip. During every block there were five repetitions of each of the conditions (agency, kinematics, goal), and the remaining video clips were always novel compared with the previous one. Object type was counterbalanced across blocks, while actors, kinematics and goals were counterbalanced within a run. The first video in each block was always excluded from analysis, as there was no previous video for it to be compared against. Altogether 128 video clips were presented in each fMRI run, so that every video clip was presented equally often (4 times) during one run. The order of blocks within the run was randomised, such that block-order was unique for every participant. The entire experiment consisted of two fMRI runs.

3.2.2.2. Attentional load task

As participants passively viewed the centrally presented action videos, they also performed high- and low-load versions of an attentional task, which involved them monitoring stimuli presented concurrently in 2 streams on both the left and right of the videos (Figure 3.3A). The stimuli for the tasks consisted of crosses that were coloured and either in an upright or inverted orientation. Different crosses were presented in the left and right streams at a rate of one every 1200 ms. The number of presented crosses was adjusted to the length of the block.

Participants were required to monitor the streams and to count the number of target crosses within each block, under both high- and low-load conditions. In the low attentional load condition, participants were asked to count the number of red crosses for each stream. In the high attentional load condition participants counted the number of upright yellow and inverted blue crosses (see Figure 3.3) (Kamke et al., 2012; Schwartz et al., 2005). Attentional load conditions were varied between blocks, with an instruction presented at the beginning of each block to indicate to participants which targets to count – for example: "red" or "up-yellow & down-blue".

The targets appeared pseudo-randomly within the sequence and care was taken that participants could not guess or anticipate their timing or left/right location within the streams. Also, streams of crosses were identical in high- and low-load conditions, so visual stimuli were perfectly matched between conditions. Between zero and six targets were presented in each block. At the end of each block, a response screen was presented with the text "Number of targets:", followed by four possible number options. Participants indicated their responses by pressing one of four buttons, corresponding to the number of targets they had counted during the block.

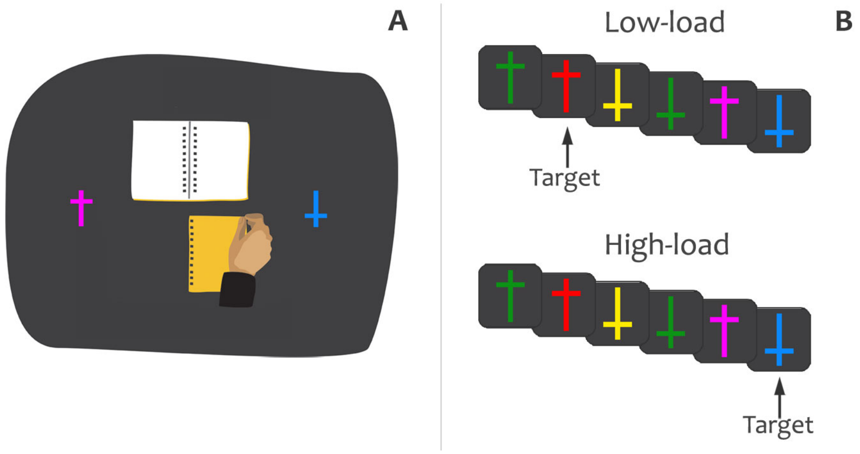

Figure 3.3. High and low load attentional task. **A|** Streams of crosses were concurrently displayed to the left and right of the video clips of the hand actions. Participants monitored the streams to count targets in high- and low-load versions of the task. **B|** Examples of low-load (target: "red" cross) and high-load streams (target: "upward yellow or inverted blue").

3.2.3. fMRI data acquisition

The fMRI data were collected using a 3-Tesla Siemens Trio MRI scanner with a 32-channel headcoil. During the fMRI acquisition participants lay supine with their head supported in a volume coil. The stimuli were presented on a screen at the head end in the bore of the scanner and viewed by participants via a mirror that was mounted on the head coil. Functional images were acquired using gradient-echo echo-planar imaging (EPI) sequence with the following parameters: 30 horizontal slices (3 x 3 mm in-plane voxel resolution and 3 mm slice thickness plus 10% gap), repetition time (TR) 2.31 s; echo time (TE) 40 ms. Two identical fMRI runs of 325 images (12 min 30 s) each were acquired. The first three TR periods from each run were discarded to allow for steady-state tissue magnetization. A three-dimensional high-resolution T1-weighted image covering the entire brain was also acquired and was used for anatomical reference (TR= 1700, TE=3.91 ms, FA=15°, 192 cubic matrix, voxel size =1.2 cubic mm).

3.2.4. fMRI analyses

Data were processed and analysed using SPM8 (Wellcome Department of Imaging Neuroscience, Institute of Neurology, London; http://www.fil.ion.ucl.ac.uk/spm), implemented in Matlab. EPI images were slice-time corrected to the middle slice acquired in time (Sladky et al., 2011) and spatially realigned to the middle image of each run for movement correction using a least-squares approach and six-parameter rigid body spatial transformations (Friston et al., 1995). Structural images were co-registered to the mean of the realigned functional images and then an inbuilt unified segmentation routine of SPM8 was applied to register the structural T1 image to the standard MNI template. The transformation parameters created by segmentation were then applied to all of the realigned functional images, subsequently resliced to 2 x 2 x 2 mm resolution and smoothed using a 7-mm full-width-at-half-maximum isotropic Gaussian filter.

An event-related approach was used to analyse the time series in a general linear model. At the single-subject level, onsets of the target words at the start of each block, onsets of each of the videos, and onsets of the end-of-block responses were modelled separately, convolved with the canonical hemodynamic response function of SPM8. Motion correction parameters from the pre-processing were also included the models. For the video-clips, the first video of each block was modelled separately and not included in any subsequent contrasts. The rest of the videos were modelled as 12 separate conditions (regressors) accordingly to a 2 x 2 x 3 design, with levels of attentional *load* (high, low), *repetition* (novel, repeated), and *action representation* (agency, kinematics, goals). All videos were modelled with duration of 2.6s, which corresponded with the duration of the video clips. The duration of the end-of-block response regressor was adjusted based on individual reaction times. The periods during the resting phase between blocks were considered as baseline and were not explicitly modelled.

For second-level random-effects analysis, we took the 12 single-condition contrasts from the first-level analysis and created a 3 x 2 x 2 full-factorial model with *action representation* (agency, kinematics and goals), *attentional load* (high-load and low-load) and *novelty* (novel and repeated trials) as the main factors. Given the complexity of this design, we only analysed selected main effects and interactions based on a priori hypotheses. As our aims were specifically to examine repetition suppression effects and their modulation by attention, we examined only main effects of *novelty* and the interactions between *novelty* and *action representation*, and between *novelty* and *attentional load*. Specific contrasts for these main effects and interaction analyses are outlined in the results section below.

We created a mask for "all-action" by combining the positive activation for novel and for repeated action videos (using the voxel-level threshold $P < 0.05$). This mask represented all brain areas showing positive activation when viewing action videos compared with the implicit resting baseline, regardless of action representations, attention or novelty conditions. By applying this mask to all contrasts from the second-level factorial model, we ensured that all reported areas showed positive activation when viewing action videos. For all contrasts, significant activation was defined by a cluster-level probability threshold of $P_{FWE} < 0.05$, corrected for the masked search volume (with clusters defined by the voxel-level threshold $P < 0.001$).

3.3. Results

3.3.1. Behavioural results

Overall participants scored well above chance (25%) in both the high-load and low-load conditions of the attentional load task (Figure 3.4). Mean percentage of correct answers (counting the number of targets) was significantly less in the high-load condition (70%, SD=0.24) than in the low-load condition (89%, SD=0.19; t(16)=3.224, p<0.05), showing that the high-load condition was indeed more difficult for participants.

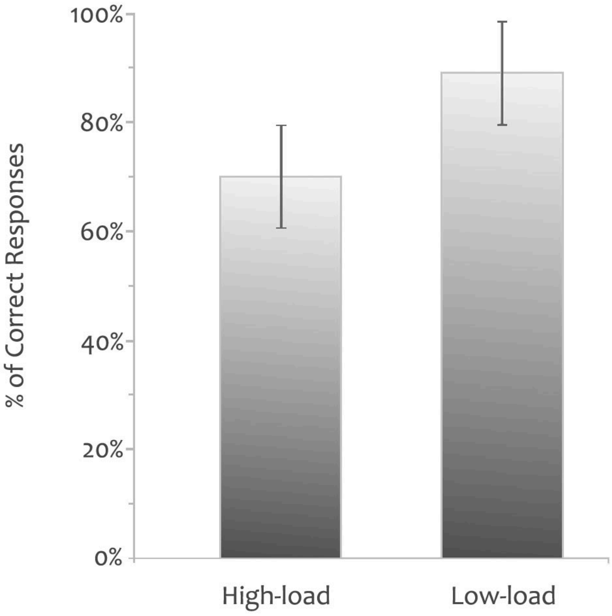

Figure 3.4. Mean percentage of correct responses (with standard error bars) in high- and low-load conditions of the attention task.

3.3.2. fMRI results

3.3.3.1. Repetition suppression across all conditions

We first identified the brain network that showed repetition suppression for repeated compared with novel actions, irrespective of attention or action representation conditions (i.e.: main effect of *novelty*, representing novel vs. repeated actions across all action representations and attentional loads). We found overall repetition suppression in a wide network (Figure 3.5). This pattern is consistent with previous reports of the action observation network, including significant repetition suppression in the lateral occipital cortex, inferior parietal cortex, the superior temporal sulcus, middle and superior temporal gyri, the inferior frontal gyrus, and dorsal and ventral premotor cortex. Repetition suppression was widespread in the supplementary motor area, as well as in midline and subcortical structures including the cingulate cortex, the thalamus, and the basal ganglia.

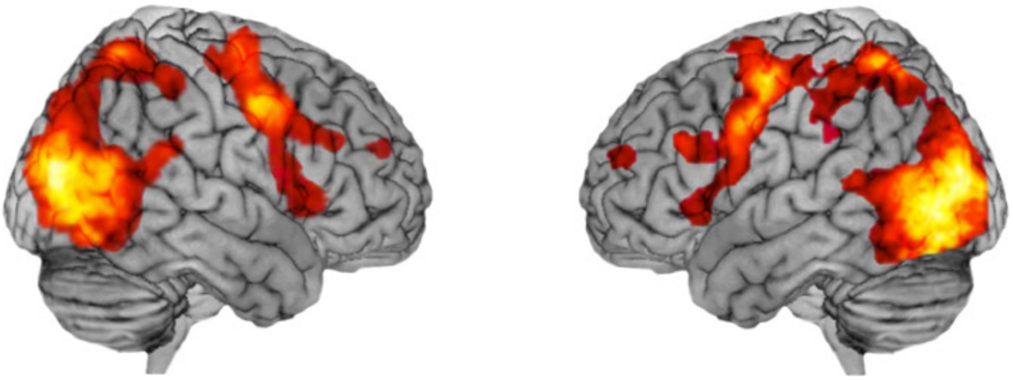

Figure 3.5. Brain areas showing overall repetition suppression, regardless of attention or action representation. These areas showed less activation for repeated compared with novel actions when averaged across repetitions of goals, kinematics, and agency, and both high- and low-load conditions.

3.3.3.2. Repetition suppression for goals, kinematics, and agency

To determine whether repetitions of different action properties showed different responses within the action observation network, we examined interaction effects between *novelty* and *action representation*. To do this, we contrasted repetition suppression effects for each action property against the other two action properties, averaged across attentional conditions (i.e., repetition suppression for goals versus agency and kinematics, repetition suppression for agency versus goals and kinematics, and repetition suppression for kinematics versus goals and agency, each calculated separately). No significant differences in repetition suppression were found in any of these interaction contrasts. Investigating the same interaction contrasts for high and low attentional load conditions separately also yielded no significant activation. This indicates that, although significant and widespread repetition suppression was found for observed actions overall, this effect did not change significantly depending on which aspect of the action was repeated. Because we found no activation differences specific to the different action representations (goals, kinematics, agents), for all subsequent analysis we combined contrasts across these action representations.

3.3.3.3. Effect of attention on repetition suppression

Next, to determine whether repetition suppression was influenced by attentional load, we investigated the interaction effects between *novelty* and *attentional load* conditions. To do this, we contrasted repetition suppression effects for high-load compared with load-load attentional conditions, averaged across action representations (i.e. novel vs. repeated for high-load compared with novel vs. repeated for low-load). Comparison of repetition suppression effects for low-load >

high-load conditions showed no significant differences. This indicates that repetition suppression effects were not *reduced* under high-load, when attentional resources available for processing observed actions are more limited. However, the comparison of repetition suppression for high-load > low-load (i.e., *greater* repetition suppression when attentional resources were more limited) showed significant effects in regions of the right superior parietal lobe, and in the left inferior frontal lobe and premotor cortex (Table 3.1, Figure 3.6).

To specifically examine whether these changes in repetition suppression arose from changes in activation to novel trials or to repeated trials with varying attentional load, we extracted the mean parameter estimate values from 5 mm radius spheres centred on these peaks and analysed by paired t-tests, comparing activation for high-load versus low-load separately for novel trials and for repeated trials (note that these comparisons are orthogonal to the contrast used to select the peaks for analysis and thus avoid any circularity; Kriegeskorte et al., 2009). As shown in Figure 3.6, the larger repetition suppression effect during high-load compared with low-load was the result of two factors: first, there was significantly greater suppression of the BOLD signal to repeated actions during high-load compared with low-load (rSP: t(16) = -2.208; lPc: t(16) = -3.163; lIF: t(16) = -3.197; all $p<0.05$); second, there was a significantly greater neural response to novel actions under high-load compared with low-load (rSP: t(16) = 3.402; lPc: t(16) = 5.065; lIF: t(16) = 4.496; all $p<0.05$).

Table 3.1.
Brain regions showing repetition suppression in high vs. low-load conditions (Anatomic locations of peaks are from the Anatomy Toolbox 1.8, Eickhoff et al., 2005).

Region	Anatomic location of peak	Number of voxels	T	P cluster corrected	MNI coordinates		
					x	y	z
R Parietal, sup.	SPL (7PC)	129	4.09	0.007	32	-50	52
L Frontal, inf.	Area 44	87	3.72	0.022	-42	6	24
L Precentral	Area 6	85	4.18	0.023	-32	-2	46

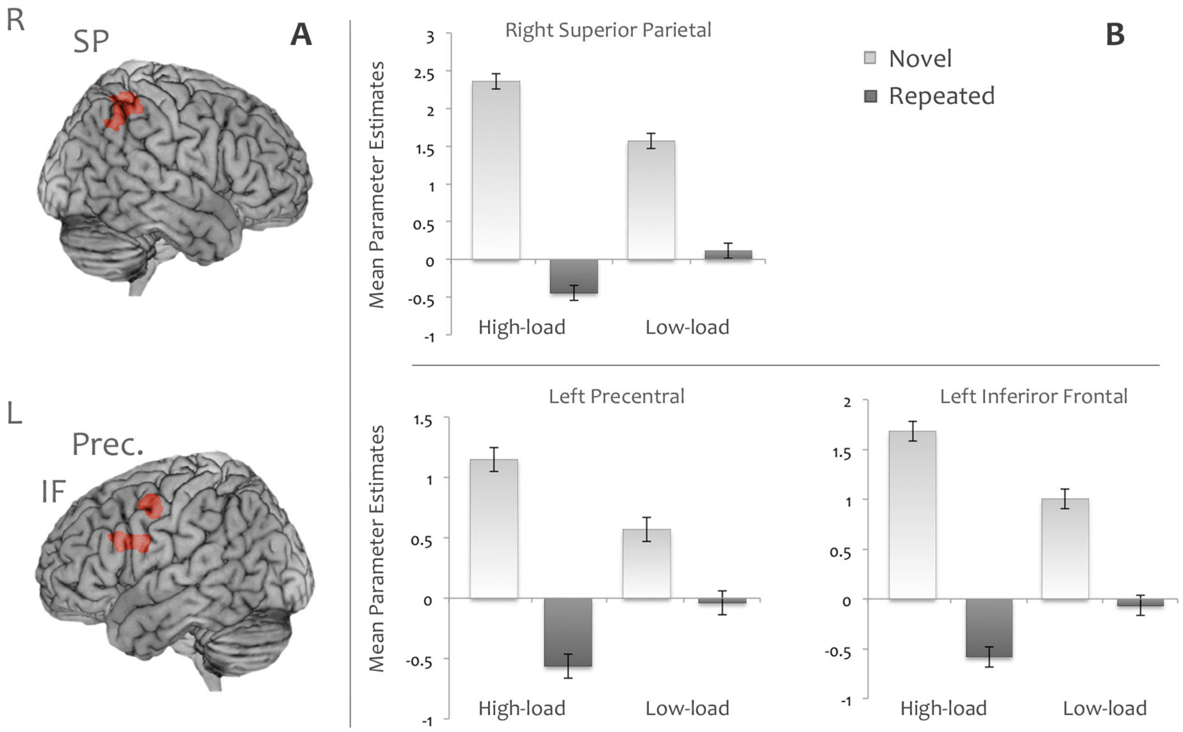

Figure 3.6. A| Brain areas showing stronger repetition suppression during high attentional load compared to low-load. **B|** Mean parameter estimates for right superior parietal (32 -50 52), left precentral (-32 -2 46), and left inferior frontal (-42 6 24) regions with standard error bars.

3.3.3.4. Effect of attention on novel and repeated actions

To further investigate the significant interaction between *novelty* and *attentional load,* we examined the effects of attention on neural responses to novel actions and to repeated actions separately. To do this, we contrasted high versus low attentional load conditions for novel trials and for repeated trials separately (i.e., high-load minus low-load for novel trials and its reverse; and high-load minus low-load for repeated trials and its reverse). From the four contrasts, the only significant effects found were greater activation for *novel actions* under high-load compared with low-load (i.e. when attentional resources for processing actions were most limited). This contrast showed significant clusters including the same peaks as those described above for effects of attentional load on repetition suppression, specifically involving the premotor cortex bilaterally extending to the inferior frontal gyrus pars opercularis and pars triangularis, and bilateral regions of the inferior parietal cortex extending towards the superior parietal lobe and postcentral gyrus (Figure 3.7, Table 3.2).

Table 3.2.

Brain regions showing significantly larger BOLD responses to novel actions under high-load compared with low-load conditions (Anatomic locations of peaks are from the Anatomy Toolbox 1.8, Eickhoff et al., 2005).

Region	Anatomic location of peak	Number of voxels	T	P cluster corrected	MNI coordinates		
					x	y	z
L Precentral	Area 6	694	5.07	< 0.001	-32	-2	48
Frontal, inf., tri.	Area 44		4.03		-34	16	24
R Precentral	Area 44	479	4.66	< 0.001	52	6	34
Precentral	Area 6		3.93		34	-2	48
R Parietal, sup.	SPL (7A)	529	4.76	< 0.001	32	-52	50
Parietal, sup.	Area 2		3.68		34	-40	48
L Parietal, sup.	SPL (7PC)	519	4.51	< 0.001	-30	-48	48
Parietal, sup.	SPL (7A)		4.16		-28	-70	30

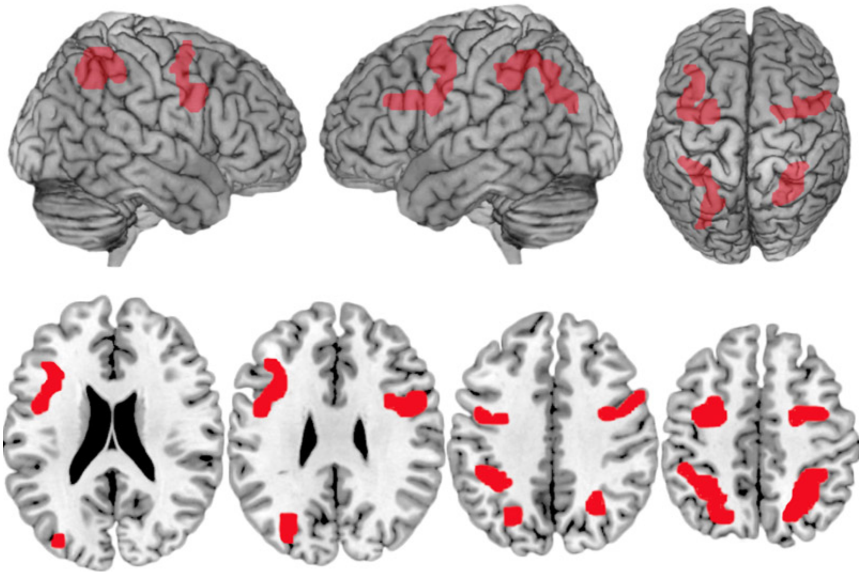

Figure 3.7. Brain areas showing significantly greater activation for novel actions during high attentional load compared with low-load (i.e., when attentional resources for processing actions are limited). Results are rendered onto the surface of a template brain using SPM8 software and overlaid on axial template slices with MRIcron.

3.3.3.5. Representation of novel agency, kinematics, and goals under high-load

Finally, to examine whether the greater activation for novel actions under high-load differed depending on which aspect of actions were novel (agency, kinematics, or goals), we conducted a voxel-wise region of interest analysis on the bilateral precentral and inferior parietal clusters identified above, using small volume correction in SPM8. We contrasted novel trials for each action representation against the other two under high-load conditions only (e.g., high-load novel agency versus high-load novel kinematics and goals). No significant clusters were found within these regions for any of the contrasts. Finally, we extracted the mean parameter estimates for novel trials of the three action representations under high-load in the inferior parietal (left: -30 -48 48; right: 32 -50 52) and precentral areas (left: -32 -2 46; right: 52 6 32). No significant differences were found between action representations in any of these areas.

3.4. Discussion

3.4.1. Neural processing of unattended actions

We used fMRI and a repetition suppression paradigm to determine whether limiting attentional resources, under high and low attentional load conditions, modulates neural responses to observed actions. We found wide-spread repetition suppression in which repeated presentation of actions compared with novel presentation was associated with significantly lower BOLD responses, even when observed actions were not the focus of attention. This widespread repetition suppression involved occipito-parietal areas, motor and premotor regions, and inferior frontal regions (Figure 3.5), corresponding to regions typically associated with action-observation (Grosbras et al., 2012; Molenberghs et al., 2012a). Importantly, in the present study, we found repetition suppression when observed actions were relatively unattended. Even when participants were engaged in the most demanding high-load attentional task, leaving limited resources for the observed actions, there was widespread activation in action observation regions of the brain that systematically changed depending on whether specific aspects of the actions were repeated or novel. This suggests that, even when our attention is engaged elsewhere and we do not consciously attend to observed actions, a wide network of brain areas is still involved in their processing.

Repetition suppression to observed actions was also evident in midline structures including the medial prefrontal and cingulate cortex. These structures are often grouped together with the temporo-parietal junction, precuneus and the STS to form the "mentalizing network" or "theory-of-mind network", which is thought to be involved in higher-level action and intention understanding (Lieberman, 2007; Spunt et al., 2011; Uddin et al., 2007; van Overwalle & Baetens, 2009). Therefore, as well as the monitoring of actions when they fall outside the current focus of attention, it appears that areas linked to higher-order action understanding are also recruited even when attention is engaged elsewhere.

3.4.2. Repetition suppression and predictive coding

Overall, we found that the level of repetition suppression changed significantly with attentional load in the right parietal cortex and showed a similar trend (P_{FWE}=0.054) in the left inferior frontal and premotor cortex. Crucially, when we examined this effect in more detail, it was the neural responses to *novel* actions that increased with attentional load more than any change in activation to *repeated* actions (Figure 3.7; Table 3.2). This result does not fit with an account of repetition suppression caused by adaptation of neural firing or neural fatigue to repeated stimuli, as that theory would predict that the level of repetition suppression depends on the level of suppression of responses to repeated presentations. Instead, our results fit with a predictive theory of action understanding whereby predictive mechanisms monitor for changes in the attributes of observed actions and enhance processing for novel actions or when some aspect of the observed actions changes (Csibra, 2007; Friston, 2005; Halász & Cunnington, 2012; Kilner et al., 2007; Wilson & Knoblich 2005). Further, this enhanced activation to novel actions, even under high attentional load, fits with the theory that these predictive mechanisms for detecting novelty-related changes are relatively automatic processes of our brain and do not rely on focussed attention (Friston, 2010).

3.4.3. Attentional load and the processing of novel and repeated actions

Specifically, with region-of-interest analysis, the change in repetition suppression we found with attentional load was the result of two factors. First, the suppression of neural responses to repeated actions was stronger under high-load than low-load. We suggest that when resources are available to process observed actions, repeated actions engage the action observation network; however, as attentional resources become more limited, this processing of (irrelevant) repeated actions is suppressed.

Second, novel actions elicited greater neural responses under high attentional load compared with low-load. These results were further investigated with whole-brain analysis of the effect of attention on neural responses to novel actions specifically, showing significantly greater activation for novel actions under high attentional load compared with low load in a bilateral network of premotor, inferior frontal, and inferior parietal regions. Chong and colleagues reported a similar pattern for high versus low attentional load, albeit more lateralized to the right hemisphere (Chong et al., 2008). These brain regions are also commonly considered as a part of an attentional system involved in the detection of salient or unexpected stimuli (Corbetta & Shulman, 2002). Corbetta and Shulman (2002) described a right ventral fronto-parietal attention network that shows increased activity to unexpected salient stimuli when they are outside the focus of attention. While our data does not show lateralization, parts of this ventral frontoparietal system, such as the inferior frontal gyrus, middle frontal gyrus and inferior parietal regions showed enhanced activation to novel actions during the high attentional load of the present experiment. According to Corbetta and Shulman (2002), this network is involved in the detection of unattended but highly salient stimuli and serves as an alert mechanism to reorient attention to stimuli of potentially high behavioural significance.

In previous studies, enhanced processing of an unattended stimulus under high load has been explained according to perceptual load theory (Chong et al., 2008; Jacoby et al., 2012; Tellinghuisen & Nowak, 2003; Lavie at al., 2004). Lavie and colleagues' load theory proposes that resources allocated for the processing of non-task relevant stimuli (in our study, the observed action videos) depend on whether the participants’ task loads perceptual or cognitive resources (Lavie, 1995; Lavie & Tsal, 1994; Lavie et al., 2004). They argue that under high perceptual load the processing of non-task stimuli is suppressed, as there are insufficient perceptual resources remaining for the processing of stimuli outside the focus of attention. By contrast, when a task heavily loads working memory, there are insufficient cognitive resources to (top-down) suppress processing of non-task relevant stimuli, and hence the processing of “distractor” stimuli (in our study, the observed action videos) increases as cognitive load on the primary task increases. This theory could explain our results if the target-detection task we used involved differing *cognitive* load; however, this commonly used task with differing colour/orientation crosses is considered to load perceptual resources rather than cognitive resources (Kamke et al., 2012; Schwartz et al., 2005). Load theory also cannot explain the increased neural responses specifically for *novel* actions, and not repeated actions, with increasing load. Our results suggest that there is an important difference in the way the brain processes novel and repeated actions.

Enhanced neural responses to novel stimuli outside the focus of attention are commonly reported and well-known in studies of visual MMN, with underlying neural sources largely overlapping with areas reported in the present experiment (Cléry et al., 2013; Kimura et al., 2010; Urakawa et al., 2010; Yucel et al., 2007). For example Cléry and colleagues (2013) reported that passive detection of infrequently occurring visual stimuli compared to repeated stimuli elicit greater neural responses in the superior occipital gyrus, middle temporal gyrus, superior and inferior parietal cortex, and anterior premotor /middle prefrontal areas. These same areas have also been implicated in change detection mechanisms across different sensory modalities (Bledowski et al., 2004; Corbetta & Shulman, 2002; Downar et al., 2001; Gur et al., 2007; Huettel et al., 2004). Importantly, recent studies also report attentional modulation of MMN (Kimura & Takeda, 2013; Parmentier et al., 2010; SanMiguel et al., 2010; Schomaker & Meeter, 2014; Wetzel et al., 2012;

Zhang et al., 2006). For example, in line with our results, Zhang and colleagues (2006) found that neural responses associated with MMN were enhanced with increasing load of a concurrent visual tracking task. Furthermore, Schomaker and Meeter (2014) reported that task-irrelevant novel visual stimuli can facilitate processing when the stimuli are complex relative to standard simple stimuli. These recent studies suggest that, in dual-task paradigms, increasing load on the primary task can facilitate or enhance processing specifically of novel rather than repeated unattended stimuli. Crucially, recent studies propose that predictive mechanisms also underlie generation of the MMN (Garrido et al., 2009a, 2009b; Wacongne et al., 2012). Wacongne et al (2012) provide compelling argument and evidence that the MMN results from active cortical predictions and, consistent with Garrido et al. (2009b), argue that the enhanced neural responses to novel stimuli seen in MMN represent a prediction error when novel or changed stimuli do not match the previously repeated stimuli. In the present experiment, we similarly propose that the enhanced neural responses we find for novel actions when attention is most engaged in the target-detection task arise from predictive processes that operate on stimuli outside the focus of attention. Our results further suggest that, when attentional resources are most limited, the neural processing of novel stimuli is prioritised over the processing of repeated stimuli that match predictions from previously repeated stimuli.

3.4.4. Action representations: Goals, kinematics, and agency

Previous studies reported repetition suppression that was specific for different action representations (Hamilton & Grafton, 2007, 2008; Kable & Chatterjee, 2006; Majdandžić et al., 2009; Ramsey & Hamilton, 2010a, 2010b; Wiggett & Downing 2011). We found no attenuated BOLD response that was uniquely correlated with the repeated presentation of the same agent, kinematics, or goal, at the whole-brain level or at the small-volume corrected level. We also extracted parameter estimates from bilateral regions of inferior parietal and precentral cortex that showed overall repetition suppression effects. There were no significant differences in repetition suppression for agency, goals, and kinematics in any of these regions.

Crucially, our study was different from all previous studies in that participants’ attention was directed away from the presented actions and engaged in a demanding secondary task. In previous studies participants' attention was either directed towards the actions in general (Hamilton & Grafton, 2008; Kable & Chatterjee, 2006) or focused on specific aspects of the actions (Hamilton & Grafton, 2007; Majdandžić et al., 2009; Ramsey & Hamilton, 2010a, 2010b; Wiggett & Downing 2011). It is possible that the lack of unique repetition suppression we found for goals, kinematics and agency was the result of the limited attentional resources available for processing specific aspects of the observed actions. Supporting this, Majdandžić et al (2009) showed specific repetition suppression only for those aspects of actions that were selectively attended, suggesting that specific representations of goals, kinematics, or agency may not be revealed when those aspects of the action are not explicitly attended. This is consistent with our results, suggesting that goals, kinematics or agency are not uniquely encoded when attention is not specifically directed toward actions. Future experiments are needed to elaborate on what we can *consciously* perceive from actions or action properties when our attention is focussed on another task. Our experiment measured only neural responses to unattended actions but as yet we do not know how this influences participants' perception or understanding of those actions.

3.5. Conclusions

It is not often in everyday situations that our undivided attention is focused solely on someone else's actions. We engage in dynamic social interactions in which there are many body movements occurring around us, or we may monitor others' movements while focussing attention on our own tasks or elsewhere. For example, we keep an eye on the kids in the back seat of the car while driving, and also manage to pay attention to our movements and to the actions and intentions of cyclists, joggers, or other drivers around us. In the present study we examined how the brain represents specific aspects of others' actions and intentions while attention is otherwise engaged. We found that the action observation network responds strongly to novel versus repeated observation of actions even when there are limited resources available to process them. Our data suggest that action understanding is a prioritised process in the brain and proceeds even when attention is focussed elsewhere. Despite this, we found that attention nonetheless influences the processing of observed actions. Neural responses to novel actions were enhanced under the most demanding attentional task, in which available resources for observed actions were most limited. We suggest that this allows early detection of novel or changed actions around us that are not predicted from the preceding events to maximize individual success in a rapidly changing and competitive environment.

Acknowledgment

This work was supported by funding of the Australian Research Council (DP110103285).

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Chapter 4

Attention and prediction influence the neural processing of observed actions

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Abstract: Whenever we observe an action, neural systems are engaged for processing the acting agent, the movement kinematics, and the possible goals and intentions behind the action. A well-described widespread network is active during action observation, involving inferior frontal, premotor, parietal, and occipital areas of the brain. However, the roles of different parts of this network for processing different aspects of observed actions and the influence of attention are still heavily debated. We used functional magnetic resonance imaging to investigate neural activation during action observation. Specifically, we examined how focused attention can influence the neural processing of observed action goals, kinematics, and agency. Participants observed short video clips of simple object-directed actions while they focused their attention on the acting agent, the goal, or the kinematics of the action. Videos were presented in a repetition suppression paradigm in which every action was coded as novel or repeated compared to the previously seen one with respect to the depicted goal, movement kinematics, or acting agent. Regardless of what aspect of the action was repeated, neural activity in the widespread action observation network showed a significant decrease for repeated compared to novel or unexpected action properties. This overall repetition suppression, however, was significantly influenced by attention in specific parts of the network. Attending to the acting agent resulted in greater repetition suppression bilaterally in the middle occipital area, including the fusiform gyrus. Attending to movement kinematics showed stronger repetition suppression in the right lateral prefrontal cortex around the insula and in the left inferior frontal gyrus. Attending to action goals elicited greater repetition suppression in the right postcentral gyrus, right superior occipital gyrus, left middle occipital gyrus, and in the left superior parietal lobule. Our results indicate that the action observation network is highly sensitive to the detection of novel action properties, and that attention can further enhance this sensitivity in areas of the network in which the attended features are processed. The present study sheds light on how attention and prediction, as two fundamental processes of perception, interact for the neural processing of observed actions.

Keywords: action observation, attention, predictive coding, agency, kinematics, action goals

4.1. Introduction

From the moment we open our eyes in the morning, our day is full of actions that we plan and execute ourselves, and that we observe, understand, and predict in others. Flawless interaction between sensory and motor areas is necessary for our own actions, just as for successfully understanding others' actions. While much is known about the extensive network active during both action execution and the perception of actions, we know little about how attention influences this network, despite the fact that attention is one of the most important modulating factors of human perception. Recent theories also highlight the importance of predictive processes during action understanding (Friston, 2010); however, our knowledge of these predictive mechanisms and their interaction with attention for action perception is still narrow. Here we aimed to investigate how focusing attention on the acting agent, to action goals, or to movement kinematics while observing actions can influence the neural activation related to the processing and perception of simple hand actions. Furthermore, we tested the neural response to novel and repeated action properties, in a repetition suppression paradigm, to investigate how predictive mechanisms during action observation are influenced by task relevance or attentional focus.

Quick and effective monitoring of actions around us, and the interpretation of the possible outcomes of a given action, are crucial for survival and successful social interactions. Consequently, the processing of observed actions is a robust mechanism involving a widespread brain network, known collectively as the *action observation network* (AON), involving inferior frontal, premotor, supplementary motor, inferior parietal and occipitotemporal regions of the brain (Caspers et al., 2010; Grafton & Tipper, 2012; Grosbras et al., 2012; Molenberghs et al., 2012). Previously, neuronal processing of observed actions, as with biological motion processing, was considered automatic and independent of attentional modulation (Blake & Schiffrar, 2007; for a review on attention and biological motion processing see Thompson & Parasurman, 2012). Emerging literature shows that attention can influence the neural processing of observed actions (Chong et al., 2008; Halász et al., 2014; Pavlova et al., 2006; Safford et al., 2010; Thornton et al., 2002). Furthermore, results suggest that different parts of the AON have different sensitivity to attentional modulation (Chong et al., 2008; Halász et al., 2014).

While the anatomical organisation of the AON is well studied, the functional organisation is still debated. Similarly to the motor system, the AON is thought to be organised in a hierarchical manner (Jeannerod, 1994; Kilner, 2011; Uithol et al., 2012; Grafton & Tipper, 2012; or for a review see Grafton & Hamilton, 2007). At the top of the motor hierarchy is an overarching goal or intention that must be achieved by completing sub-goals. These sub-goals are built from low-level motor commands and those movements are built from individual muscle activations. It is hypothesized that the action observation network has a similar hierarchical organization in which different aspects of actions (e.g. goals, kinematics, agents) are represented at different neural levels (Hamilton & Grafton, 2007).

Observed actions are information-rich stimuli and, as such, attentional focus is crucial to select and focus processing resources on the action representation that is important to us in any given situation. In most everyday situations, people tend to show a strong preference to interpret other's actions in relation to goals and intentions (Csibra & Gergely, 2007; Grafton & Tipper, 2012). In most cases, focus is on *why* a given action has been performed (goals) rather than specifically *how* the action has been performed (kinematics). Indeed, previous research has shown that memory recall is faster and more accurate for an observed action's goal compared to its kinematics (Baldwin & Baird, 2001, Loucks & Sommerville, 2013; Spunt et al., 2011). Because these different aspects of action representations are differently attended during normal action observation, the control of attention or task-relevance when observing actions should be vital in experiments focusing on the function of the action observation network.

A number of studies have investigated the different representations of actions within the AON and generally report that action goals are localized to the anterior parietal areas, action kinematics in occipitoparietal and inferior frontal areas, and agency in occipitotemporal and fusiform areas of the brain (Di Dio et al., 2013; Hamilton & Grafton, 2007, 2008; Kable & Chatterjee 2006; Majdandžić et al., 2009; Ortigue et al., 2009; Ramsey & Hamilton, 2010a, 2010b; Wiggett & Downing 2011). However, most earlier experiments have not controlled attention or task-relevance of the observed actions (Hamilton & Grafton, 2006, 2007; Ramsey & Hamilton, 2010a, 2010b). For example, in one experiment participants were asked to report if they noticed a stop in the videos (Hamilton & Grafton, 2008), or had to answer a question on every 9th video (Ramsey & Hamilton, 2010a). In the first case, participants only had to pay attention to whether there was movement on the screen versus a still image; in the second case, they could easily predict which video they had to attend and which they could ignore. Only one previous study has tested the direct effect of attention on the processing of different aspects of action representations. Hamilton and Grafton (2007) asked participants to observe and mentally perform simple object directed actions and required them to answer a question presented randomly after five to ten video clips that was related to a specific aspect of the action in the last video clip. Participants were allocated to one of four groups, and each group were asked questions that were related to different aspects of the action, such as the "object", the type of "grip", the "weight" or the "location" of the manipulated object. The authors reported no effect of task at all, but suggested that the manipulation of the attentional task was somewhat weak as participants were not told in advance about what aspects of action to attend during the task. It is also important to note that some conditions only had three subjects per group. Nonetheless, the control of attention to different aspects of actions by manipulating task relevance is an important avenue for research to understand function within the action observation network.

Importantly, many studies in this area of research have used a technique called *repetition suppression* to assess the functional localization of the AON (Di Dio et al., 2013; Hamilton & Grafton, 2007, 2008; Kable & Chatterjee 2006; Majdandžić et al., 2009; Ortigue et al., 2009; Ramsey & Hamilton, 2010a, 2010b, Wiggett & Downing 2011). Repetition suppression is based on the principle that repeated exposure to the same stimulus results in a reduced fMRI BOLD signal in brain regions that are sensitive to that specific stimulus (Grill-Spector, et al., 2006; Krekelberget al., 2006). Thus, comparing trials in which action goals or kinematics are repeated with trials in which they are new or novel should result in a decreased BOLD response in the population of neurons that uniquely code those specific action representations. Importantly, attention can be a modulating factor of the repetition suppression effect (Eger et al., 2004; Halász et al., 2014; Murray & Wojciulik, 2004). However, because the task relevance of different aspects of actions during action observation has generally not been controlled in previous repetition suppression experiments, our knowledge is limited on how attention to specific action properties can effect repetition suppression for actions.

Recent theories and studies on the origin of repetition suppression effects suggest that this phenomenon mainly arises from *predictive mechanisms* (Friston, 2005, 2006; Friston et al., 2010, 2011; Kovács et al., 2012; Larsson & Smith, 2012; Summerfield et al., 2008). According to predictive theories of action understanding, during action observation predictions are formed regarding the observed actor's goals, intentions, and the sensory consequences of the observed action. These predictive processes are suggested to be part of a universal brain mechanism that helps us to adjust our own motor behaviour to the dynamic environment, described under the free-energy principle (Friston, 2009, 2010). The core idea of the free-energy principle is a system that constantly updates predictions to tries to minimise its energy state by reducing the occurrence of "prediction error". In this case, prediction error is defined as an elevated neural response related to an unexpected or novel sensory state (Kilner et al., 2007). Repetition suppression is explained by predictive coding theories as follows: A repeated presentation of the same action leads to lower neural activation compared to a novel or unexpected goal, because the unexpected novel action leads to additional neural activation as a prediction error. Importantly, this line of argument predicts that the magnitude of repetition suppression should correlate with the relative expectation of a given stimulus, as indeed reported by several recent experiments (Andics et al., 2013; Kovács et al., 2012; Larsson & Smith, 2012; Summerfield et al., 2008).

Predictive theories and most notably the free-energy principle make predictions about how attention should modulate repetition suppression (Friston, 2005, 2009; Feldman & Friston, 2010). If we accept that the brain is using Bayesian principles to estimate or predict future sensory states based on incoming sensory states and prediction errors, attention is a factor that weights the incoming data in proportion to their estimated precision (Feldman & Friston, 2010). By this logic, in an every-day situation, we rely more on predictions and are more sensitive to violations (generating prediction errors) from a specific modality when we are attending to that modality. Attention can therefore help us making better predictions by increasing the gain, or enhancing prediction errors, and thereby increasing the distinction between expected and unexpected sensory states (Kok et al., 2012; Jiang et al., 2013). In terms of repetition suppression, this would be observed as a stronger repetition suppression effect for attended stimuli in regions of the brain specific for encoding those stimuli.

Along with attention, prior expectations and learnt regularities of the world are primary modulating forces of perception (Hemholtz, 1867; Fiser et al., 2010; Kersten et a., 2004). For example, Fitts's law, a model of human movement, which defines how distance and target size effect the speed of movement, holds true equally for imagined and -most importantly for the present argument- for perceived actions (Fitts, 1954; Decety & Jeannerod, 1995; Grosjean et al., 2007). However, often in experimental conditions we can acquire a new working model, which describes the regularities of the current context (Fiser et al., 2010). In the present paradigm, novel and repeated action properties are presented in a random order; henceforth participants cannot learn regularities tied to context. Predictions must rely on existing regularities of the world. In most everyday experience actions or goals remain the same over short timescales, thus *"no change"* is often the most precise prediction we can form (Koster-Hale & Saxe, 2013; Wacogne et al., 2012). In this sense, novel is unexpected and repeated action properties are expected in the present paradigm.

Repetition suppression is a very well described and replicated effect in the action observation literature; however, we still don't understand the precise neural mechanisms responsible for repetition suppression and we know very little about how attention can modulate this effect. In our previous study, we reported that even unattended actions can elicit repetition suppression in the traditional AON (Halász et al., 2014). Furthermore, we found that attention can modulate the magnitude of repetition suppression for observed actions. Participants completed an attentionally demanding visual task while non task-relevant videos of object-directed hand actions were presented centrally in their visual field. Although participants could ignore the actions, neural activity in the AON showed widespread repetition suppression to repeated compared with novel properties of the actions. Furthermore, when the distracting attentional task was more difficult, and attentional resources for processing observed actions were most limited, neural responses specifically to novel or unexpected action properties were even further enhanced in bilateral inferior frontal, premotor, and parietal brain regions. We argued that the reported areas could play an important role in alerting us to unexpected changes in the environment that violate predictions, even when attentional resources are most limited, as such changes often signal threat, danger or the need to disengage from a current task (Halász et al., 2014). In this previous study, however, actions were always non task-relevant and could be ignored. It is still not known how attention can influence the processing of novel or unexpected compared with repeated actions when only specific aspects of the action are task-relevant and therefore attended.

In this study, we investigated how attention can influence the processing of specific aspects of observed actions, as reflected by the repetition suppression effect in different regions of the AON. We asked participants to monitor one property of simple object-directed hand actions (action goals, movement kinematics, or the acting agent). We presented a series of videos while manipulating specific aspects of the actions to be repeated or novel in consecutive video clips. We also manipulated task-relevance of different action properties by asking participants to monitor either for a specific action goal, movement speed, or agent in different blocks. We measured repetition suppression elicited by repeated compared with novel action properties and investigated how task relevance or attention to specific action properties influences the neural processing of those specific action properties. Similar to our previous study (Halász et al., 2014), we expected to find strong overall repetition suppression effects in the AON tied to the novel or repeated presentation of the different properties of observed actions. Additionally, we expected to find that attention enhances the neural signal in brain areas in which the attended features are processed, as in previous studies (Chelazzi et al, 1998; Corbetta et al., 1990; Kastner et al., 1999; Spitzer et al., 1988; Yeshurun & Carrasco, 1998; Treue & Trujillo, 1999). Specifically, we expected that attention to the different action properties would modulate or sharpen predictive mechanisms, further enhancing the difference between novel and repeated action properties and resulting in stronger repetition suppression effects in task specific areas of the action observation network.

4.2. Materials and methods

4.2.1. Subjects

Twenty healthy, young volunteers took part in the study, ranging in age from 18 to 40 years. The final dataset contained 17 participants (M = 24.8, SD = 5.9 years; 6 males); one participant's data was discarded because of scanner failure, and two because of excessive head movement during the scans. Volunteers were right handed, had normal or corrected to normal visual acuity, and no history of mental or neurological diseases. Participants gave informed consent and received $20 as reimbursement. Approval for this study was granted by the University of Queensland Medical Research Ethics Committee.

4.2.2. Stimuli and procedure

4.2.2.1. Video clips and the one-back repetition suppression paradigm

Sets of video-clips were created depicting either a male or female hand, acting either to open or to close a book or a pencil case, and moving with either fast or slow kinematics (See Figure 4.1 for stimuli & Figure 4.2 for the paradigm). The actors wore a black tight-sleeved shirt so that only their hands below the wrist were visible. Every video-clip was cut so that it showed only the right hand and forearm reaching into the frame and then either opening or closing the book or pencil case. Importantly, the goals of both opening and closing the object were shown with similar kinematics of actual hand movement and grasp, therefore allowing the independent manipulation of goals and kinematics. We carefully matched the actions filmed in the video-clips so that all actions were as similar as possible between actors and goals.

Video clips therefore differed based on the agency, goals of the actions, and kinematics of the actions depicted. For agency, two hand-actors were selected, one male and one female. They were specifically chosen so that, even when only their hands were visible in the clips, they could be clearly identified as male and female, allowing participants to recognise the different agency between the clips. For goals, actions depicted either opening or closing of the book or pencil case object. For all clips, two of the same object were always shown: in the case of books, one open and one closed; in the case of pencil cases, one closing to the left and one closing to the right. This manipulation prevented participants from judging the nature of the action (opening or closing) purely based on the objects shown prior to the actions. Video clips then depicted the hand reaching in to either open or close one of the objects. The position of the open/closed objects, whether they were at the top or at the bottom of the screen, and the object that the action was directed towards were counterbalanced throughout. For movement kinematics, two distinct profiles of movement speed throughout the reach and object interaction were created by video-editing software (Adobe PremierePro). In half of the videos, the hand approached slowly towards the object then acted quickly upon it. In the other half of videos, after a quick approach the hand acted slowly upon the object. These two levels of movement kinematics were named "fast" and "slow" referring only to the part of the movement when the hand manipulated the object.

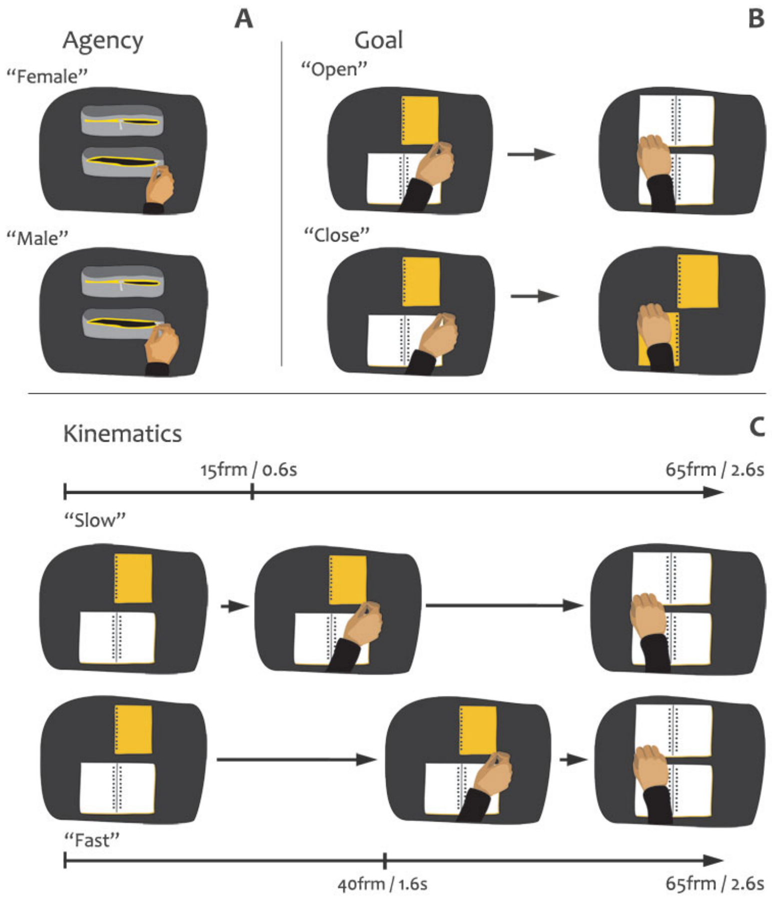

Figure 4.1. Examples of video clips from the three repetition suppression conditions. **A|** Agency, showing "female" and "male" hands; **B|** Goals, showing "open" and "close" actions; and **C|** kinematics showing "slow" and "fast" movements when interacting with the objects.

All videos were edited so that they consisted of exactly 65 frames (2.6 seconds) from the point when the hand first appeared in the video until the movement on the object was completed. In the "fast" condition, the action on the object lasted for 25 frames (1 second), while in the "slow" condition the action lasted for 50 frames (2 seconds) (See part (c) of Figure 4.1). The aspect ratio of the video clips was 640x480 pixels. Altogether 32 videos were created as follows: 2 objects (book, pencil case) x 2 actors (female, male) x 2 goals (open, close) x 2 types of kinematics (slow, fast) x 2 object-positions (top, bottom).

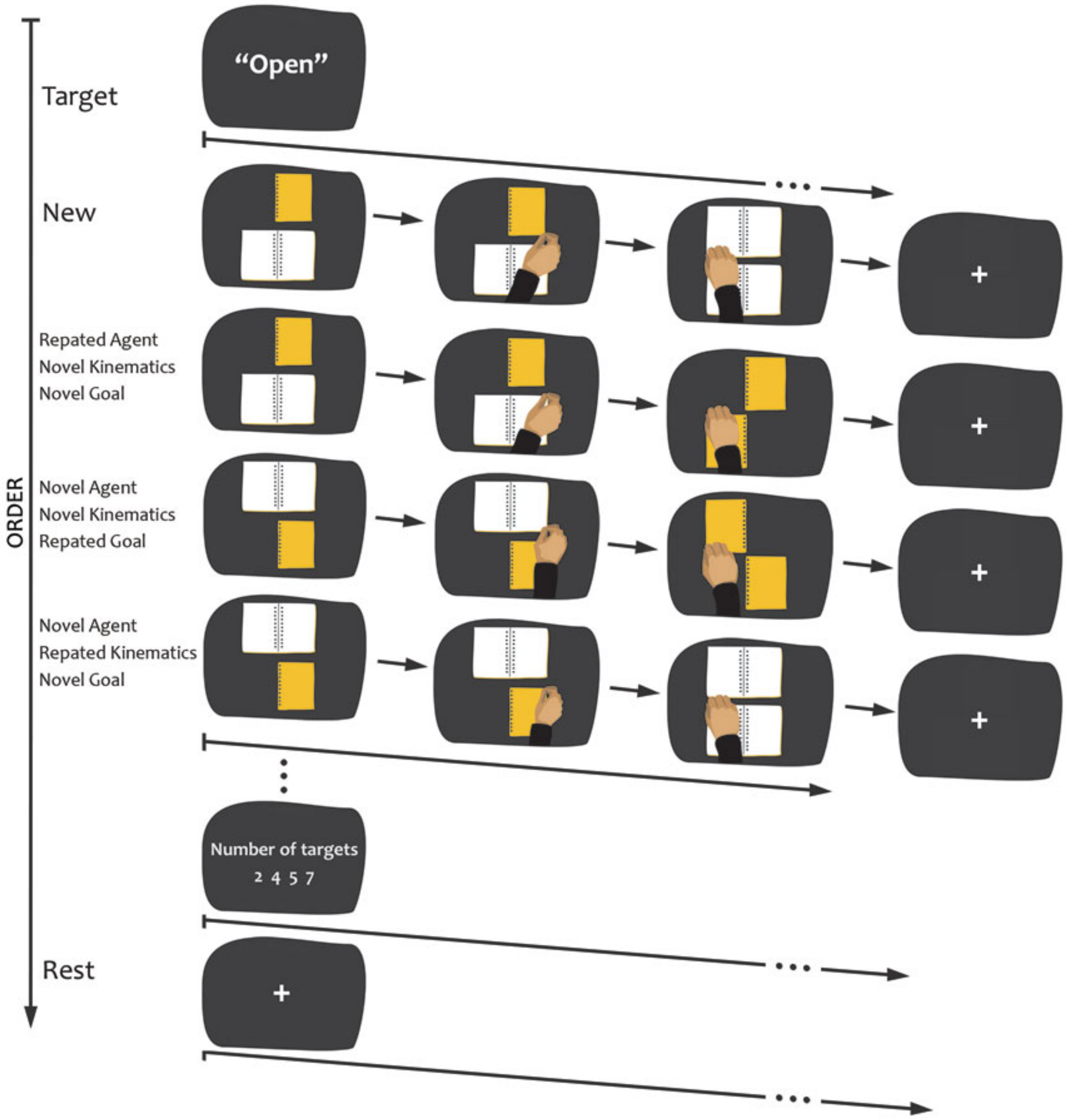

Figure 4.2. Experimental time course in a block of the repetition suppression paradigm. Every block started with the presentation of the target word for the attentional task. Blocks contained 13 to 16 videos, played sequentially and separated by 0.4 s blank screen; at the end of the block participants were prompted to indicate the number of targets in the block, followed by a 15 s rest. The video-clips were presented in a pseudo-random order. Every video was defined as either novel or repeated compared to the previous one and thus served both as a prime for the following video clip and a target in the repetition suppression analysis.

A one-back repetition suppression paradigm was used (Hamilton & Grafton, 2008), as shown in Figure 4.2. Every video-clip was defined as either novel or repeated for agency, kinematics, or goals compared to the immediately preceding stimulus. For example, if the first clip depicted the female hand opening a book and the second depicted the female hand closing a book, the second stimulus would be coded as repeated agency (for the female hand repeated) but novel goal (for “closing” after previously viewing “opening” goal). In this way every video clip was both a prime for the following video clip and a target in the repetition suppression analysis.

Between 13 to 16 video clips were shown consecutively, with 400 ms blank screen between clips (39 to 48 s duration), and constituted one block. Each fMRI run contained 10 blocks, with 15 s rest between blocks. Videos were shown in a pseudo-random order based on the one-back repetition suppression paradigm in which each of the videos was defined as novel or repeated relative to the previous video clip. During every block there were five repetitions of each of the conditions (agency, kinematics, goal), and the remaining video clips were always novel compared to the previous one. Object type was counterbalanced across blocks, while actors, kinematics and goals were counterbalanced within a run. The first video in each block was always excluded from analysis, as there was no previous video for it to be compared against. Altogether 128 video clips were presented in each fMRI run, thus every video clip was presented equally often (4 times each) during one run. The order of blocks within the run was randomised, thus the block-order was unique for every participant. The entire experiment consisted of three fMRI runs. Experimental data was collected in the same session as for the experiment described in Chapter 3, but task order was counter-balanced between participants.

4.2.2.2. Attentional task

Participants were required to monitor the video clips and count the number of cued target features that occurred within each block. These features were related to the three action representation conditions: agency, kinematics and goals (Figure 4.1). A target word was presented at the beginning of each block: "female" or "male" for agency; "fast" or "slow" for kinematics; and "open" or "close" for action goals. Thus, for example, if the cue “female” was presented before the stream of videos, participants were required to count the number of video clips containing the female actor’s hand, or if the cue “close” was presented participants counted the number of times a book was shown being closed. The attentional conditions were varied between blocks, counterbalanced across the experiment, and randomly ordered for every participant. Based on the number of video clips in each block, the possible number of targets varied between five and nine. At the end of each block, a response screen was presented showing four possible number options and participants indicated their responses by pressing one of four buttons corresponding to the number of targets they had counted during the block.

4.2.3. fMRI data acquisition

The fMRI data was collected on a 3-Tesla Siemens Trio MRI scanner with a 32-channel headcoil. During the fMRI acquisition participants lay supine with their head supported in a volume coil. The stimuli were presented on a screen at the head end in the bore of the scanner and viewed by participants via a mirror that was mounted on the head coil. Functional images were acquired using gradient-echo echo-planar imaging (EPI) sequence with the following parameters: 30 horizontal slices (3 x 3 mm in-plane voxel resolution and 3 mm slice thickness plus 10% gap), repetition time (TR) 2.31 s; echo time (TE) 40 ms. Two identical fMRI runs of 325 images (12 min 30 s) each were acquired. The first three TR periods from each run were discarded to allow for steady-state tissue magnetization. A three-dimensional high-resolution T1-weighted image covering the entire brain was also acquired and was used for anatomical reference (TR= 1700, TE=3.91 ms, FA=15°, 192 cubic matrix, voxel size =1.2 cubic mm).

4.2.4. fMRI analyses

Data was processed and analysed using SPM8 (Wellcome Department of Imaging Neuroscience, Institute of Neurology, London; http://www.fil.ion.ucl.ac.uk/spm), implemented in Matlab. EPI images were slice-time corrected to the middle slice acquired in time (Sladky et al., 2011) and spatially realigned to the middle image of each run for movement correction using a least-squares approach and six-parameter rigid body spatial transformations (Friston et al., 1995). Structural images were co-registered to the mean of the realigned functional images and then an inbuilt unified segmentation routine of SPM8 was applied to register the structural T1 image to the standard MNI template. The transformation parameters created by segmentation were then applied to all of the realigned functional images, subsequently resliced to 2 x 2 x 2 mm resolution and smoothed using a 6-mm full-width-at-half-maximum isotropic Gaussian filter.

An event-related approach was used to analyse the time series in a general linear model. At the single-subject level, onsets of the target words at the start of each block, onsets of each of the videos, and onsets of the end-of-block responses were modelled separately, convolved by the canonical hemodynamic response function of SPM8. Motion correction parameters from the pre-processing were also included the models. For the video-clips, the first video of each block was modelled separately and not included in any subsequent contrasts. The rest of the videos were modelled as 18 separate conditions (regressors) according to a 3 x 2 x 3 design, with levels of *attentional task* (agency, kinematics, goals), *repetition* (novel, repeated), and *action representation* (agency, kinematics, goals). All videos were modelled with a duration of 2.5s as this was the actual duration of the video clips. The duration of the end-of-block response regressor was adjusted based on individual reaction times. The periods during the resting phase between blocks were considered baseline and were not explicitly modelled.

The main focus of the group-level analysis was to specifically examine changes in *repetition suppression* (i.e. novel minus repeated activation differences) across attention and action representation conditions. Therefore, in the first-level analysis, contrasts of "novel minus repeated" were calculated for the three action representation conditions (i.e. repetition suppression for agency, kinematics, and goals) at each level of the attentional task (attending to agency, kinematics, goals), resulting in nine first-level contrasts. For second-level random-effects analysis, these contrasts were analysed in a full-factorial model with main effects of action representation and attentional task (3 x 3 ANOVA design).

We also created a mask for "all-action effects" by combining the positive activation across all 18 video-condition regressors (using the voxel-level threshold $P < 0.05$). This mask represented all brain areas showing positive activation when viewing action videos compared with the resting interval between blocks, regardless of action representations, attention, or novelty conditions. By applying this mask to all contrasts from the second-level factorial model, we ensured that all areas reported to show repetition suppression differences between conditions were areas that also showed significant positive activation when viewing action videos compared with resting. For all contrasts, significant activation was defined by a cluster-level probability threshold of $P_{FWE} < 0.05$, corrected for the masked search volume (with clusters defined by the voxel-level threshold $P < 0.001$).

4.3. Results

4.3.1. Behavioural results

Participants' accuracy in counting the number of video clips containing the relevant feature was well above chance level (25%) in all three attentional conditions (Figure 4.3). One-way ANOVA showed a significant difference in accuracy between the attentional tasks, $F(1.39,22.29)=11.99$, $p< .001$. Accuracy for identifying particular agency (69%, SD=.29) or particular goals were not significantly different (79%, SD=.18; $p=.105$, ns). However, accuracy for identifying the movement kinematics (45%, SD=.25) was significantly worse compared to agency ($p=.018$) and goal conditions ($p<.001$), suggesting that identifying cued features of the movement kinematics was more challenging for participants.

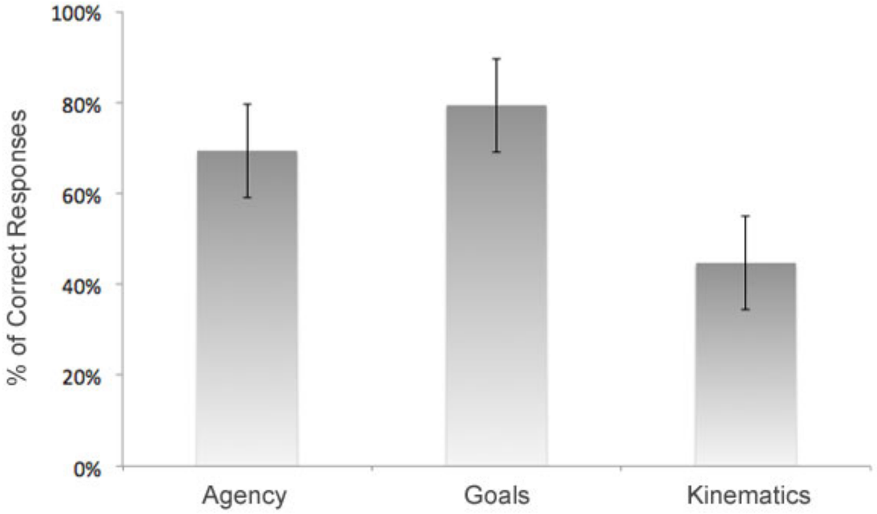

Figure 4.3. Mean percentage of correct responses (with standard error bars) when counting the number of videos containing cued features in the three attentional conditions (agency, goals, kinematics).

4.3.2. fMRI results

4.3.2.1 Overall effect of attention

As behavioural results showed a significant difference in difficulty when participants were required to attend to movement kinematics compared with action goals or agency, we examined the overall effect of attention to different aspects of actions averaged across novelty and action representation conditions. We created a new factorial model to contrast all activation to videos (novel and repeated combined) when attending to agency versus goals and kinematics, when attending to goals versus agency and kinematics, and when attending to kinematics versus agency and goals. None of these contrasts showed significant differences, even with a liberal 0.01 uncorrected threshold level. This result indicates that changing task relevance of specific action properties does not influence overall activation of the action observation network, and that specific differences reported below in repetition suppression effects between conditions are not merely related to differences in task difficulty.

4.3.2.2. Overall Repetition Suppression

When contrasting novel versus repeated actions averaged across attention and action representation conditions, repetition suppression was evident in a widespread network (Figure 4A). Significantly greater activation for novel compared with repeated presentations of action properties was found in the lateral occipital cortex, inferior parietal cortex, the superior temporal sulcus, middle and superior temporal gyri, the inferior frontal gyrus, dorsal and ventral premotor cortex, and the supplementary motor area. These areas are typically identified as part of the action observation network and closely follow results of our previous study (Halász et al., 2014).

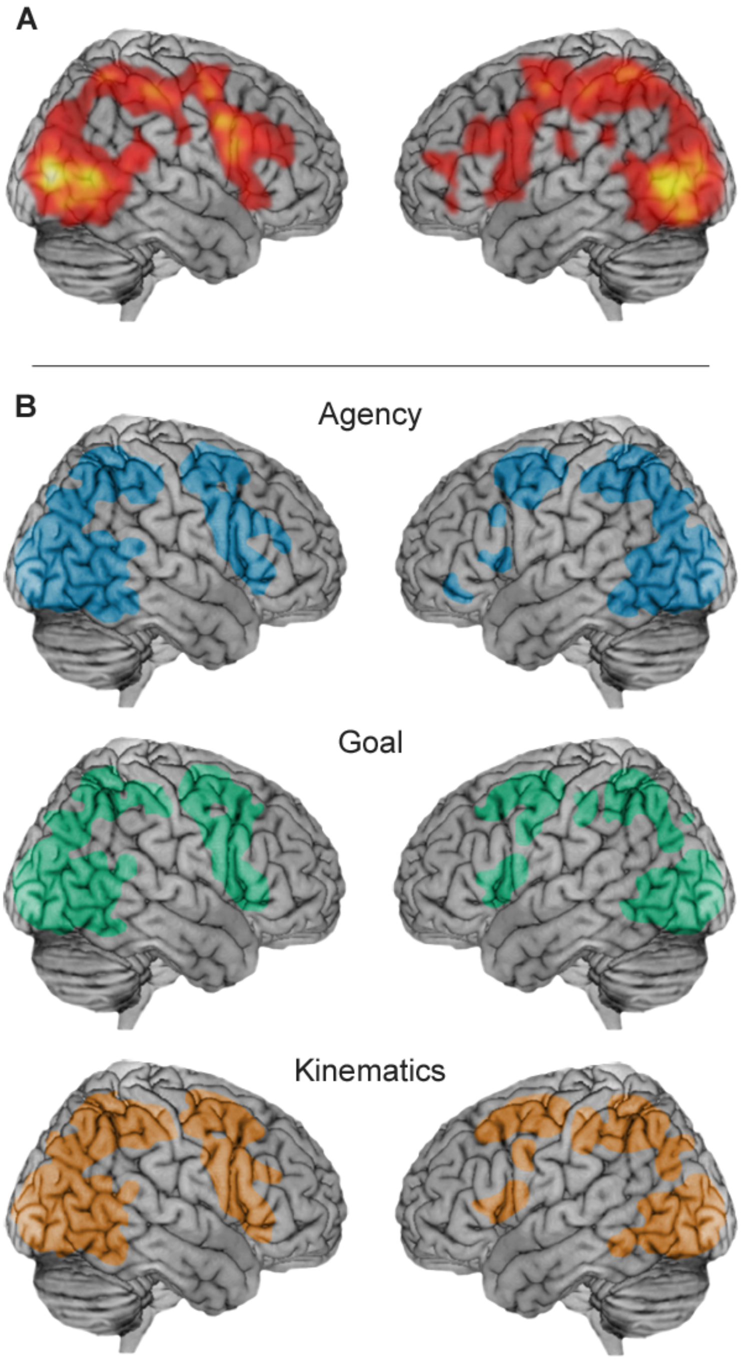

Figure 4.4. A| Brain areas showing overall repetition suppression, regardless of attention or action representation. These areas showed less activation for repeated compared with novel actions when averaged across attentional conditions and repetitions of goals, kinematics, and agency. **B|** Brain areas showing repetition suppression separated for repeated presentation of agency, goals, or kinematics, averaged across attentional conditions.

When examining repetition suppression specifically for repetitions of goals, kinematics, or agency, averaged across attention conditions, the same widespread patterns of repetition suppression were found in all cases (Figure 4.4B). To test for differences in repetition suppression depending on which aspects of actions were repeated, we contrasted repetition suppression for goals versus agency and kinematics, repetition suppression for agency versus goals and kinematics, and repetition suppression for kinematics versus goals and agency. These contrasts revealed no significant differences between conditions. Similar to our previous results (Halász et al., 2014), this lack of action representation specific repetition suppression suggests that the detection of novelty or response to novel compared with repeated action properties in the AON probably reflects a robust, generalised process that does not depend on which aspect of the action is repeated.

4.3.2.3. Effect of attention on repetition suppression

Finally, we examined interaction effects between attention and repetition suppression by examining overall repetition suppression (regardless of which aspects of actions were repeated) when participants were attending to agency versus goals or kinematics, when attending to goals versus agency or kinematics, and when attending to kinematics versus goals or agency. These contrasts all showed significant differences in repetition suppression depending on which aspects of actions were attended.

4.3.2.3.1 Attending to agency

When the agency of actions was task-relevant and attended, significantly greater repetition suppression was found in two occipital brain areas (Figure 4.5A). One cluster showed a significant peak in the right lingual gyrus, and the second showed a peak in the left middle occipital gyrus, extending to the fusiform gyrus and to inferior occipital areas (Table 4.1). To further examine the nature of this interaction effect, we calculated mean parameter estimate values for a 5 mm radius sphere centred on these peaks and plotted across attention and novelty conditions. As shown in Figure 4.5B, attending to agency has a dual effect of both increasing activation to novel actions and reducing activation to repeated actions in both these regions as compared with attending to either action goals or kinematics (when agency is not task-relevant).

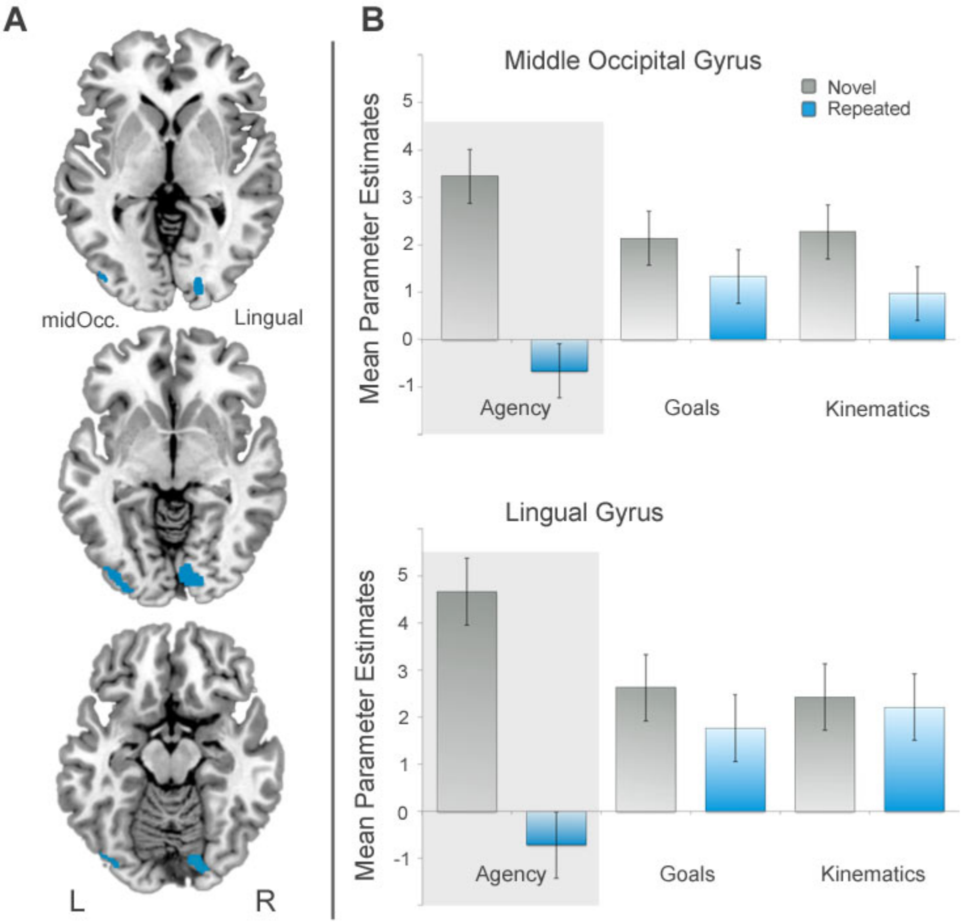

Figure 4.5. **A|** Brain areas showing stronger repetition suppression when attending to the agent of observed actions compared to action goals or kinematics. **B|** Mean parameter estimates for novel and repeated actions across attention conditions for peaks in the right lingual gyrus (16 -90 -10), and left middle occipital gyrus (-38-88 -6), with standard error bars.

4.3.2.3.3 Attending to goals

When the goals of actions were task-relevant and attended, significantly greater repetition suppression was found in four brain areas (Figure 4.6A). These clusters included the right postcentral gyrus, the right superior occipital areas extending towards the superior parietal lobule, the left inferior and superior parietal lobule, and the left middle occipital gyrus (Table 4.1). Mean parameter estimates were calculated for a 5 mm radius sphere centred on these peaks and plotted across attention and novelty conditions. As shown in Figure 4.6B, attending to action goals also had the dual effect of both increasing activation to novel actions and reducing activation to repeated actions in all areas as compared with attending to either agency or kinematics (when goals were not task-relevant).

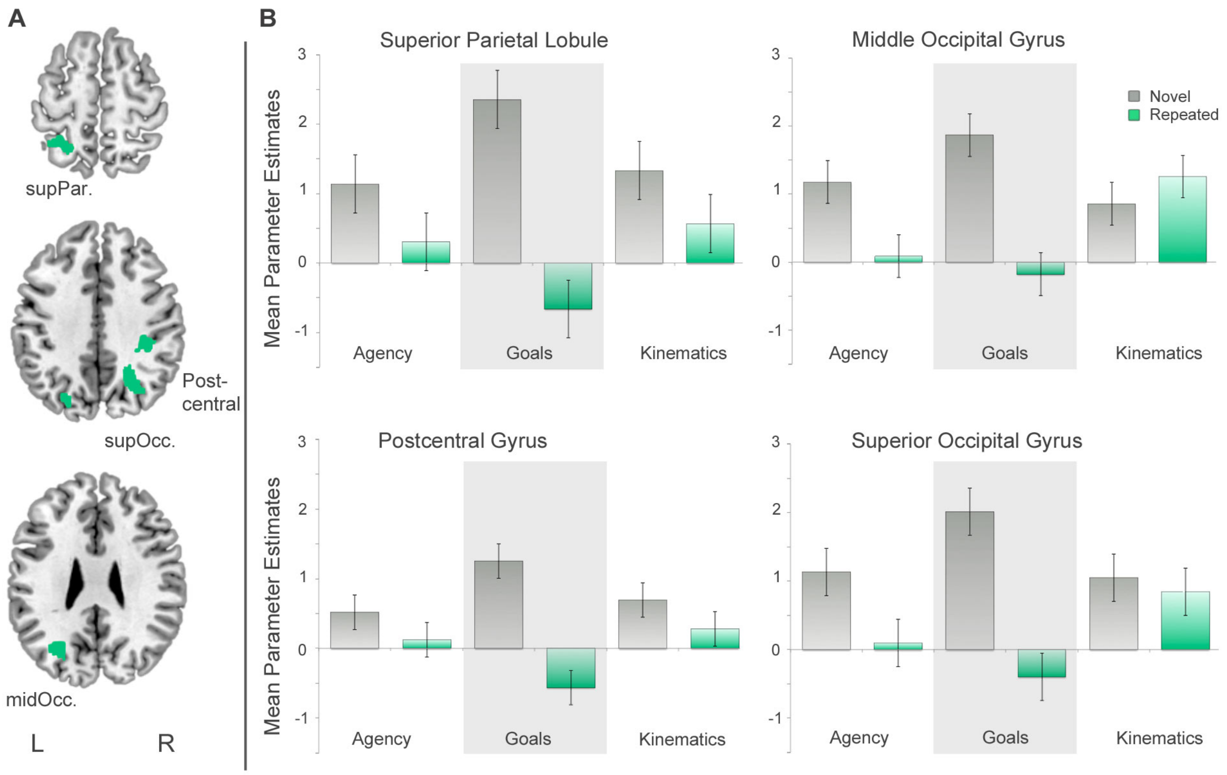

Figure 4.6. A| Brain areas showing stronger repetition suppression when attending to the goal of observed actions compared with movement agency or kinematics. **B|** Mean parameter estimates for novel and repeated actions across attention conditions for peaks in the right postcentral gyrus (38 -32 40), right superior occipital gyrus (26 -64 38), left superior parietal lobul (-24 -54 64), and left middle occipital gyrus (-30 -68 28), with standard error bars.

4.3.2.3.4 Attending to kinematics

When the kinematics of actions were task-relevant and attended, increased repetition suppression was found in the left inferior frontal gyrus, pars opercularis, extending also into the precentral gyrus, and a significant cluster in the triangularis part of the right inferior frontal gyrus extending towards the right insula (Table 4.1; Figure 4.7A). Mean parameter estimates were again calculated for a 5 mm radius sphere centred on these peaks and plotted across attention and novelty conditions. As shown in Figure 4.7B, attending to movement kinematics also had the same dual effect of both increasing activation to novel actions and reducing activation to repeated actions as compared with attending to either goals or agency (when kinematics were not task-relevant).

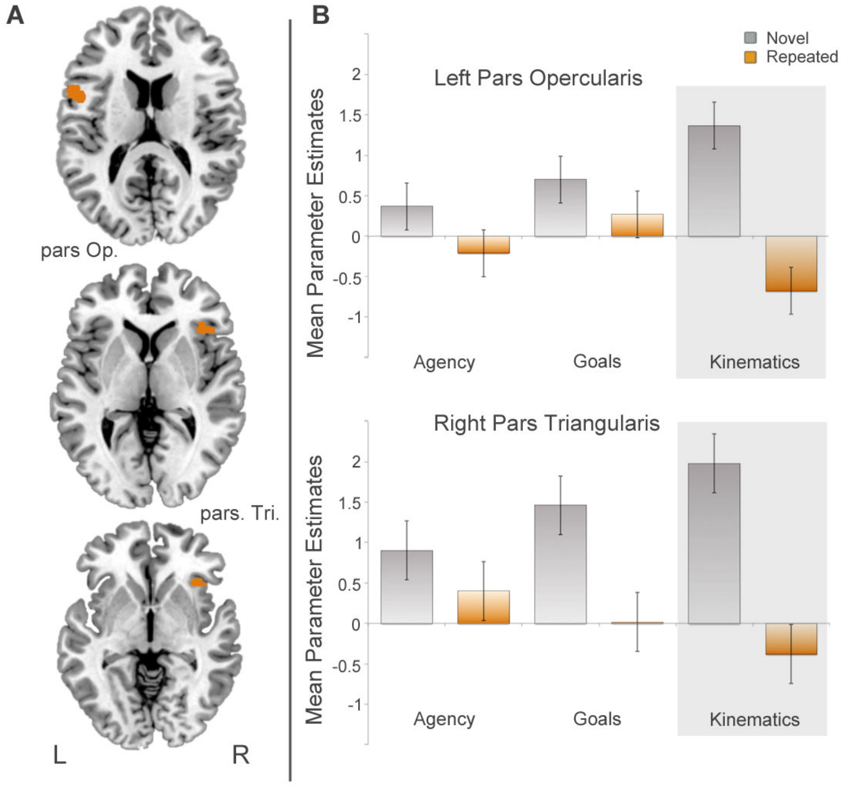

Figure 4.7. A| Brain areas showing stronger repetition suppression when attending to kinematics of observed actions compared with goals or agency. **B|** Mean parameter estimates for novel and repeated actions across attention conditions for peaks in the right (36 26 0) and left inferior frontal gyrus (-56 6 14), with standard error bars.

Table 4.1.

Brain regions showing significantly stronger repetition suppression when attending to agency, goals, and kinematics.

Condition Region	Anatomic location of peak	Number of voxels	T	P cluster corrected	MNI coordinates		
					x	y	z
Agency							
R Lingual	Area 18	245	4.58	< 0.001	16	-90	-10
L Occipital, mid.	hOC4v	97	4.65	0.016	-38	-88	-6
Goal							
R Postcentral	Area 2	223	5.03	0.001	38	-32	40
R Occipital, sup.	SPL (7A)	271	4.74	< 0.001	26	-64	38
L Parietal, sup.	SPL (7A)	127	4.92	0.007	-24	-54	64
L Occipital, mid.	hIP3	166	4.29	0.003	-30	-68	28
Kinematics							
R Frontal, inf. tri.	Area 45	76	3.94	0.029	36	26	0
L Frontal, inf. op.	Area 44	111	4.79	0.011	-56	6	14

4.4. Discussion

In the present experiment we investigated how attending to various aspects of observed actions can influence the neural processing of those actions. Our results revealed that the typical AON shows a widespread suppression in BOLD responses to the presentation of repeated compared with novel properties of actions, regardless of attentional focus. Compared to previous research we did not find attenuation of the neural signal uniquely tied to repetitions of agency, kinematics, or action goals. However, we found that specifically focusing attention to one aspect of an observed action enhances the processing of any novel information in areas specialised to process the attended feature, while repeated presentation leads to a stronger suppression effect in the same area.

4.4.1. Processing of actions & the general repetition suppression effect

Observation of novel versus repeated action properties elicited a strong attenuation of the BOLD response in an extensive network (Figure 4.4). Previous reports describing neural activation during action observation are consistent with our results; typically, the lateral occipital cortex, inferior parietal cortex, the superior temporal sulcus, middle and superior temporal gyri, the inferior frontal gyrus, the dorsal and ventral premotor cortex, and the supplementary motor area are involved in action observation (Caspers et al., 2010; Grafton & Tipper, 2012; Grosbras et al., 2012; Molenberghs et al., 2012). Furthermore, these results are highly similar to our previous repetition suppression study in which participants passively observed actions (Halász et al., 2014).

Interestingly, repetitions of any of the three action representations resulted in similar patterns of repetition suppression that were consistent with the overall repetition suppression across all attention and action representation conditions (Figure 4.5). This suggests that no matter which action representation was repeated or novel, the same widespread regions of the AON were equally involved in the neural processing of the observed action. In particular, we found no significant differences in repetition suppression for repeated presentations of agency, goals, or kinematics, which appears at odds with previous results. Several previous studies have shown repetition suppression effects, often in pre-defined regions of interest, that are uniquely linked to repeated goals, kinematics, or agency (Di Dio et al., 2013; Hamilton & Grafton, 2006, 2007, 2008; Kable & Chatterjee 2006; Majdandžić et al., 2009; Ortigue et al., 2009; Ramsey & Hamilton, 2010a, 2010b; Wiggett & Downing 2011). While most of these studies did not control task-relevance or attention to the observed actions, our results show that attention is a crucial factor in mediating repetition suppression effects. We found significant differences in repetition suppression across different regions of the AON depending on which aspects of the observed actions were task-relevant or attended by participants.

4.4.2. Representation of agency, goals, and kinematics

When the agency of observed actions was task-relevant and attended by participants, repetition suppression effects were enhanced in bilateral clusters localised in the fusiform gyrus and middle occipital regions (Figure 4.6). This result overlaps with many studies reporting body-selective regions in the occipitotemporal regions, specifically involving the fusiform body area (FBA) and the extrastriate body area (EBA) (recent review & commentaries: Downing & Peelen, 2011). Repetition suppression studies have also reported strong attenuation of neural activity upon repeated presentation of the same actor in the occipitotemporal regions, suggesting the encoding of personal identity or agent-specific information (Ewbank et al., 2011; Ramsey & Hamilton, 2010b).

In their recent review, Downing and Peelen (2011) argued that the EBA and FBA are distinct functional units involved in body perception, but with only a limited role in processing of higher-order aspects such as personal identity. Contrary to this view, many commentaries on Downing and Peelen's review argued that these occipitotemporal regions are bidirectionally connected to other cortical areas involved in higher-order processing of identity and agency, in line with a predictive coding account (Ewbank, 2011; de Lange & Bekkering, 2011; Ramsey et al., 2011; Quadflieg & Rossion, 2011). Importantly, the function of these regions is shown to be heavily dependent on the context in which they are recruited (de Lange & Bekkering, 2011). In other words, by a predictive coding account, these areas may pass face or body specific information to higher-level areas that formulate accurate predictions regarding high-order representations such as identity and agency, and in turn these areas also evaluate those predictions based on incoming lower-level sensory information when required by the task or the context. Our data is consistent with this, showing that when the acting agent is task-relevant and attended, the sensitivity of these regions to novel or repeated presentations is greatly enhanced resulting in greater repetition suppression effects.

When the goals of observed actions were task-relevant and attended by participants, significantly greater repetition suppression was found bilaterally in the middle occipital, superior and inferior parietal areas, and in the right postcentral gyrus. Earlier studies reported repetition suppression for goals in a similar but wider network including inferior frontal, precentral, superior parietal, lateral occipital and inferior parietal regions (Hamilton & Grafton, 2006, 2007, 2008; Majdandžić et al., 2009; Ortigue et al., 2009; Ramsey & Hamilton, 2010a, 2010b). Importantly, the definition of "goals" has not been consistent between these studies, but has varied to include object-related goals (e.g. grasping a cookie versus grasping a disk) and higher-order intentions (e.g. switching off or on a lamp), and may therefore account for the large range of regions attributed to the representation of "goals" (for a review on the importance of clear definitions in the action understanding literature see Uithol et al., 2011). Nevertheless, research using single cell recording on macaques, human neuroimaging and patient studies support the involvement of the parietal areas in the processing of action goals (Rizzolatti et al., 2014; Fogassi et al., 2005). Our study further suggests that middle occipital, superior and inferior parietal areas are not only sensitive for novel and repeated action properties, but are strongly influenced by the context in which actions are observed.

When the kinematics of movements were task-relevant and attended by participants, significantly stronger repetition suppression was found in the pars opercularis region of the left inferior frontal gyrus, left precentral gyrus, and a marginally significant cluster in the right insula cortex. Previously, bilateral inferior frontal, left parietal, and bilateral inferior lateral occipital areas were reported to show kinematics-related repetition suppression effects (Di Dio et al., 2013; Hamilton & Grafton, 2006, 2007, 2008; Majdandžić et al., 2009). In prefrontal areas, Press and colleagues (2012) reported repetition suppression in the left inferior frontal gyrus, with very similar coordinates as ours (-56, 2, 20), when different types of actions were repeated (precision grip or ring pull), irrespective of whether participants observed, executed, or imitated (i.e. observed and executed) the actions. Importantly, the participants' task was to perform and observe simple grip or pull actions that were not associated with any higher-level intentions, and therefore involved focus primarily on the form of the movement itself, similar to our kinematics condition, rather than any focus on higher-order goals or intentions. Similarly, Johnson-Frey and colleagues (2003) described strong bilateral precentral gyrus, pars triangualris and opercularis activation upon the observation of still images of different grasps of the same object. Overall, repetition suppression and lesion studies generally point to primarily left pars opercularis and triangularis regions of the inferior frontal cortex for processing *how* an action is being executed (Grafton & Tipper, 2012; Buxbaum et al., 2005; Johnson-Frey et al., 2003; Pazzaglia et al., 2008).

4.4.3. Attention and prediction of actions

An important aspect of our results is that our repetition suppression effects that were enhanced by attention always involved the dual effect of greater activation to novel actions as well as greater suppression to repeated actions than when those particular properties of actions were not attended. Overall, regardless of the attentional task, our present results are consistent with our previous study showing a strong, uniform pattern of repetition suppression in the AON, even when attention is directed away from actions (Halász et al., 2014). This suggests an automatic system that is involved in the processing of observed actions and, in particular, detecting novel action properties even when the observed actions are not task-relevant. However, our present data extend on those previous findings by further showing that attention does modulate the neural processing of observed actions. Our results suggest that attention enhances the processing of novelty, causing greater repetition suppression in brain regions important for processing those specific aspects of actions that are task relevant and attended.

In the present paradigm, the attentional task forced participants to make rapid judgements on specific properties of actions in every video they saw. Our data indicates that whenever novel action properties were presented or encountered by the AON, neural activity was increased in specialised areas of the brain where those attended properties of the actions are typically analysed. We hypothesise that, upon focusing on a behaviourally relevant property of the actions, processing in the task-relevant brain areas was boosted to allow more precise and/or faster discrimination between target or non-target action features. Increased neural responses and improved behavioural performance upon attending to task-relevant stimuli is a well-described phenomenon (Chelazzi et al, 1993, 1998; Corbetta et al., 1990; Kastner et al., 1999; Spitzer et al., 1988; Yeshurun & Carrasco, 1998; Treue & Trujillo, 1999).

It is also important to note that attention did not simply increase overall neural activation for the attended feature, but enhanced the sensitivity to novel compared with repeated action properties, demonstrating a clear interaction effect between attentional and predictive processes. Kok and colleagues (2012) reported a similar interaction between attention and prediction in early visual areas, in which the effect of attention varied with participants' expectations and was specifically localised to a part of the visual cortex normally associated with processing of the expected sensory information. In line with the theories of predictive coding, it is suggested that attention acts as a scaling factor or gain control, sharpening the perceived difference (i.e.: increasing the difference between neuronal activity) between expected and unexpected sensory states (den Ouden et al., 2012; Feldman & Friston, 2010; Jiang et al., 2013). This is entirely consistent with our present results in which the distinction between novel and repeated actions was greater in regions of the AON associated with the processing of the action property that was attended.

Lastly, we must note that repetition suppression reported here is unlikely to be the sole result of predictive brain mechanisms, but most likely arises from multiple neural factors such as low-level sensory adaptation, fatigue, neural sharpening, and prediction related activity (Grill-Spector et al., 2006; Larsson & Smith, 2012; Summerfield & Egner, 2009; Todorovic & de Lange, 2012). Emerging literature provides evidence that predictive processes play an important role in observed repetition suppression effects, together with the lower-level neural adaptation assumed in earlier studies, since attention and the relative expectation of a given stimulus can modify the magnitude of repetition suppression (Halász et al., 2014; Kok et al., 2012; Kovács et al., 2012; Larsson & Smith, 2012; Summerfield et al., 2008). In the present study, we suggest that the very widespread nature of repetition suppression evident throughout the AON, and fact that processing for novelty specifically was enhanced by attention (i.e. not merely greater suppression for repeated stimuli), indicate the involvement of brain mechanism involved in predictive processes (Friston, 2005, 2010).

4.5. Conclusions

We showed that widespread brain areas involved in action observation are highly sensitive to the presentation of novel compared with repeated properties of the observed actions, showing strong repetition suppression effects across widespread cortical areas. Furthermore, we found that attending to the acting agent, the goal, or the kinematics of the observed action selectively enhanced the repetition suppression effect in brain areas that are typically involved in the processing of the attended properties. Our results suggest that when specific aspects of observed actions are attended or task-relevant, sensitivity to novel action properties is enhanced, in line with theories of predictive mechanisms (Friston, 2005, 2009; Feldman & Friston, 2010). Therefore, while the AON network overall appears highly sensitive to the detection of novel action properties, as consistent with our previous study (Halász et al., 2014), attention also plays a crucial role to further enhance sensitivity in regions of the AON important for processing the features of actions that are most relevant and selectively attended.

Acknowledgment

This work was supported by funding of the Australian Research Council (DP110103285).

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Chapter 5

Interaction of concurrent motor plans and perceived actions on neural oscillations

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Abstract: Existing theories suggest a bi-directional information flow between motor and perceptual brain areas and posit the importance of sensorimotor rhythms in the communication between functionally connected brain areas. Here we aimed to examine how cortical oscillatory activity changes over time during concurrent action observation and execution. Magnetoencephalography recordings were collected from 20 participants while they performed and observed simple hand gestures. Visual images of either congruent or incongruent hand gestures were presented either during movement preparation or movement initiation. Sensor level analysis revealed greater neural activity over the motor cortices during the observation of congruent hand gestures. Time-frequency analysis linked strong theta activity over central regions to sensorimotor integration, reflecting computational processes near behavioural decision points. Beta frequency changes displayed movement related power suppression over motor cortices, reflecting the timing component of the prepared movements and increased power over parieto-occipital areas specifically linked to congruency between planned and observed actions. Alpha activity peaked over central motor areas during the observation of incongruent actions, possibly reflecting conflict-monitoring processes. These findings give a comprehensive picture of neuronal processes behind the integration of sensory and motor information tied to the early processing of observed actions.

Keywords: action observation, action preparation, hand gestures, oscillation, magnetoencephalography, congruency

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5.1. Introduction

In natural settings we often deal with complex situations when we need to perform actions while also observing others act. The neural circuitry involved in the processing of actions overlaps extensively with brain areas involved in the execution of actions, a connection that supposedly plays a crucial role in action understanding (Bonini et al., 2010; Kilner, 2013; Rizzolatti & Sinigaglia, 2010). As action execution and action understanding rely on the same neural sources, it raises the question of how a common system can deal with the parallel processing of our own and other's actions.

Recent theoretical models claim that the brain's primary task is to predict future sensory states and to infer the causes of perceived sensory input (Friston, 2009, 2010, 2011). For example, during action planning, incoming sensory information is used to adjust planned movement to reach intended consequences or goals. Predictive theories thus claim an ongoing information flow between perceptual and motor areas during motor cognition. Communication between distant neural populations involves synchronised cortical oscillations that have also been linked to predictive processes (Arnal & Giraud, 2012; Buzsáki & Draguhn, 2004; Engel et al., 2001). In the present experiment, our aim was to measure frequency changes related to the observation of an action when participants prepared to execute matching or non-matching actions. We were interested to investigate neural changes linked to the processing of an "erroneous" sensory stimulus that is not in line with predicted movement outcome. To give a comprehensive picture of neural activity related to action observation, we analysed event-related magnetic field activity and power changes in theta, alpha and beta frequency bands. Furthermore, we investigated how neural activity related to action observation is influenced by concurrent action preparation.

5.1.1. Predictive coding

According to predictive theories, action production and action understanding share a common neural network, just as they share a common neural mechanism: The brain predicts sensory states to minimise surprise and to save energy (Friston, 2009, 2010, 2011). During action preparation, the brain predicts the sensory consequences of the action (Csibra, 2007; Halász & Cunnington, 2012; Kilner et al., 2007; Kilner, 2011). This mechanism helps us to plan and execute actions in a way to reach a desired sensory state or to fulfil goals. For example, if I am planning to lift a cup to drink, I create a motor plan of how far I need to reach and roughly how much force I need to use to lift the cup. Whenever there is a mismatch between the goal of the motor plan and the actual sensory state (e.g. I use too much force to lift the cup and some of its content spills) an error signal manifests in the brain, known as *prediction error*. This error signal is used to modify motor behaviour until the desired goal is reached. Similar processes are suggested to be present during action observation, but the brain infers goals and intentions, which in turn lead to sensory predictions (Clark, 2013; Friston, 2010; Kilner, 2011). When these predictions are not met, the brain creates new predictions about the possible goals until they match with the incoming sensory information. Crucially, the nature of this error signal changes depending on the exact type of the error (e.g.: low-level visual incongruency vs. higher-level cognitive discrepancy), the brain areas involved in the generation of the signal, and its functional role in a given neural process (for a review see den Ouden et al., 2012).

5.1.2. Neural oscillations

Changes in neural oscillations are linked to the communication and predictive processes of different functional units of the brain (for recent review see: Arnal & Giraud, 2012; Buzsáki & Draguhn, 2004; Fries, 2005;). Cortical rhythms have also long been implicated in motor cognition (Gastaut & Bert, 1954; Hari, 2006). Research using electroencephalography (EEG) and magnetoencephalography (MEG) led to the general conclusion that neural oscillations during action execution and observation show great similarity (Cheyne, 2013; Hari, 2006). The alpha (8-13 Hz) and beta (14-30 Hz) rhythms are the most studied frequency ranges in relation to sensorimotor activity. Both frequencies show a strong suppression before voluntary or passive movement, followed by a “rebound” of oscillatory power after movement execution over the motor cortices. Action observation and even motor imagery elicit a very similar but somewhat weaker neural pattern (Hari, 2006). Research on non-human primates and human neuroimaging studies point to the wider sensorimotor cortex as the generator of these oscillatory mechanisms (Cheyne, 2013). Despite being well-established phenomena, the exact function of alpha and beta oscillatory activity during visual-motor tasks is not clear.

As well as the motor-related alpha changes over sensorimotor cortex, alpha frequency oscillations are also typically observed over the parieto-occipital region and show a more generalised neural function. Parieto-occipital alpha is linked to cortical inhibition and its elevated amplitude allegedly reflects the disengagement of task-irrelevant neural populations (Palva & Palva, 2007; Händel et al., 2011; Jensen & Mazaheri, 2010; Kelly et al., 2006). Research also shows an inverse relationship between perceptual performance and alpha amplitude (van Dijk et al., 2008; Wyart & Tallon-Baudry, 2009).

In terms of beta band activity, neuroimaging studies and research on patients with movement-related disorders suggest that beta frequency oscillations play an important part in the neural communication between the basal ganglia and motor cortex (Cheyne, 2013). It is argued that beta activity helps to maintain the current motor state and, the suppression of beta band activity over the motor cortex prior to movement execution helps the preparation and initiation of movements (Engel & Fries, 2010; Jenkinson & Brown, 2011).

An additional important property of the beta range oscillation is the sensitivity to movement related anticipatory/predictive mechanisms (Donner et al., 2009; Press et al., 2011; Tzagarakis et al., 2010; Quandt et al., 2013). For example, Press et al. (2011) showed that beta power during action observation was modulated by the kinematics of the observed actions in such a way that the neural pattern temporally predicted the action dynamics. The changes in beta power were similar as if the observer had executed the actions, but occurred in advance of the observed actions.

While alpha and beta band have a well-founded link to movement related activity, newly emerging literature has also revealed the importance of oscillatory activity in the theta band. Cortical theta activity shows a narrow frequency band (usually 4-8 Hz) and maximal amplitude over frontal midline electrodes (Mitchell et al., 2008). While this cortical activity has been implicated in various cognitive functions, recent literature presses its importance in sensorimotor integration during movement initiation (Bland & Oddie, 2001; Cheyne et al., 2012; Cruikshank et al., 2012; Rawle et al., 2012; Perfetti et al., 211; Tombini et al., 2009). Theta band activity is reported to show an increased amplitude before movement execution, a reverse pattern compared to alpha and beta related oscillation, but at the same sensorimotor location (Cruikshank et al., 2012). Theoretical models hypothesise that theta activity is strongest around behavioural decision points because this oscillatory band is involved in the selection or decision processes related to movements (for a review see Womelsdorf et al., 2010).

Other theories claim that mid-frontal theta activity reflects a generic process related to performance monitoring (Cavanagh et al., 2012a; Nigbur et al., 2011, 2012; Ullsperger et al, 2014). A wide variety of tasks can induce a strong mid-frontal negativity, roughly around the 300ms time-point after stimulus presentation, including the *mismatch negativity* (MMN) reflecting unexpected sensory information, the *feedback related negativity* (FRN) after feedback that indicates poor performance, and the *control-related negativity* occuring following response inhibition or response conflict (Cavanagh et al., 2012b; Grafton & Tipper, 2012; Nigbur et al., 2011, 2012; Folstein & van Petten, 2008). Cavanagh and colleagues (2012b) reported that tasks commonly used to elicit MMN, FRN, or control-related negativity all show an elevated theta activity over medial prefrontal regions, claiming that neural activity in the theta frequency range plays a key component in the processing of novelty, conflict, punishment and error.

5.1.3. Erroneous actions

Observed actions may also be considered *correct* or *incorrect* in relation to predicted or concurrently planned actions. The observation of an everyday action can lead to prediction error when that action fails to produce the expected sensory states (e.g.: seeing someone spilling their drink). In this context, actions are “incorrect” or incongruent with the predicted action goal. Experiments on correct and incorrect actions point to the importance of investigating differences in neural oscillations across different frequencies. For example, van Schie and colleagues (2008) asked participants to observe simple finger movements and report when they diverted from external cues. The amplitude of evoked magnetic fields over the motor cortices was insensitive to the correctness of the observed action; however, further analysis of the data indicated that there was a stronger decrease in the beta frequency range during observation of incorrect versus correct actions over the motor cortices (Koelewijn et al., 2008). Finally, de Bruijn and colleagues (2007) showed that the observation of erroneous everyday actions is different from the processing of more symbolic errors. In their study, incorrect responses during the Flanker task elicited strong amplitudes at fronto-central electrodes, while unexpected outcomes of everyday actions yielded significantly higher P300 amplitudes over parietal sources. Furthermore, while theta band activity showed error related power increases during the Flanker task, the observation of erroneous actions did not significantly modulate theta band activity.

5.1.4. Concurrent action production and observation

There are only a handful of studies that have investigated the effect of concurrent motor plans on the perception of actions, and their results indicate a somewhat complex relationship between an active motor plan and an observed action. For example, Stanley and Miall (2007) reported that action incompatible stimuli elevated the blood-oxygen-level dependent (BOLD) response in the primary visual cortex, in the superior parietal lobule, and in the dorsal premotor cortex, while a compatible stimulus showed stronger neural response in the primary motor cortex and central and postcentral gyri. Similarly, Press and colleagues (2010) described both facilitative and attenuative forces on early event-related potentials (ERP) with EEG measurement. In their study, the early visual N1 component was increased for spatially compatible actions but attenuated for kinematically compatible actions, while the later N2 component was attenuated for both.

As of today, we know only one experiment focusing on neural oscillatory patterns during concurrent action preparation and observation. Silas and colleagues (2012) asked participants to execute simple button presses as quickly as possible while observing congruent, incongruent or irrelevant actions. The analyses focused only on the alpha frequency range over the central electrodes and measured whether congruency affected movement-related decreases in alpha oscillations. EEG measures indicated that both congruent and incongruent actions elicited stronger alpha suppression than irrelevant actions. Interestingly, while behavioural measurements showed faster reaction times for congruent actions, alpha suppression was not different between congruent and incongruent conditions. As all the above results indicate, there is a lack of consensus in the literature about how and in which frequency band congruency between observed and executed actions manifests.

One explanation for these divergent findings is that attentional focus and the relative timing of the observed actions relative to planned or executed actions can modulate early visual responses to the observed actions (Bortoletto et al., 2011, 2013). In a study by Bortoletto et al (2011), images of congruent or incongruent gestures were presented on the screen while participants were waiting for a "go" cue to initiate an already planned gesture. Early visual components 170ms after the presentation of the static gesture image were elevated when the planned actions were different from the observed one. This congruency effect was significant at sensors over the occipital cortex as well as at a central location over the motor cortex. In a follow-up study, the same authors modified the paradigm such that the observed gestures acted as a "go" cue for participants to initiate their own actions (Bortoletto et al., 2013). Furthermore, in this second experiment the attentional focus of the participants was also modulated. After performing the gesture, participants were required to report back either the executed or the observed action. Interestingly, this attentional modulation altered the congruency effect on the N170 component. When participants focused their attention on the observed action, the active motor plan did not modulate the N170; however, when their attentional focus was on the executed action, the presentation of a matching gesture elicited a larger N170. Importantly, the different results between the first and second experiment of Bortoletto's raises the question whether the relative timing of the prepared and observed action to each other could be a modulating factor of the underlying neural pattern. It is possible that during action preparation there are more neural resources to analyse and match incoming stimuli with the concurrently planned one, resulting in higher activation related to error or conflict processes. In contrast, during action execution or at the time of initiation, sensory feedback that is in line with current plans may elicit more neuronal activity. These seemingly conflicting results from Bortoletto and colleagues' study can be explained by predictive coding theories. Longer reaction times and elevated neural activity can signal the additional neural resources related to prediction error. Furthermore, recent experiments show that attentional processes can modulate and even reverse the effect of predictive processes by increasing neural selectivity to goal-relevant stimuli (Jiang et al., 2013; Kok et al., 2012). Thus, the attentional focus on planned actions and the temporal proximity to action execution could reduce error related signals and strengthen the neural processing of the sensory stimulus that is in line with task demands.

5.1.5 Present experiment

Overall, previous literature highlights the importance of investigating congruency related effects with a broader scope, focusing on multiple frequencies and spatial locations. As apparent from these previous studies, results are not consistent throughout the literature and replications of results are sparse. The effect of observed actions on motor plans seems to be mostly clear, showing a facilitation effect if observed and planned actions are congruent. The effect of the motor system on action observation is less straightforward. EEG, fMRI and MEG experiments have reported facilitation as well as attenuation, depending on attentional focus, measurement type, and examined frequency band.

The main aim of the present experiment was to investigate early frequency changes during concurrent action preparation and observation. Based on the reviewed literature, we identified three key points that were addressed with the present study. Firstly, there is a lack of research exploring multiple frequency ranges focusing on neural activity from all brain regions during concurrent action execution and observation. We investigated three oscillatory bands most commonly linked to action observation and execution: theta, alpha and beta frequencies. Furthermore, to offer a thorough description of neural activity, we analysed sensor-space event-related fields (ERFs) and implemented source-reconstruction methods. Secondly, previous literature on concurrent action preparation and observation failed to investigate how this dual task differs from either simple action observation or action execution alone. Here we measured neural activity related to action observation in the absence of an active motor plan. We used this "baseline" condition to examine how a concurrent motor task affects action observation related neural oscillations. Thirdly, the two reviewed experiments of Bortoletto and colleagues (2011, 2013) suggest that the neural response to observed action might be influenced by whether it is observed during action preparation or initiation. We modulated the relative timing of the observed and planned actions such that observed actions were presented either during action preparation or at the time of action initiation.

Here, we present a replication and extension of Bortoletto and colleagues' paradigm, using magnetoecephalography (MEG) and focusing on the first 500 ms after the processing of a gesture. During the experiment, participants prepared to execute simple hand gestures while we presented images of either congruent or incongruent gestures. We measured neural activity related to action observation in the absence of an active motor plan to examine the general effect of a concurrent motor plan on neural patterns. Based on previous research, we expected to see an overall elevated neural pattern for conditions in which participants were planning an action over conditions in which they only observed one. We predicted stronger cortical theta activity and lower beta activity in central locations in the presence of a motor plan. Based on the results of Silas and colleagues (2012), we anticipated no congruency effect in the alpha range, but a stronger suppression of the beta band in the incongruent condition in line with the results of Koelewijn et al. (2008). In comparison to Bortoletto and colleagues EEG study (2013), here (1) we used MEG for greater sensitivity to sources; (2) analysed three oscillatory bands, ERFs and implemented source reconstruction for a comprehensive picture on neuronal activity; (3) investigated the effect of an active motor plan over baseline action observation; and (4) modulated the relative timing of action observation and execution in one design to explore the complex interactions behind concurrent action observation and execution.

5.2. Materials and methods

5.2.1. Participants

Twenty healthy, young volunteers took part in the study, ranging in age from 21 to 39 years (M = 26.3, SD = 4.9 years; 10 males). All participants were right handed, had normal or corrected to normal visual acuity, and no history of mental or neurological diseases. Participants gave informed consent and received $40 as a reimbursement. Approval for this study was granted by The University of Queensland in accordance with the Australian Health and Medical Research Council's guidelines.

5.2.2. Stimuli and procedure

Participants attended two recording sessions, one week apart, to complete the *"preparation"* and *"initiation"* parts of the task in a counterbalanced order. Each session lasted around an hour. Before recording, participants performed a short training while seated in the magnetically shielded room. The schematic of the experimental paradigm is illustrated in Figure 5.1. During the experiment, an initial word cue indicated one of four possible hand gestures ('OK', 'Peace', 'Thumbs-Up', 'Point'). Participants prepared and performed the cued gesture with their right hand as quickly as possible in response a 'Go' cue (66% of trials). In the action *initiation task* 'Go' cues consisted of a static image of a hand gesture that either matched (*"congruent"*) or did not match (*"incongruent"*) the cued and executed action. In the action *preparation task* a green circle served as a 'Go' cue, and 500ms (+/- 100ms) before this 'Go' cue a static image of a hand gesture was presented and was not task-relevant for participants. One third of the trials served as *"baseline"* when, instead of the initial word cue, the hand image was presented, thereby involving no concurrent motor task. In all conditions, evoked neural responses were measured in relation to the presented hand gesture image, either presented at the time of movement initiation, during motor planning, or with no concurrent motor task. The delays between the word cue and the 'Go' cues, and between the hand image and the following cues, were jittered to rule out processes linked to temporal expectation. After performing the action, participants were required to report the action they had just performed by selecting the correct response among four possible gestures. The inter-trial delay varied between 1000 and 2000ms. The overall number of specific gestures performed and presented was equal across all conditions and the order randomised individually for each participant. Each session consisted of five blocks of 72 trials (360 trials total), giving a total of 120 trials each for *congruent*, *incongruent* and *baseline* conditions per session.

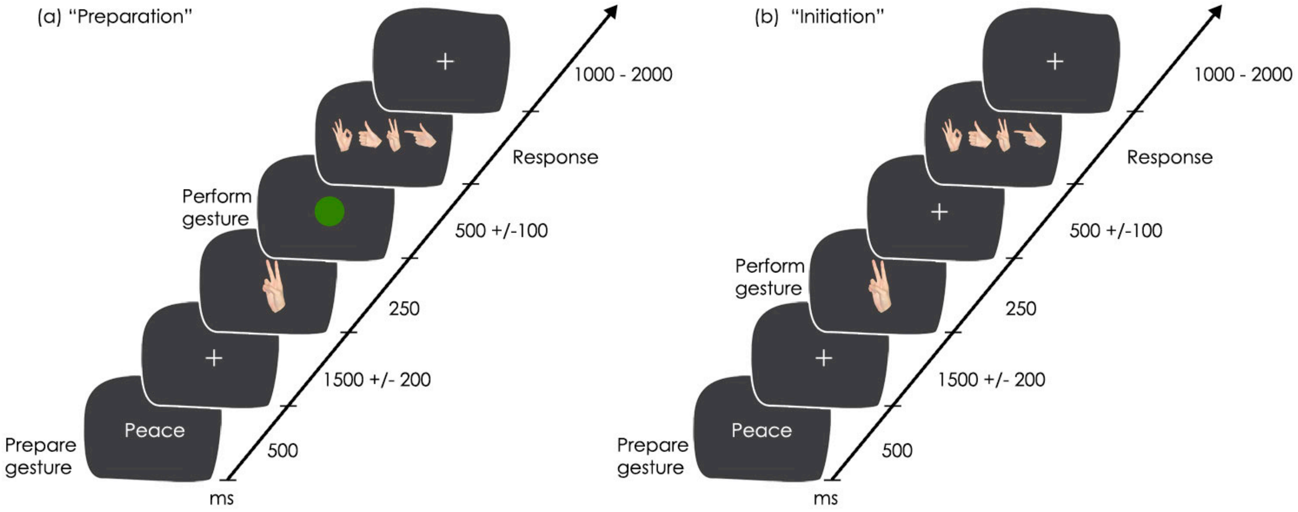

Figure 5.1. Time course of a typical trial of the *Preparation* **A|** and *Initiation* **B|** parts of the experiment.

The participants' hands were resting on a table, with their right index finger on a resting-position button. They were asked to perform the action as quickly as possible upon presentation of the 'Go' cue and return to the starting position after movement. Participants' actions and their hand-positions were monitored by the experimenter via a camera. However, participants were prevented from seeing their own actions by a cardboard box covering their right hand. The participants' left hands were positioned on a four-button, MEG-compatible response box for reporting the performed actions. Stimuli were presented centrally at fixation and projected into a screen positioned 90 cm in front of participants.

5.2.3. Structural MRI recording

Individual magnetic resonance images (MRI) were obtained during separate sessions for source space coregistration. A 3-Tesla Siemens Trio MRI scanner (Siemens Medical Solutions, Erlangen, Germany) with a 32-channel headcoil was used to acquire high-resolution T1-weighted images, covering the entire brain (TR= 1900, TE=2.52 ms, FA=9°, 176 cubic matrix, voxel size =1 cubic mm).

5.2.4. MEG data acquisition

Brain activity was recorded in a magnetically shielded room, using a whole-head, 306-sensor (102 magnetometers and 102 pairs of orthogonally oriented planar gradiometers) Elekta Neuromag TRIUX system (Elekta Neuromag Oy, Helsinki, Finland). Signals were sampled at 1 kHz and on-line band-pass filtered between 0.1-300 Hz. Head position inside the MEG helmet was continuously monitored using five head tracking coils, three positioned on the forehead and two behind the ears. The location of these coils with respect to anatomical fiducials was determined before each recording session with an electromagnetic digitizer system (FastTrak, Polhemus, Colchester, VT, USA).

5.2.5. MEG data analyses

5.2.5.1. Preprocessing

Initial pre-processing of the MEG data used the temporal extension of the Signal-Space Separation (SSS; Taulu and Simola, 2006) method implemented in the Max-Filter software (Elekta Neuromag, Helsinki, Finland). During this step the active noise cancellation signal was removed from the data and bad channels were interpolated.

Subsequent pre-processing steps were carried out using SPM12 (Wellcome Trust Centre for Neuroimaging, University College London, UK) implemented in MATLAB 12b (The MathWorks, Inc., Natwick, MA, USA). Data were downsampled to 500 Hz and band-pass filtered at 1-45 Hz (Butterworth), then epoched between -400 to +800ms relative to the visual onset of the presented hand image in each trial. For sensor level statistics, data from the two recording sessions was merged into a single file with six conditions and baseline corrected from -200 to -25ms pre-stimulus. Sensor data were averaged per participant and per condition with SPM’s robust averaging algorithm (Litvak et al., 2011). This method can supress artefacts with narrow time and frequency ranges without the necessity of rejecting the affected trials. The algorithm allocates weights to each trial based on how artefactual the given trial is, so the effect of outlier trials on the averaged data is minimised (Litvak et al., 2011). As robust averaging can introduce high-frequency noise to the data, a 45 Hz low-pass filter was applied after averaging.

5.2.5.2. Source space modelling

For source space modelling we kept the two recording sessions separate and applied robust averaging to individual files, followed by filtering the data with 45 Hz low-pass filter. We tested several source reconstruction methods implemented in SPM: hyperprior models (IID & COH), normal and iterative multiple sparse priors methods as individual inversion (GS & MSP) or as group inversion (MSP). These statistical analyses yielded no significant differences between conditions even at a very lenient $P < 0.001$ uncorrected threshold level. Here we describe the procedure of group inversion with the MSP method, which we used to illustrate the overall source reconstruction of neural activity during the task conditions.

Individual structural scans were used to create canonical head model meshes. Coregistration was based on three fiducial points (nasion, left and righ pre-auricula) and headshape points, followed by forward computation using a single shell model. Group inversion with multiple sparse priors methods were used for two time windows, based on a priori hypotheses: 50-200ms (“early” responses, primarily focusing on the M170 response) and 220-400ms (“later” responses, mainly around 300ms). The three experimental conditions were inverted together. Inversion was based on the combined data of magnetometer and gradiometer channels, restricted to the 1-45Hz frequency range. A hanning taper was applied to reduce noise around the edge of the time windows. Source inversion results were summarized as 3D NIfTI images for each subject, recording session, and condition, smoothed by a 8 × 8 × 8mm full-width-at-half-maximum (FWHM) Gaussian kernel. For the “early” time window, images were saved between 160-190ms and 70-190ms. For the “late” responses, we used three time windows: 250-280ms, 290-340ms, and 250-400ms. These different time-windows were created to allow an overall picture of earlier and later responses and also to specifically encapsulate neural responses at significant time-points based on a priori knowledge (e.g.: 160-190ms time-window for visual response at 170ms after stimulus onset). These images were analysed with random-effects analysis, based on the general linear model. Factorial models were built for each time window and action phase (preparation, initiation) with factors of *participants* and *condition* (baseline, congruent, incongruent). Based on these 10 models, no contrasts between conditions (i.e.: congruent versus baseline) yielded significant results on the $P < 0.001$ uncorrected threshold level. In the results section below, we present only the source reconstruction results linked to 160-190ms and 290-340ms time windows.

5.2.5.3. Sensor space analysis

The Neuromag system contains planar gradiometers that measure the spatial gradient of the magnetic field: two directions in a plane parallel to the head surface. When combined for a single location, the planar field gradient gives the maximal signal typically located above the neural source

(Hämäläinen et al., 1993; Parkkonen, 2010). For this reason, gradiometer data is more suitable for sensor-level data analyses than magnetometers. We combined the averaged event-related fields of planar gradiometers at any sensor location and converted this data into 3D spatiotemporal volumes. As the present experiment aimed to investigate early neuronal responses, we restricted our time-frame to 80-500ms. For each time point within this time-window, we created a 2D scalp map applying linear interpolation between sensors with a dimension of 64 pixels in each spatial direction. These scalp maps were then stacked over peristimulus time and smoothed by a 7 × 7mm × 1ms FWHM Gaussian kernel. The above steps resulted in 3D images with space (x, y) and time (z) dimension and were further analysed by the traditional second-level SPM analyses based on the general linear model. A flexible factorial model was built with main factors of *participants*, *action phase* (preparation, initiation) and *condition* (baseline, congruent, incongruent).

5.2.5.4. Time-frequency analysis

Time-frequency representations of the spectral power were computed using Morlet wavelet method with a fixed time-window (-100 and +700ms) on the combined gradiometer data. Four wavelet cycles for theta band (4-8 Hz), five for alpha (8-12 H), and six for beta (13-30 Hz) were applied. For each frequency band, the log-power was calculated, baseline-corrected, and scaled compared to the -100 and 0ms pre-stimulus time-window. Next, 3D images (space × space × time) of averaged power for each frequency band between 80 and 500ms post-stimulus were saved individually for every participant. These images were then smoothed with a 3 × 3mm × 1ms FWHM Gaussian kernel and analysed with a flexible factorial model with *participants*, *action phase* (preparation, initiation) and *condition* (baseline, congruent, incongruent) as the main factors.

Other studies of frequency changes associated with movement tasks have focussed on "mu" rhythms, which are composed of a combination of alpha and beta frequency oscillations (Hari, 2006). Here we report motor-related changes in alpha and beta frequencies separately and for clarity refer to these specifically as alpha and beta frequencies, although results are comparable with other studies that label such activity as "mu" rhythms.

For all contrasts, significant activation was defined by a cluster-level probability threshold of $P_{FWE} < 0.05$, corrected for the whole time-space search volume (with clusters defined by the voxel-level threshold $P < 0.001$).

5.2.5.5. Visualisation of frequency amplitude changes compared to baseline

In order to visualise changes in theta, alpha, and beta frequency signals over time during action observation with concurrent movement preparation/initiation compared with observation alone (baseline condition), we extracted and plotted field intensity values for each condition over selected sensor locations. Difference scores between each concurrent observation/execution condition and the baseline observation condition alone were calculated for each frequency band, focusing on central and left parieto-occipital areas (e.g.: beta preparation congruent versus beta preparation baseline, based on four sensor values averaged over central motor areas). Field-intensity values were extracted from grand average results. Locations were selected based on those showing the strongest modulation during the frequency analyses. Similarly, in order to visualise differences between congruent and incongruent conditions, we extracted field-intensity values for difference waves of congruent minus incongruent conditions, calculated separately for preparation and initiation conditions in theta, alpha, and beta frequency ranges. Field-intensity values extracted from grand average results, based on the average of four electrodes over central and parieto-occipital regions.

5.3. Results

5.3.1. Source space modelling

Figures 5.2 and 5.3 show the source reconstruction results for neuronal activity at around 170ms and 300ms after action observation. Neuronal sources were present in brain areas commonly linked to action perception: occipital, parietal, postcentral, supplementary motor area, and in the middle frontal gyrus. Additionally, sources in the middle temporal gyrus, fusiform gyrus, and parahippocampal regions also show a common activation in all conditions linked to the observation of actions.

Comparing Figure 5.2 and Figure 5.3, neural sources appear to be more widespread at 300ms compared to 170ms. Further visual inspection shows some common trends between experimental conditions in both time-points. Sources linked to action initiation appear stronger than sources linked to action preparation. Baseline action observation seems to elicit less strong sources than congruent or incongruent conditions overall. Regardless of action phase, incongruent actions appear to yield somewhat stronger source activation than congruent actions. Furthermore, based on Figure 5.2 and Figure 5.3, sources over the motor cortex appear to be stronger when there is an active motor plan (i.e.: congruent and incongruent versus baseline) compared to baseline observation. However, as we noted in the methods section, contrasts between experimental conditions did not reach statistical significance on a $P < 0.001$ uncorrected threshold level, therefore none of the apparent differences in source activity between these conditions are statistically significant. Nonetheless, the apparent differences here in source space are in similar locations across conditions as the statistically significant effects found in sensor-level analysis reported below.

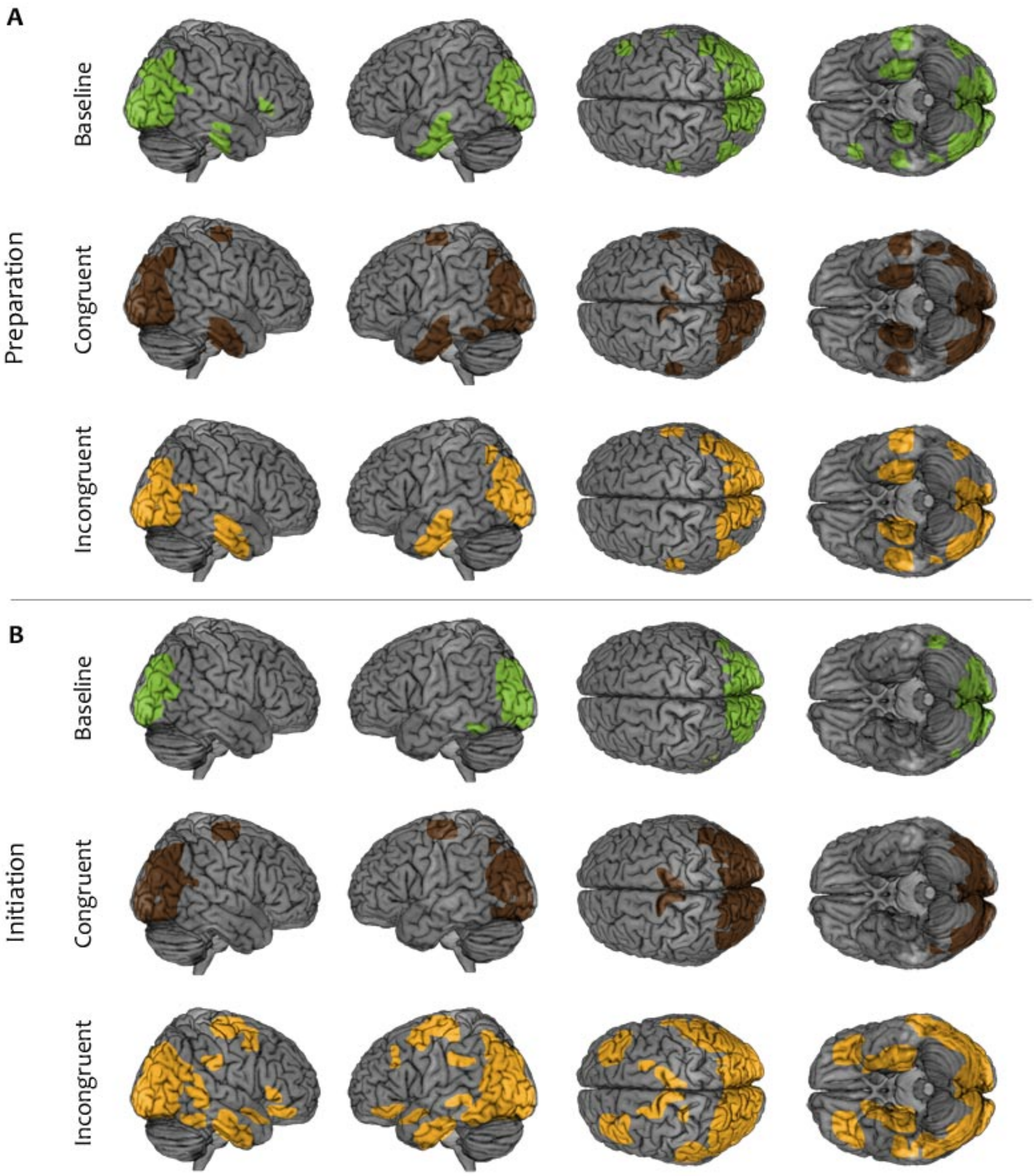

Figure 5.2. Source reconstruction results rendered to individual template brain to illustrate the overall effects of baseline, congruent or incongruent action observation separately for **A|** action preparation and **B|** initiation, at the 160-190ms time-window.

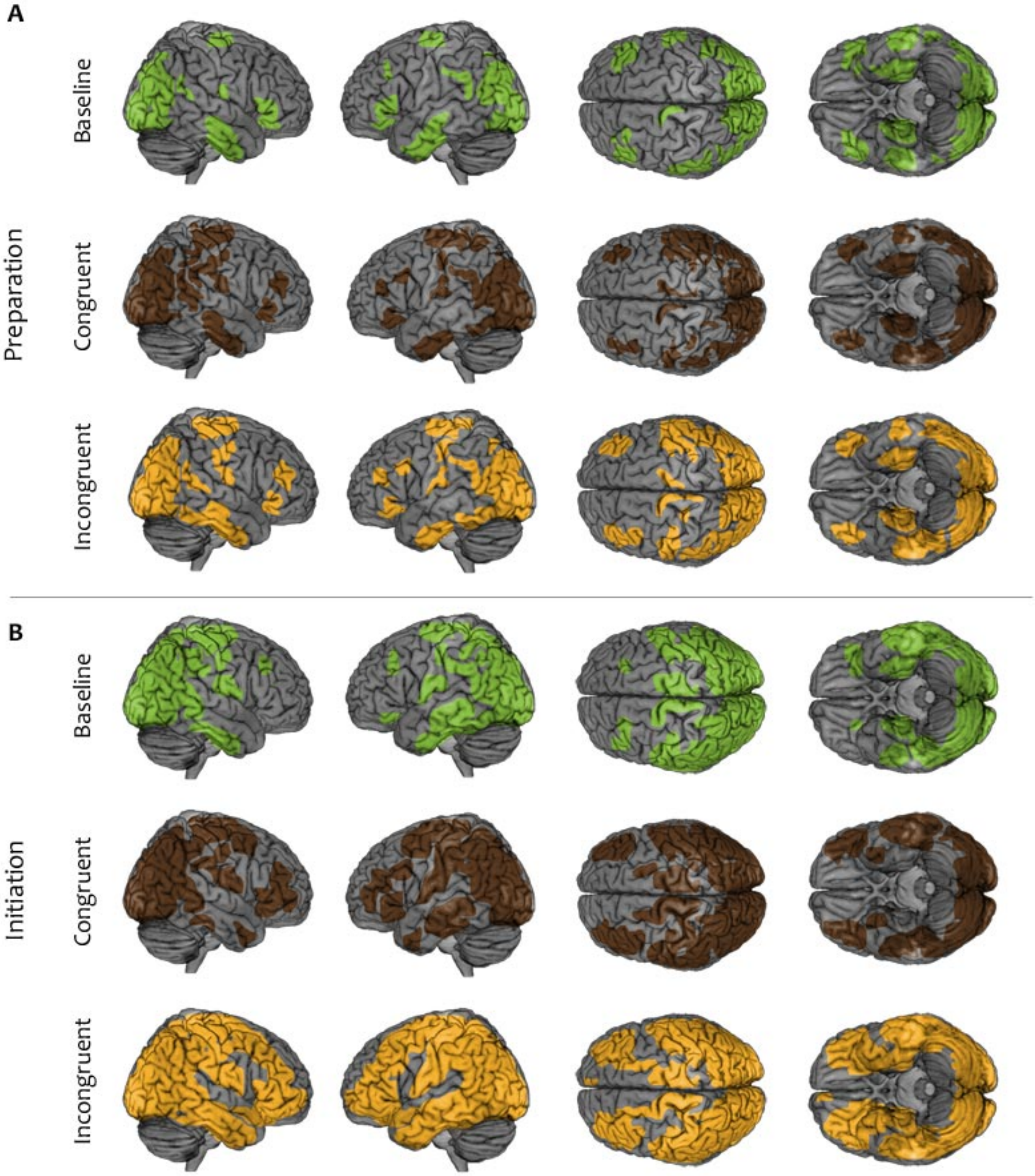

Figure 5.3. Source reconstruction results rendered to individual template brain to illustrate the overall effects of baseline, congruent or incongruent action observation separately for **A|** action preparation and **B|** initiation, at the 290-340ms time-window.

5.3.2. Sensor space analysis

Results for the ERF analysis are shown in Figures 5.4 and 5.5. These figures depict two-dimensional statistical maps showing significant sensor-space differences based on the factorial model of *participants*, *action phase* (preparation, initiation) and *condition* (baseline, congruent, incongruent). To illustrate the time course of the significant effects we also provided plots of field-intensity values over the regions showing significant differences.

Sensor-space analysis revealed stronger ERFs over central electrodes whenever participants had an active motor plan compared to baseline action observation (Figure 5.4). This elevated ERF also showed a unified temporal pattern across both preparation and initiation conditions, significant between ~ 150-200ms after action observation (see Table 5.1 for the list of significant time points). Furthermore, during action preparation (Figure 5.4A), the observation of congruent actions compared to baseline elicited a significant neural response over the left occipital electrodes, showing a strong peak around 170ms. During action initiation, congruent actions showed stronger ERFs over bilateral inferior frontal areas peaking around 300ms after action presentation (Figure 5.4B). Baseline versus congruent or incongruent contrasts did not reveal significant clusters.

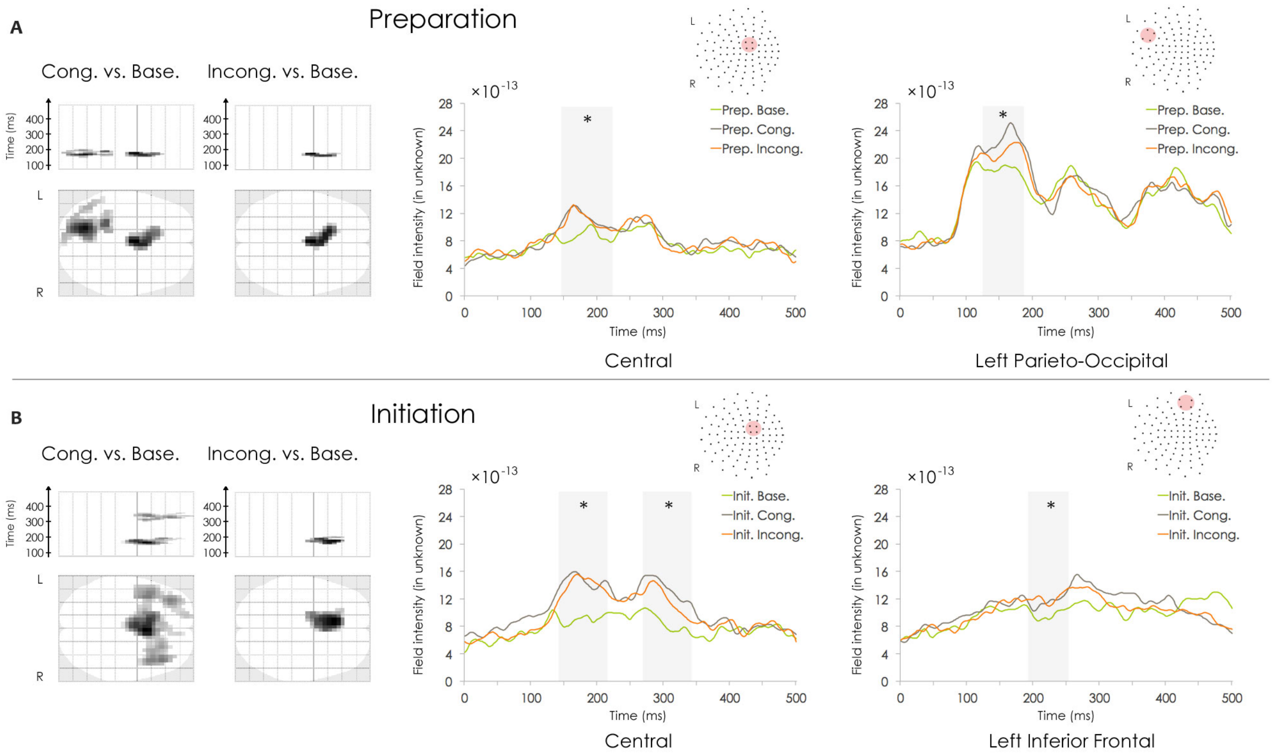

Figure 5.4. Significant sensor-space differences and their time course on averaged field-intensity values. **A|** On the left, two-dimensional statistical maps showing significant sensor-space differences in the congruent vs. baseline and incongruent vs. baseline contrasts during action preparation. Top row shows space and time dimension, bottom row 2D sensor space. On the right, the average field-intensity

values of four sensors, in a central and left occipital locations. **B|** Two-dimensional statistical maps showing significant sensor-space differences in the congruent vs. baseline and incongruent vs. baseline conditions during action initiation. On the right, the average field-intensity values of four sensors, in a central and left inferior frontal region. Shaded areas and * denotes significant differences corresponding to statistical maps.

Table 5.1.

Significant amplitude differences in the sensor space analysis.

Condition Sensor-space	Number of voxels	Z	P cluster corrected	mm	mm	ms
Prep. Cong. vs. Baseline						
Central	415	4.51	0.001	0	-3	176
		4.27		4	2	162
		3.84		-8	18	174
Left Occipital	655	4.38	< 0.000	-17	-68	166
		3.94		-21	-41	188
		3.74		-13	-73	194
Prep. Incong. vs. Baseline						
Central	267	4.26	0.006	0	-3	174
		4.13		0	8	162
		3.39		-13	24	174
Init. Cong. vs. Baseline						
Central	1005	5.08	< 0.000	4	8	160
		4.58		0	-3	172
		4.05		42	29	186
Left Frontal	457	4.01	0.001	-38	13	340
		3.96		-34	40	328
		3.90		-17	8	344
Central	175	3.88	0.021	-8	8	312
		3.73		4	24	322
		3.65		4	13	314
Init. Incong. vs. Baseline						
Central	596	4.12	< 0.000	-8	24	174
		4.02		-8	18	164
		3.88		-8	8	188

Focusing on congruency effects, we found that congruent versus incongruent actions during action preparation showed a stronger neural response over right-central electrodes, around 100ms after action presentation (Figure 5.5A, Table 5.2). Furthermore, congruent actions versus incongruent actions during initiation elicited stronger ERFs over right frontal electrodes around 100ms. Incongruent versus congruent contrasts did not reach significance during the first 500ms after stimulus presentation.

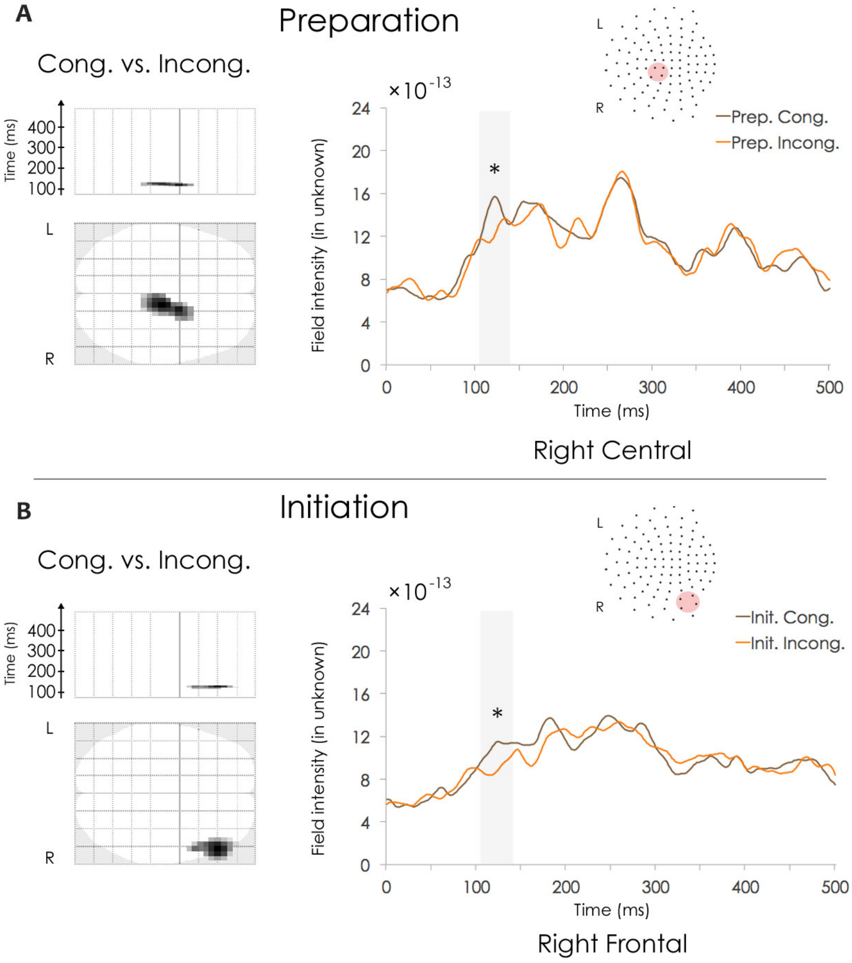

Figure 5.5. Significant sensor-space differences and their time course on averaged field-intensity values. **A|** On the left, two-dimensional statistical maps showing significant sensor-space differences in the congruent vs. incongruent contrast during action preparation. Top row shows space and time dimension, bottom row 2D sensor space. On the right, average field-intensity values of four sensors, in central location. **B|** Two-dimensional statistical maps showing significant sensor-space differences in the congruent vs. incongruent condition during action initiation. On the right, average field-intensity values of four sensors, in the right frontal region. Shaded areas and * denotes significant differences corresponding to statistical maps.

Table 5.2.

Significant amplitude differences in the sensor space analysis.

Condition Sensor-space	Number of voxels	Z	P cluster corrected	mm	mm	ms
Prep. Cong. vs. Incong						
Central	201	4.59	0.039	13	-19	120
		4.42		17	-3	118
Init. Cong. vs. Incong						
Right Frontal	124	3.98	0.047	55	34	122
		3.56		55	13	122

5.3.3. Time-frequency analysis

5.3.3.1. Theta band

Results of the sensor level analysis of the theta frequency band are illustrated in Figure 5.6 and Table 5.3. Focusing on the time window of 80-500ms after stimulus presentation, we investigated how the theta frequency band changes as a function of *action phase* (preparation, initiation) and *condition* (baseline, congruent, incongruent).

Theta frequency changes indicated stronger neuronal responses during action initiation compared to action preparation, and overall lower amplitudes in the baseline condition compared to congruent or incongruent conditions. Baseline versus congruent or incongruent contrasts did not reveal significant clusters in the theta band. During action preparation (Figure 5.6A), left parietal sensors showed significantly higher theta amplitudes for congruent actions versus baseline conditions between 150 and 300ms after stimulus onset, while incongruent actions versus baseline resulted in greater neuronal responses over central regions from 150ms onwards (Table 5.3). In the movement initiation phase (Figure 5.6B), both congruent and incongruent actions elicited very similar patterns over central and bilateral frontal sensors. Neural responses to observed actions during concurrent action compared to baseline action observation revealed higher theta amplitudes between ~ 170 - 500ms after stimulus onset. Theta band did not show any significant difference between congruent and incongruent actions.

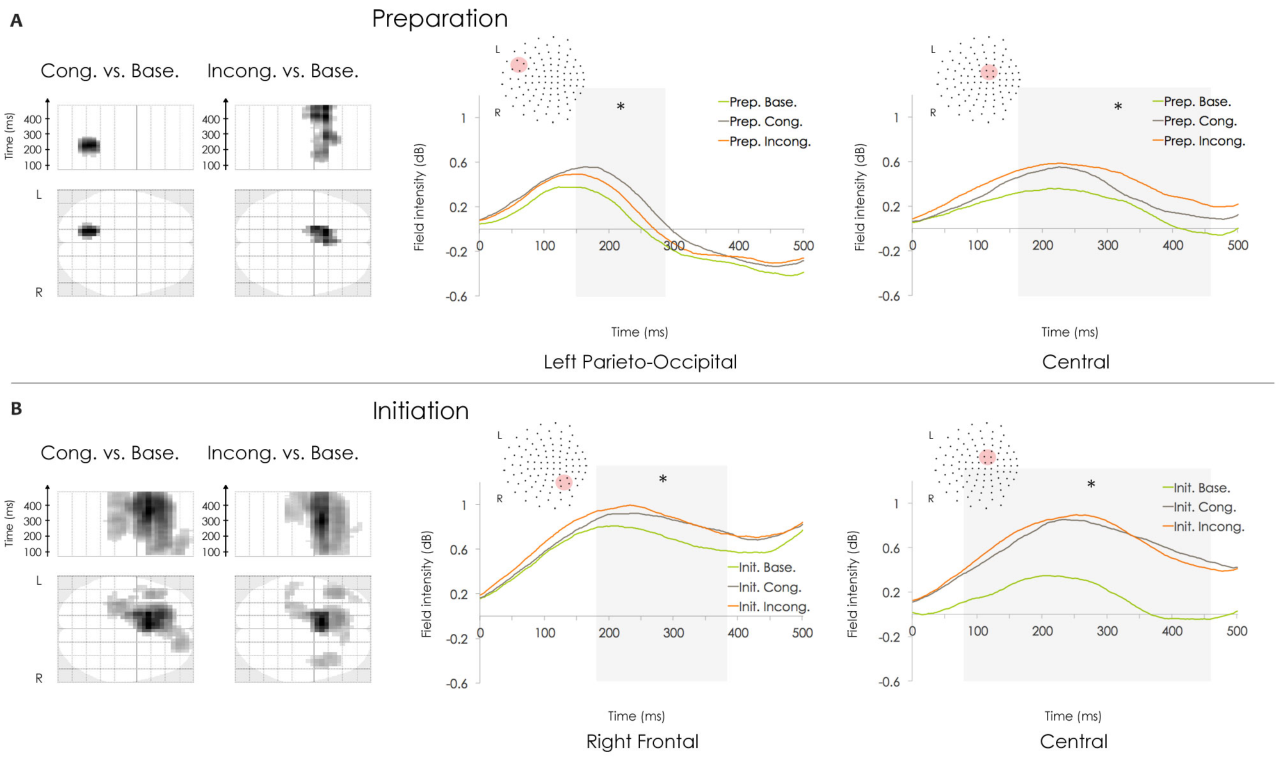

Figure 5.6. Significant sensor-space differences in the theta band and their time course on averaged field-intensity values. **A|** On the left, two-dimensional statistical maps showing significant sensor-space differences in the congruent vs. baseline and incongruent vs. baseline contrasts during action preparation. Top row shows space and time dimension, bottom row 2D sensor space. On the right, the average field-intensity values of four sensors, in central and left parietal regions. **B|** Two-dimensional statistical maps showing significant sensor-space differences in the congruent vs. baseline and incongruent vs. baseline conditions during action initiation. On the right, the average field-intensity values of four sensors, in left and right frontal regions. Shaded areas and * denotes significant differences corresponding to statistical maps.

Table 5.3.
Power differences between congruent and incongruent versus baseline conditions, in the theta frequency range.

Condition Sensor-space	Number of voxels	Z	P cluster corrected	mm	mm	ms
Prep. Cong. vs. Baseline						
Left Parieto-Occ.	782	4.37	0.015	-13	-62	230
		4.22		-13	-57	246
		3.95		-8	-57	202
Prep. Incong. vs. Baseline						
Central	2911	4.65	< 0.000	-13	13	428
		4.56		-13	13	484
		4.55		-13	13	494
Init. Cong. vs. Baseline						
Central	17779	6.58	< 0.000	-4	13	366
		6.46		-17	13	388
		6.29		-13	13	436
Left Frontal	584	4.22	0.031	-42	18	362
		3.89		-42	29	362
		3.28		-51	2	364
Init. Incong. vs. Baseline						
Central	13363	7.33	< 0.000	-8	8	302
		7.18		-8	8	318
		7.02		-8	8	338
Left Frontal	2062	4.49	< 0.000	-42	29	296
		4.46		-42	29	268
		4.35		-42	18	336
Right Frontal	1921	4.19	< 0.000	42	8	138
		4.17		47	8	164
		4.09		47	8	154

5.3.3.2. Alpha band

The results of the factorial model of *participants*, *action phase* (preparation, initiation) and *condition* (baseline, congruent, incongruent) based on alpha frequencies are illustrated in Figure 5.7. The congruent versus baseline contrast during action initiation revealed a left inferior frontal area that showed elevated alpha amplitudes around 400ms. Incongruent versus baseline contrast was significant an earlier time point, around 300ms over central sensors (Table 5.4).

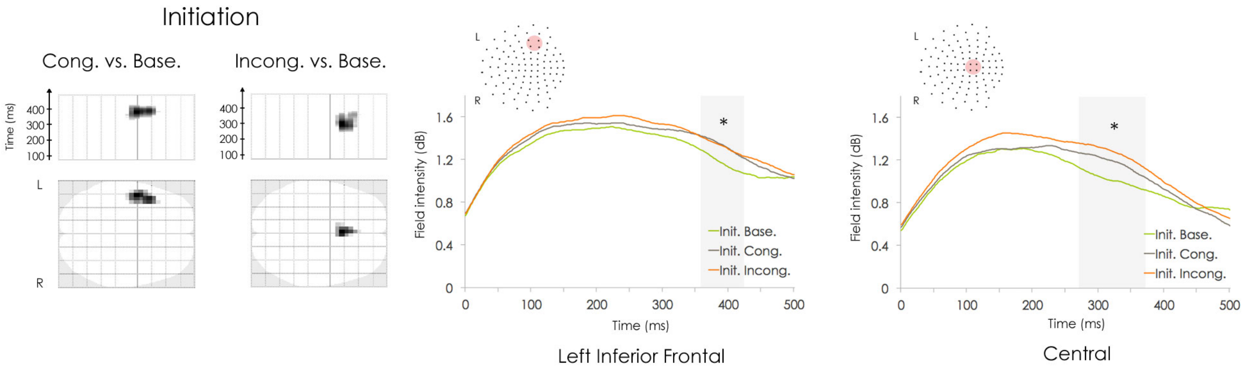

Figure 5.7. Significant sensor-space differences in the alpha band and their time course on averaged field-intensity values. On the left, two-dimensional statistical maps showing significant sensor-space differences in the congruent vs. baseline and incongruent vs. baseline contrasts during action initiation. Top row shows space and time dimension, bottom row 2D sensor space. On the right, the average field-intensity values of four sensors, in central and left inferior frontal regions. Shaded areas and * denotes significant differences corresponding to statistical maps.

Table 5.4

Power differences between congruent and incongruent versus baseline conditions during action initiation phase, in the alpha frequency range.

Condition Sensor-space	Number of voxels	Z	P cluster corrected	mm	mm	ms
Init. Cong. vs. Baseline						
Left Central	614	4.33	0.010	-47	-3	386
		4.16		-42	13	396
Init. Incong. vs. Baseline						
Central	577	4.89	0.012	0	13	296
		4.88		0	13	310
		3.69		0	29	362

5.3.3.3. Beta band

Significant results of the beta frequency range based on the factorial model of *participants*, *action phase* (preparation, initiation) and *condition* (baseline, congruent, incongruent) are illustrated in Figures 5.8 and 5.9 and Tables 5.5 and 5.6. Oscillatory changes indicated overall stronger beta suppression for both conditions with an active motor plan versus baseline action observation (Figure 5.8). This effect was present during action preparation and initiation over the right central sensors. During action initiation, this suppression effect was significant at an earlier time point (~ 200ms) than during action preparation (~300ms), in correspondence with the temporal proximity of the actual movement (Table 5.5).

Table 5.5

Power differences between baseline versus congruent and incongruent conditions, in the beta frequency range.

Condition Sensor-space	Number of voxels	Z	P cluster corrected	mm	mm	ms
Prep. Baseline vs. Cong.						
Right Central	360	4.32	0.018	26	13	486
		4.26		26	8	494
		3.88		21	-3	494
Prep. Baseline vs. Incong.						
Right Central	577	4.26	0.004	17	24	324
		3.76		17	40	292
		3.75		21	29	292
Right Central	787	4.23	0.001	17	18	488
		4.22		21	18	466
		4.21		21	18	456
Right Frontal	399	3.86	0.014	51	24	370
		3.78		51	24	390
		3.72		51	34	444
Init. Baseline vs. Cong.						
Right Central	4247	5.48	< 0.000	30	2	394
		5.46		30	2	380
		5.39		30	8	412
Init. Baseline vs. Incong.						
Right Central	1454	4.42	< 0.000	26	13	500
		4.18		21	13	444
		4.13		21	13	434

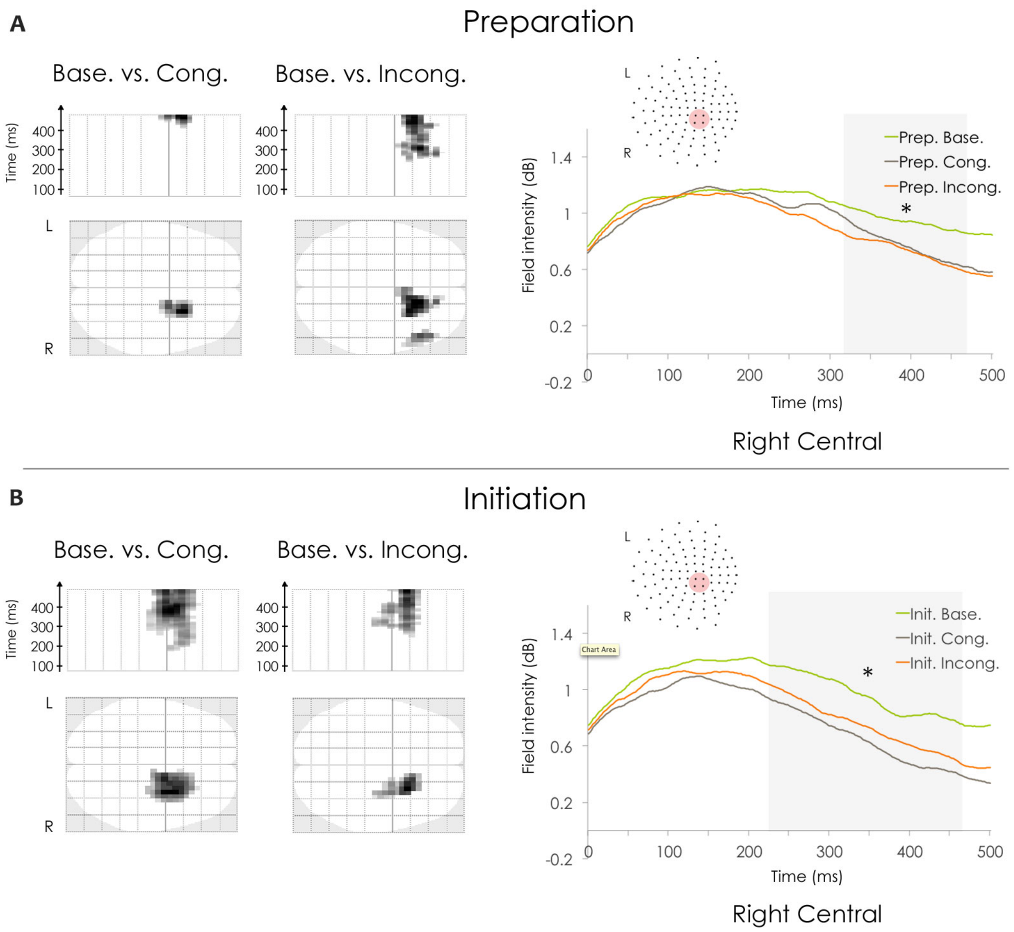

Figure 5.8. Significant sensor-space differences in the beta band and their time course on averaged field-intensity values. **A|** On the left, two-dimensional statistical maps showing significant sensor-space differences in the baseline vs. congruent and baseline vs. incongruent contrasts during action preparation. Top row shows space and time dimension, bottom row 2D sensor space. On the right, average field-intensity values of four sensors, in central location. **B|** Two-dimensional statistical maps showing significant sensor-space differences in the baseline vs. congruent and baseline vs. incongruent conditions during action initiation. On the right, average field-intensity values of four sensors, in central location. Shaded areas and * denotes significant differences corresponding to statistical maps.

Congruent and incongruent versus baseline contrasts in the beta frequency band yielded one significant effect (Figure 5.9). Congruent versus baseline during the action initiation condition revealed a significant left occipital area. As Table 5.6 shows, congruent actions resulted in stronger neural responses in two time windows, between ~270-300ms and ~350-450ms. When we investigated the congruency effect on beta band oscillation, we found that this left occipital area also showed stronger activity during congruent versus incongruent conditions over similar timepoints as mentioned above. We also found that beta band suppression was reliably stronger for incongruent actions during movement initiation over the left inferior frontal area.

Table 5.6

Power differences between congruent and baseline and congruent versus incongruent conditions, during action initiation phase, in the beta frequency range.

Condition Sensor-space	Number of voxels	Z	P cluster corrected	mm	mm	ms
Init. Cong. vs. Baseline						
Left Parieto-Occ.	1293	4.88	< 0.000	-17	-78	264
		4.57		-17	-78	246
		4.63		-17	-78	376
Init. Cong. vs. Incong						
Left Parieto-Occ.	316	4.04	0.026	-17	-78	272
		3.81		-13	-84	282
		3.37		-8	-87	304
Left Parieto-Occ.	361	4.00	0.018	-13	-73	368
		3.81		-13	-78	390
		3.55		-17	-78	408
Left Frontal	317	3.95	0.025	-26	45	354
		3.86		-26	45	338
		3.81		-26	45	328

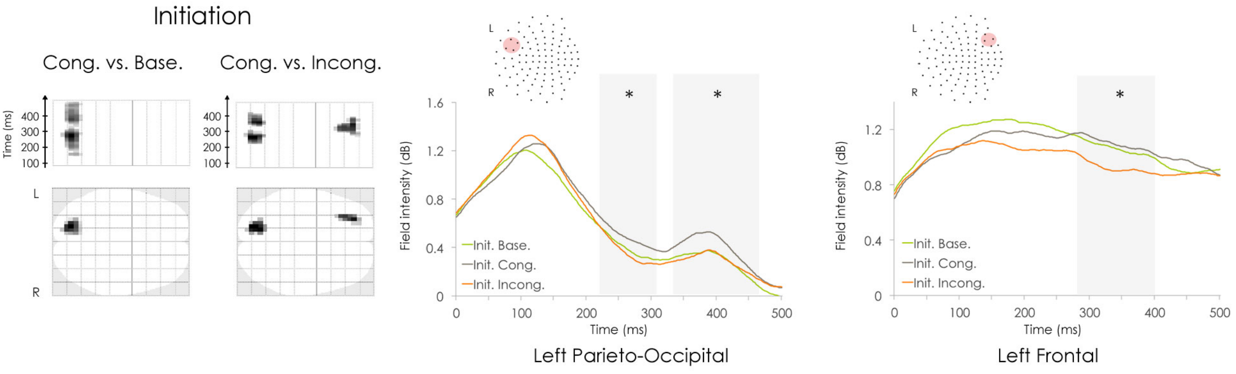

Figure 5.9. Significant sensor-space differences in the beta band and their time course on averaged field-intensity values. On the left, two-dimensional statistical maps showing significant sensor-space differences in the congruent vs. baseline and congruent vs. incongruent contrasts during action initiation. Top row shows space and time dimension, bottom row 2D sensor space. On the right, the average field-intensity values of four sensors, in left occipital and left frontal regions. Shaded areas and * denotes significant differences corresponding to statistical maps.

5.3.3.4. *Power changes during concurrent action preparation and observation*

In the following section we will summarise the power changes of the three investigated frequency bands demonstrated during our paradigm. Figure 5.10 displays how theta, alpha and beta frequencies during concurrent action observation and preparation differ from baseline action observation. We have chosen to focus on the central motor area and the left parieto-occipital area as our paradigm modulated these two locations most significantly.

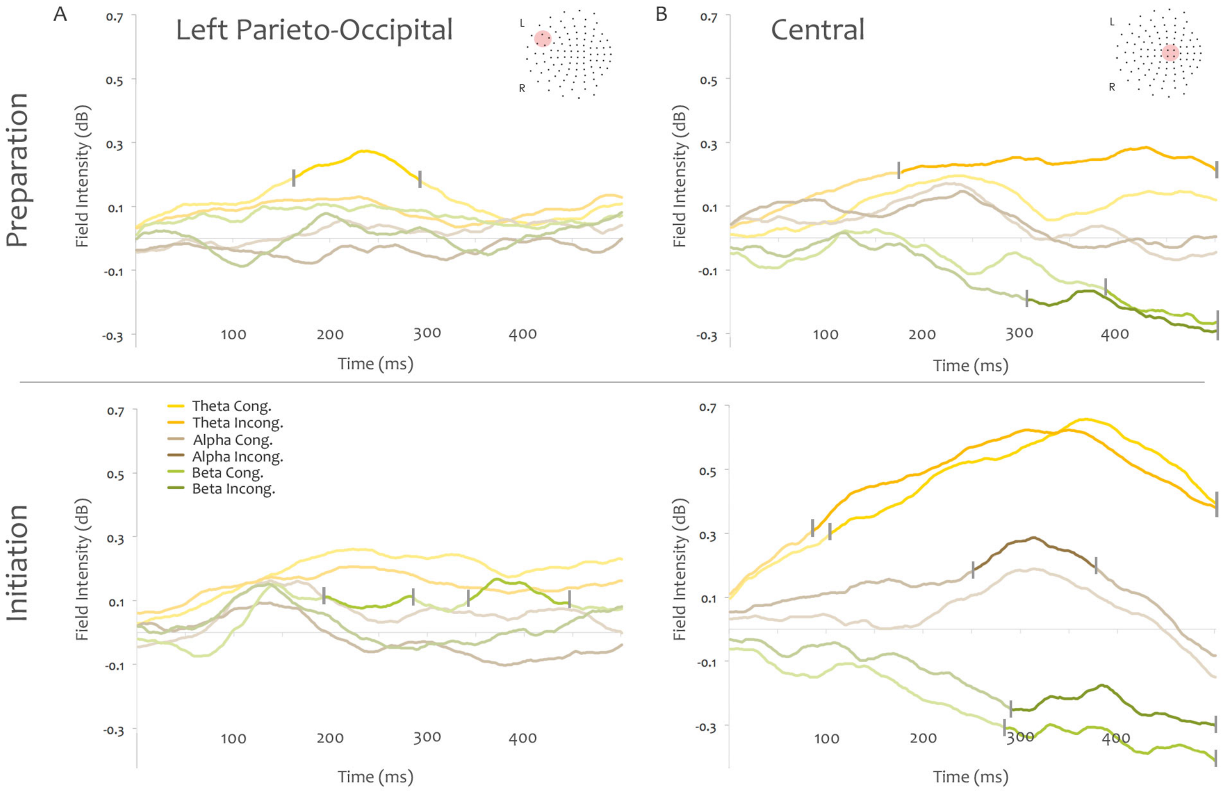

Figure 5.10. Time-course of averaged field-intensity values in theta, alpha and beta bands for congruent and incongruent conditions compared to baseline action observation. **A|** Average field intensity values of four sensors over the left-parieto-occipital regions during the preparation and initiation conditions, in the first 500ms after action observation. **B|** Average field intensity values of four sensors over the central motor regions during preparation and initiation conditions, in the first 500ms after action observation. Highlighted sections between the horizontal markers indicate significantly different values compared to baseline action observation.

Regardless of conditions, theta frequency activity displayed the strongest divergence from baseline, indicating that it is most sensitive to the modulation of a motor plan over and above action observation alone. Over the central motor location, theta band activity showed a significant increase in amplitude linked to action initiation (Figure 5.10B). Theta activity also displayed a tendency to be modulated by congruency during action preparation over the parietal regions. In comparison, beta power changes showed a reverse pattern compared to theta band, with decreasing amplitudes approaching the execution of the planned action (Figure 5.10B). This well-documented effect of beta suppression was characteristically different from the amplitude change we found over the parietal cortex. Over left parieto-occipital sensors, stronger beta amplitudes were recorded for the observation of actions matching concurrently prepared ones. Finally, alpha band activity revealed relatively weak effects of our experimental manipulations, displaying strong central amplitudes for incongruent actions (Figure 5.10B).

5.3.3.5. Congruency between observed and planned actions

Our results indicated a relatively small congruency effect across sensor and frequency band analyses. The analyses of ERF amplitudes indicated higher amplitudes for congruent versus incongruent actions over central and right frontal sensors at a very early 100ms time point. Similarly, we found greater beta power for congruent versus incongruent conditions in the beta frequency range, but over parieto-occipital areas. Lowering the threshold to a more liberal 0.01 uncorrected level revealed several sensor locations showing a congruency effect. To illustrate some of these, we prepared Figure 5.11 that shows field intensity values for the “Congruent minus Incongruent” contrast over central and left parieto-occipital areas in theta, alpha and beta frequency ranges. Visual inspection of Figure 5.11A shows that congruent actions generally elicit stronger activity over parietal areas than incongruent actions. In comparison, central brain regions seem to be more strongly influenced by incongruent actions compared to congruent ones (Figure 5.11B).

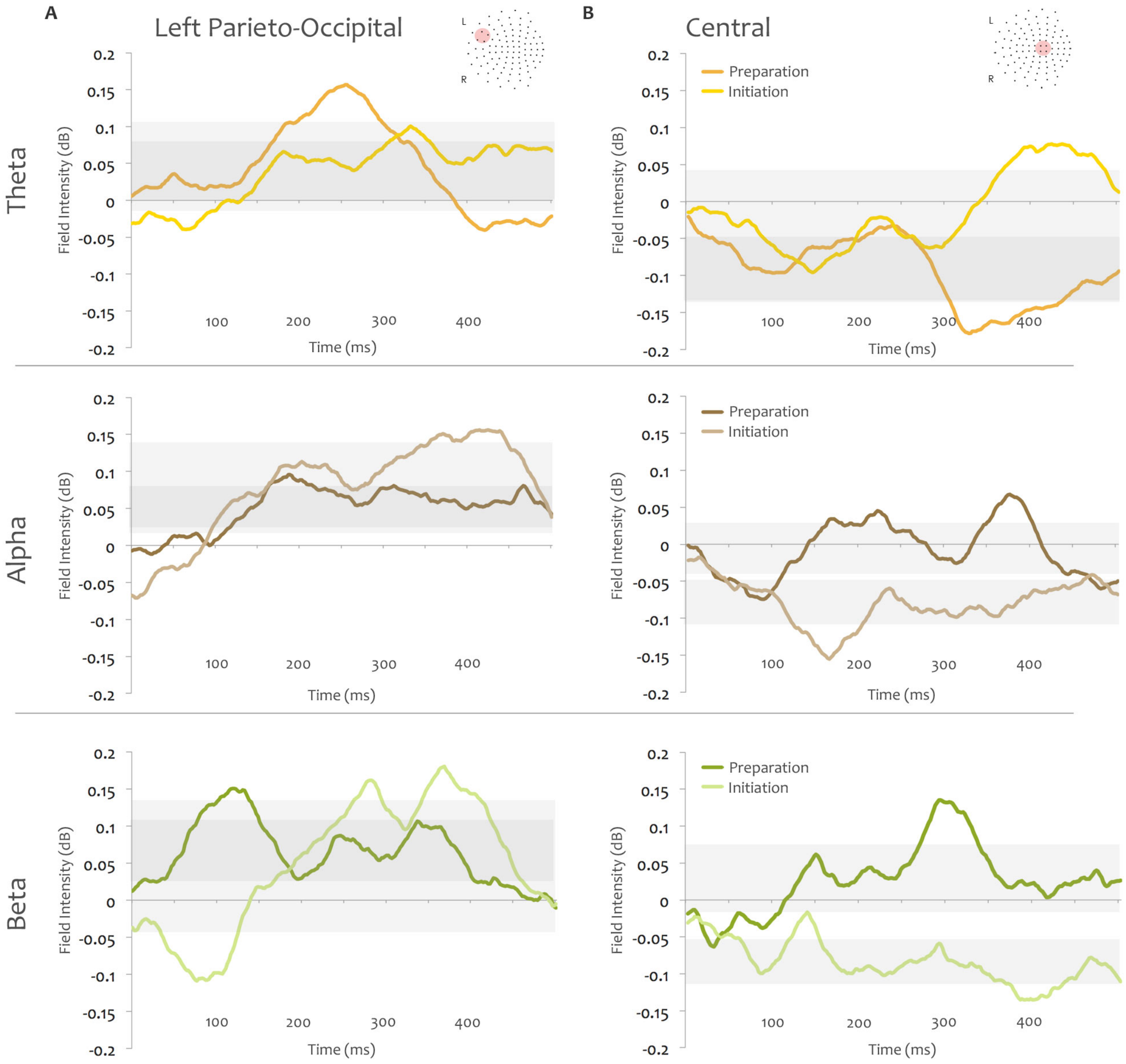

Figure 5.11. Time-course of averaged field-intensity values in theta, alpha and beta bands for congruent minus incongruent conditions. **A|** Average field intensity values of four sensors over the left-parieto-occipital regions during the preparation and initiation conditions, in the first 500ms after action observation. **B|** Average field intensity values of four sensors over the central motor regions during preparation and initiation conditions, in the first 500ms after action observation. Shaded areas indicate standard deviations. Positive values indicate stronger sources for congruent, negative values stronger neural activity for incongruent actions.

5.4. Discussion

The main focus of the present study was to investigate the neural pattern linked to the observation of actions in the presence of concurrent motor plans. Our results show a wide network of sensory, motor and frontal areas involved in concurrent motor preparation and action observation. We found that neural activity in response to observed actions shows modulation by the congruency between planned and observed actions as early as 100ms after action onset. Our data indicates that theta and beta frequency bands are the most sensitive to the concurrent effects of action execution and observation, especially over the motor cortex. Beta and theta frequency bands displayed an opposite neural pattern: theta amplitudes increase closer to action initiation, while beta amplitudes show a strong suppression compared to baseline action observation. The fact that beta and theta amplitude changes are closely linked to action execution phases suggests that their function is also related to the timing aspects of motor plans. In comparison, alpha frequency activity showed very little modulation by concurrent motor and perceptual tasks, probably representing neural processes related more to attentional mechanisms than motor preparation. We discuss our results in details in the following sections.

5.4.1. Neuronal network for concurrent action preparation and observation

Source reconstruction of neural activity in the present action observation and preparation paradigm identified a wide network of active brain areas, similar to the *action observation network* (AON) typically seen in fMRI studies. The AON includes regions of the lateral occipital cortex, the superior temporal sulcus, the middle and superior temporal gyri, the inferior parietal lobule, inferior frontal gyrus, and the dorsal and ventral premotor cortex (Grosbras et al., 2012; Molenberghs et al., 2012). As Figures 5.2 and 5.3 show, source reconstruction based on MEG signals confirms the involvement of these regions during concurrent action observation and execution. Visual inspection of the results suggested that the presence of a motor plan increases neural activity compared to baseline action observation. Based on Figures 5.3 and 5.3 it appears that action initiation linked to more widespread neural sources than the action preparation phase. Finally, actions that did not match with existing motor plans seemed to involve wider activation of brain areas than the observation of actions that did match concurrently planned actions. We should emphasise, however, that comparisons between conditions for these source localisation results did not show any statistically significant differences on the whole brain level.

5.4.2. Sensor level analysis

In contrast, sensor level analysis revealed several major differences between conditions. The main findings of the sensor level analysis were: (1) motor system activity linked to combined action observation and preparation; (2) effect of congruency and task demands on occipital and frontal areas; and (3) congruency effects at 120ms after stimulus onset. We will discuss these results in detail in the following sections.

5.4.2.1. Early integration of observed and planned actions

In line with the apparent differences in source localisation results, sensor level analysis indicated significantly greater neural activity when participants had an active motor plan compared to baseline action observation. Central ERFs were present during both action phases with peaks at 170-200ms after action presentation. Looking at the temporal distribution (Figure 5.4), we can see that this effect was specifically locked to the presentation of the hand gesture and showed no modulation linked to the execution of planned action. As this temporal pattern indicates, activation over the motor cortex reflects the combined effect of action preparation and execution rather than the effect of motor preparation alone.

Amongst the traditional early visual components elicited by images of hand gestures, the Vertex Positive Potential (VPP) shows a very similar temporal and spatial distribution to this central ERF (Bortoletto et al., 2011; Kovács et al., 2006). Indeed, research suggests that premotor areas of the brain are actively involved in action processing around the same time interval (Cattaneo et al., 2011). Bortoletto and colleagues (2011) reported a congruency effect on the VPP, which showed larger amplitude for incongruent actions during action preparation. In the present study, we did not find significant differences between congruent and incongruent gestures at the sensor level around the 170ms time point. With the computation of combined gradiometers we transformed our data to show a spatial distribution closer to actual neural sources, similar to EEG, but it is still unclear how exactly EEG results translate to MEG results.

Altogether, we found strong neural sources over central motor areas during combined action preparation and observation, similar to the VPP component typically reported in EEG studies. This central activity was not modulated by action phase or congruency, but showed a consistent temporal pattern linked to action observation. We hypothesise that this elevated neural signal is the result of processes integrating observed and planned actions.

5.4.2.2. Effect of congruency and task demand on occipital and frontal areas

Congruent actions elicited stronger amplitudes than baseline during action preparation over the left occipital area 170ms after stimulus onset. On closer inspection of the time-course (Figure 5.4A), it is apparent that both congruent and incongruent actions yielded a greater neural response compared with baseline in this location at the 170ms time-point, and that amplitudes for congruent actions were greater than for incongruent actions. Importantly, only the difference between congruent actions and baseline during action planning was significant, and not during action initiation conditions or for incongruent conditions. Thus, given the temporal and spatial location, we postulate that this neural pattern is linked to the early processing of observed actions when the observed action is consistent with the concurrent planned action.

Sensors over motor and bilateral middle frontal regions displayed a significantly stronger effect during the observation of a congruent action when participants were initiating motor actions. Amplitudes showed two peaks, around the 170ms and 300ms time points. This effect was also absent for conditions when observed and planned actions did not match, and when participants were in the action preparation phase. Thus, this bilateral frontal effect also showed the combined effects of congruency and action phase.

We hypothesise that the results of occipital and frontal areas reflect a mechanism that links observed actions to active motor tasks and concurrent task demands. During action initiation, the participants' primary task is to detect a Go-cue, but there are still neural resources available to process external sensory information when that information is consistent with the action they are preparing to initiate. During action initiation, the participants' task is to execute the prepared action as quickly as possible. The presentation of an observed action elicits increased activity once again in task relevant areas, but only when that action is consistent with the active motor tasks.

It is a well-described phenomenon that attention enhances the neural signal in brain areas in which attended features are processed (Chelazzi et al, 1998; Corbetta et al., 1990; Kastner et al., 1999; Spitzer et al., 1988; Yeshurun & Carrasco, 1998; Treue & Trujillo, 1999). We know that action processing involves sensory and motor areas as well, thus it could be possible that the enhanced neural activity we report here merely reflects task-related attentional enhancements. However, if our results show only a neural enhancement related to attentive processes, we would see enhanced neural activation during the incongruent versus baseline conditions as well, given that the motor tasks are the same between these conditions. We hypothesise that sensory information that is not matching with the actual goal-directed behaviour is probably attenuated or filtered out to facilitate the execution of prepared actions. To summarise, our results point to a neural mechanism governed by both bottom-up processes enhancing sensory processing of task relevant information and top-down forces attenuating or filtering out sensory stimuli that are incongruent with behavioural goals, all within the early processing window of 500ms after stimulus presentation.

5.4.2.3. Congruency effect

Our results also showed stronger neural sources for congruent actions compared to incongruent actions during both action preparation and initiation, as early as ~100ms after stimulus onset. EEG studies typically report an occipital P100 ERP component linked to the early processing of a visual stimulus, but our results showed a different spatial location for neural responses at this time. The congruency effect during action preparation was significant over central motor areas, while the congruency effect during action initiation was significant over right frontal sensors. Bortoletto et al. (2013) reported greater ERP amplitudes for congruent versus incongruent actions during action initiation; however, their analysis focused on the 170ms time point. Field intensity values on Figure 5.4 also suggest similar albeit non-significant trends in left occipital regions during action preparation, and at central and frontal regions during action initiation. We postulate that these results reflect similar neural processes as we described in the previous section. The processing of the sensory information that is in line with the current motor task is facilitated compared to a stimulus that is in conflict with the current motor task. Importantly, we found the congruency effect at a very early processing stage, approximately 100ms after stimulus presentation. Furthermore, this congruency effect occurred in task-specific brain areas. We found greater activity for congruent actions during action preparation over the pre-supplementary motor (pre-SMA) area, which is traditionally involved during action preparation, while middle-frontal areas showed increased neural activity for the observation of congruent actions during action initiation (Rae et al., 2014; Usami et al., 2013; Ullsperger et al., 2014).

Overall, we found that sensory information that is consistent with concurrent behavioural goals elicits stronger neural activation. The literature describes shorter reaction times for action execution upon the processing of congruent versus incongruent actions. Thus, it is possible that stronger neural sources are linked to faster action execution. However, during the present paradigm we did not collect reaction-time data, and further studies are needed to clarify the association between neural and behavioural congruency effects.

5.4.3. Theta band activity

The analysis of theta frequency activity displayed neural processes related to the integration of visual and motor-related processes. Our data indicated strong task-related power changes linked to active motor plans over central motor regions. In the context of existing theories we will discuss the lack of congruency effect on theta amplitudes and lastly we will examine our result related to changes in parietal theta power.

5.4.3.1. Cortical theta activity, behavioural decision points and conflict monitoring

Power changes in the theta band showed primarily the effect of a motor plan; theta activity was overall higher when participants had an active motor plan compared to baseline action observation (Figure 5.6). Looking at the temporal pattern of our results, it is clear that field intensity values were strong throughout the investigated 500ms in the initiation versus baseline conditions. Our data is in line with previous experiments, suggesting the crucial role of theta activity in movement related brain processes.

Several previous experiments explained central theta power increases with neural processing related to either sensorimotor integration or to behavioural decision points (Cheyne et al., 2012; Cruikshank et al., 2012; Rawle et al., 2012; Womelsdorf et al., 2010). Furthermore, experiments reported increased theta activity during action initiation compared to action preparation (Cheyne et al., 2012; Cruikshank et al., 2012). For example, Cheyne et al. (2012) described that theta power showed a consistent increase related to action execution, with maximal power around 100ms before action execution. In line with these results, Figure 5.6 suggests a more wide-spread and stronger theta power during action initiation than action preparation.

However, the overall picture of our results suggests that our data can also support theories claiming the involvement of theta band in performance monitoring (Cohen & Donner, 2013; Nigbur et al., 2012; Ullsperger et al, 2014). The incongruent versus baseline contrast during action preparation showed a spatially and temporally similar effect to results in the action initiation phase (Figure 5.6A). However, this activity was absent during the congruent versus baseline contrast. This pattern suggests that central cortical theta is modulated by the action phase and somewhat by the congruency with observed actions.

A variety of tasks related to the processing of novelty or conflict in relation to action performance have shown increased theta amplitudes over central regions, around the 300-400ms time-point after stimulus presentation (Cavanagh et al., 2012b; Grafton & Tipper, 2012; Cohen & Donner, 2013; Harper et al., 2014; Nigbur et al., 2011, 2012; Ullsperger et al, 2014). Our results indicate that theta power compared to baseline action observation was smallest when further in time from action execution (i.e. during action planning) and in the absence of conflict (congruent condition), and showed the greatest difference from baseline in the incongruent condition during action initiation. This effect is illustrated in Figure 5.12.

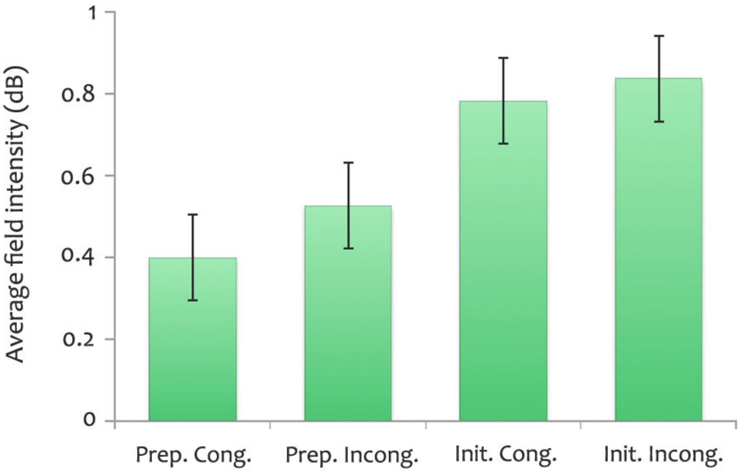

Figure 5.12. Field intensity differences in the theta band versus baseline action observation, at 300ms after stimulus presentation.

Somewhat surprisingly, we did not find any significant congruency effect analysing the theta band, even though we expected that the processing of incongruent actions would elicit greater neural activity in line with conflict monitoring processes. Based on the whole brain analysis, we found only a trend towards this pattern. For example, during action preparation, central theta amplitude was higher for the observation of an incongruent action than for a congruent one (Figure 5.6A). This result is in line with the findings of de Bruijn et al. (2007) who reported no significant error related theta activity for the observation of erroneous everyday actions. Our data indicates that central theta activity is most sensitive to action preparation/initiation, and show only an additional weaker effect related to conflict processes. Furthermore, the present result can be explained by the lack of attentional resources allocated to the monitoring of congruent and incongruent stimuli. During the entire length of the present experiment, participants could ignore the *content* of the presented hand gesture images. We hypothesise that this lack of task relevance is the main factor in the somewhat weak congruency effect that our results show.

5.4.3.2. Theta signal over parieto-occipital regions

Our data indicated theta power changes related to the integration of visual information and motor plans over parieto-occipital regions. We found stronger theta activity for congruent versus baseline observation of an action. This effect started around 170ms, with similar spatial distribution as the same contrast during the sensor level analysis. Working-memory related brain processes are often linked to increase in theta power over parietal electrodes, contralateral to the visual hemifield where to-be-memorised items are located (Klaver et al., 1999; Vogel & Machizawa, 2004). Recent theories claim that theta activity is involved in the integration of memory representations with current motor plans, rather than working-memory activity per se (Rawle et al., 2012, Womelsdorf et al., 2010). For example, Rawle and colleagues (2012) reported stronger theta power increase over parietal areas after participants observed a precue, and stronger theta power at frontal sites following a response signal. Importantly, the neural activity we report here is located ipsilateral to the active motor cortex and thus contralateral to the visual hemifield where the planned action would appear. Predictive coding models claim that during action preparation the brain anticipates the sensory consequences of the prepared action (Clark, 2013; Friston, 2010; Kilner, 2011). We speculate that this significant power increase is related to the integration or matching of observed action to the predicted sensory image that would result from executing the prepared action.

Interestingly, this power increase is absent during action initiation or when the observed action does not match the prepared one. This pattern suggests that neural processes behind parietal and central theta sources represent somewhat distinct functions. It is possible that parietal theta activity represents the integration of visual information that is in line with previous expectations based on motor plans, but missing when the stimulus is in conflict with current goals. Alternatively, this elevated amplitude might be related to a so called “prediction code” or “representation units” that signals a fulfilled prediction (Friston, 2005; Feldman & Friston, 2010; Summerfield & Egner, 2009).

To summarise, our findings indicate that cortical theta activity is closely linked to motor tasks and the integration of sensory and motor related information. Activity in the theta band showed increased amplitudes whenever an active motor plan existed over baseline action observation. Power in the theta frequency was strongest during movement initiation compared to movement planning, and our data suggested functional differences between central and parietal theta processes. Overall, our finding was in line with the theory that theta band is involved in sensorimotor integration and that it reflects computational processes near behavioural decision points (Cruikshank et al., 2012; Rawle et al., 2012; Womelsdorf et al., 2010).

5.4.4. Alpha band activity

Analysis of the alpha frequency range showed very limited modulation by our experimental conditions. Significant results were found during action initiation over left fronto-parietal and central motor areas, possibly reflecting working memory and action-related conflict managing processes respectively.

Our results did not show any significant changes in alpha power over parietal sensors. Parieto-occipital alpha oscillation is generally linked to spatial attentional processes, with previous research suggesting specifically the suppression of alpha amplitudes following sensory stimuli at corresponding sensory areas contralateral to the attended hemifield (Palva & Palva, 2007; Thut et al., 2006). The lack of significant differences suggests that the processing of gesture stimuli at the parieto-occipital areas was relatively similar attention-wise, regardless whether actions were observed while an active motor plan existed or not. This lack of significant difference can be explained by two reasons. First, stimuli were always presented centrally on the screen, hence no observed difference based on attended hemifields is visible. Secondly, in the present paradigm, participants did not have an active task related to the observed action. During action preparation they could ignore the gestures altogether, while during action initiation they only needed to register whether any visual information appeared on the screen to start to execute the prepared movement.

Interestingly, alpha oscillation over central sensors also showed little modulation by our experimental conditions. Cumulative research evidence has shown the suppression of alpha power before movement execution and to a somewhat lesser extent during action observation (Cheyne, 2013; Hari, 2006). We found no difference in alpha amplitudes during active motor preparation and baseline action observation. Similarly, Silas and colleagues (2012) reported no amplitude differences between the observation of congruent and incongruent actions.

However, sensors over the left inferior frontal regions and central areas showed stronger alpha oscillation in congruent and incongruent conditions versus baseline, during action initiation (Figure 5.7). These results fit with the view that alpha amplitudes can reflect short-term and working-memory related neural processing in the frontoparietal network (Jensen et al., 2002; Sauseng et al., 2005; Palva & Palva, 2007). We argue that the increased alpha amplitude over the left inferior-frontal area during congruent versus baseline conditions probably reflects the stronger involvement of the contralateral frontal areas linked to action production. Previous research has shown that alpha range modulation is strongest over the contralateral hemisphere compared to the location of an expected hand image (Quandt et al., 2012, 2013). In our paradigm, action stimuli were always presented centrally, but participants performed gestures with their right hand. Thus, our data points to the conclusion that the main modulating factor on this left frontoparietal alpha activation is the motor plan participants were just about to perform, and the fact that planned / predicted actions are congruent with the observed action.

Several neuroimaging studies, as well as studies of direct cortical stimulation, point to the pre-SMA, dorsal medial prefrontal cortex, and adjacent rostral cigulate zone as key regions to process unexpected actions (Schiffer et al., 2014), motion-related conflicts, or involvement in motion selection and stopping (for a recent meta analysis see Rae et al., 2014; Usami et al., 2013). Our data indicated stronger alpha amplitudes for incongruent versus congruent conditions over SMA/preSMA regions. While not significant at the whole brain level, our data displayed a trend of stronger alpha power at this central location for incongruent actions over congruent action observation, as apparent in Figure 5.7. We postulate that this stronger alpha frequency activity may represent pre-SMA activity due to the conflicting motor programs between observed and planned actions. In line with predictive coding models, this activity could represent “prediction error” that is elevated due to the discrepancy between predicted neural states and observed sensory information (den Ouden et al., 2012; Friston, 2010, 2011; Kilner, 2011).

Altogether, we found that attention-related alpha oscillation in the occipital region showed no modulation by our experimental conditions. However, we found significant alpha power increases close to action initiation. Sensors over inferior frontal areas of the brain contralateral to the executed action showed strong alpha amplitudes around the time of movement onset. Conflicting motor plans during the incongruent condition yielded strong alpha power compared to baseline action observation, possibly linked to the conflict processing mechanism of pre-SMA.

5.4.5. Beta band activity

Activity in the beta frequency band displayed the well-documented strong power suppression linked to an active motor plan. While the cortical extent of the suppression appeared wider for incongruent actions, amplitude differences indicated stronger beta sources for congruent versus incongruent actions over frontal and left parieto-occipital regions. Our results indicate that, beyond modulation by motor plans, beta frequency sources at left frontal and parietal areas are sensitive to concurrently observed actions.

5.4.5.1. Beta suppression

Amongst the analysed frequencies, only the beta band showed a stronger neural response during baseline conditions compared to conditions with concurrent action preparation and observation tasks. This pattern is in line with the view that beta activity is involved in the maintenance of motor “status quo”, and that beta power decrease is crucial for movement preparation and initiation (Cheyne, 2013; Engel & Fries, 2010; Jenkinson & Brown, 2011). Our results show a similar spatial pattern for all contrasts where baseline conditions were compared to congruent or incongruent conditions (Figure 5.8).

Looking at action initiation and preparation, we can see that the temporal pattern of beta oscillation is reflective of the timing of action execution. Cumulative research evidence suggests that beta frequency suppression increases from action preparation until just before action execution (Cheyne, 2013; Hari, 2006; Kilavik et al., 2013). Furthermore, beta suppression is suggested to be reflective of predictive brain mechanisms (Donner et al., 2009; Press et al., 2011; Tzagarakis et al., 2010; Quandt et al., 2013). In the present paradigm, significant results appeared around 350ms post stimulus during action preparation, while during action initiation this effect was already present at 250ms after stimulus onset. This temporal difference indicates that beta suppression in our paradigm is closely linked to the timing of the planned and executed action, rather than the timing of the observed action.

5.4.5.2. Congruency effects

Along with earlier findings and our predictions, our data indicated stronger beta power suppression for incongruent compared to congruent actions. Sensors over the left occipital and left frontal areas were sensitive to the congruency of action execution and observation (Figure 5.9). In a paradigm similar to ours, Koelewijn et al. found (2008) stronger suppression of beta power for actions that were incongruent with planned actions and violated a pre-existing cue. The stronger decrease in beta power was localised over the precentral gyrus and SMA, while our results appeared over left hemisphere sensors and in a more frontal location. We argue that theories claiming that beta oscillation is linked to maintain motor “staus quo” can explain our results. Observed incongruent actions are in conflict with active motor plans and potentially able to interfere with or alter planned movements compared to congruent actions. Field intensity values extracted over left frontal regions (Figure 5.9) showed lower beta amplitudes for incongruent actions compared to congruent actions as early as 200ms after stimulus presentation. Our results suggest that the suppression of the beta band might reflect the difference between the planned and observed actions, but our present paradigm is not able to clarify this correlation. Nonetheless, stronger suppression for incongruent than congruent actions seems to be a consistent effect. Looking at Figures 5.8 and 5.9, it appears that beta power was lower for incongruent versus congruent actions in all of our conditions.

Finally, we found that sensors over the left parieto-occipital area showed higher beta amplitudes during congruent versus incongruent actions. Figure 5.9 demonstrates that this effect occurred between ~250 - 450ms. We found a very similar pattern of significant sensors looking at the congruent versus baseline contrast during action initiation. Also, the same location showed elevated activity at source level and in theta amplitudes during congruent versus baseline contrasts. These results suggest that this parieto-occipital area is modulated specifically by observed actions that are congruent with concurrent motor plans, above the effect of congruency alone or the baseline versus concurrent observation-execution task.

The enhanced neural activity presented in beta, theta and sensor level analyses probably reflects the integration of visual information and motor activity. Animal and human studies indicate that the parietal cortex is strongly involved in sensorimotor tasks, transforming visual information into motor plans, and in the selection of motor plans based on sensory information (Deiber et al., 1996; Sakata et al., 1994; Beurze et al., 2010; Lehmann & Scherberger, 2013; Shibata & Ioannides, 2001; Sugarawa et al., 2013). Shibata and Ioannides (2001) measured brain activity during a Go/NoGo task with MEG. Their data indicated a strong signal around 300ms after the Go cue in the parietal cortex contralateral to the planned movement. As an alternative hypothesis, these stronger neural activities at the parieto-occipital region could signal that observed actions met with predicted sensory states based on planned actions. This interpretation would be in line with predictive coding theories and may represent the neural manifestation of “prediction code” or “representation units” (Friston, 2005; Feldman & Friston, 2010; Summerfield & Egner, 2009). Altogether, our results show the involvement of theta and beta frequencies during sensorimotor integration, and indicate that this parietal region is sensitive to the congruency of planned and observed actions.

5. Conclusions

More often than not our brain is forced to process abundant information related to various actions. We often concurrently acting and watching others act. As these two processes share neural circuitry, the question arises as to how the brain deals with concurrent action monitoring and motor behaviour. The main aim of the present experiment was to investigate power changes in theta, alpha and beta bands to understand better how motor and perceptual systems interact on the neuronal level.

Our data outlined the complex changes in ERFs, theta, alpha and beta frequency ranges in relation to concurrent action observation and execution. We found that all investigated frequency bands showed modulation during concurrent action observation and preparation compared to baseline action observation alone. Sensor and source level analyses displayed an extensive network of brain areas that are commonly involved in this task, and reflective of the complexity of concurrently observing and executing actions. Magnetic sources over motor and inferior frontal areas of the brain already at 100 ms show stronger responses when observed actions are in line with planned ones. This result suggests a very rapid mechanism that enforces the activation of motor plans when conflicting motor information could interfere with the primary goal of the individual. Interestingly though, observed actions, even when they are fully irrelevant for the task exert a very strong influence to motor, inferior frontal, and parietal areas of the brain.

Throughout our experiment we found that activity in different frequency bands shows very different modulation based on experimental conditions, sensor locations, and temporal patterns. The correlation between oscillatory activity and cognitive functions is complicated and suggests that to link single frequency ranges to specific functional processes is problematic. We found that power changes in beta and theta bands are closely linked to action preparation, while alpha frequency range showed primarily the effect of attentive processes due to the experimental tasks.

Results of the sensor level analysis reflected that the central motor areas are involved in the early processing of observed actions. We found that observed actions consistent with an active motor plan elicited greater neural activity in motor and inferior frontal areas compared to actions that differed from active motor plans. Theta frequency changes also showed predominantly motor system related activity. However, while sensor level results showed a close temporal link to the timing of the observed action, theta band activity reflected activation primarily linked to the timing of the prepared movement. Similarly, beta power changes indicated that sources close to central motor areas show a strong bond to different phases of action planning and execution.

We found that all frequencies showed some tendency to be modulated by the conflict between prepared and observed actions. The strongest effect was found in beta frequency activity over the left parieto-occipital area. This specific sensor location displayed constant strong neural sources for observed actions matching concurrent motor plans in beta and theta band, as well as greater amplitudes in sensor level analysis. Our data also showed the combined effect of action preparation and conflict processing on theta amplitudes over central motor areas. Similarly, alpha frequency changes around inferior frontal and pre-SMA areas showed unique activation for congruent and incongruent actions respectively.

Overall our experiment highlighted some of the complex interactions between motor and perceptual systems during concurrent action planning and observation. We described and linked several results from sensory and frequency level analyses to give a comprehensive picture of neuronal processes behind integrating sensory and motor information.

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Chapter 6

Summary and conclusions

The present thesis examined the neural correlates of motor cognition. Analysis of fMRI and MEG data mapped a widespread cortical network actively involved in action observation and preparation, and displayed strong modulation by attentional and predictive forces. The results suggest that actions are processed in a holistic way even when only one specific feature of them is task relevant. In this last chapter I review the main findings of my experiments specifically focusing on the various aspects of attention across experiments, shortly outline my results in relation to predictive processes, and indicate future research questions in relation to action observation.

Summary of the main results

Action observation relies on a widespread neural network, which shows activity tightly linked to the detection of novel or unexpected action features, even when actions are not task relevant. Attentional focus directed to one specific action features does not eliminate the overall activation of the AON, but enhances the precision of those processes by which we can make task-relevant decisions. Importantly, the present experiments highlight the importance of attentive and task-related effects on the processing of observed actions. The results suggest the existence of a neural mechanism that shows high automaticity in the processing of actions, albeit not completely free of attentional modulation. When actions are task irrelevant, this mechanism is primarily involved in the detection of unexpected changes in actions. However, when actions become task relevant, attentional focus sharpens neural processing of the same basic neural mechanism to facilitate perceptual discrimination or behavioural changes in line with task requirements.

Furthermore, our results suggest that predictive processes play a crucial part in action observation. We used power changes in theta, alpha and beta bands to examine neural patterns reflective of attentive and predictive processes. Our data indicated that, as early as 100ms after observing an action, parieto-occipital areas show a neural pattern that is indicative of the predicted or unpredicted nature of the observed action. Theta, alpha and beta frequency bands play a unique but not unified role throughout action observation. Beta oscillation over central motor cortex are linked strongly to preparatory motor activity, while parieto-occipital beta amplitudes show changes in relation to the processing of predicted or unpredicted sensory information. In contrast, alpha frequency changes display functional involvement of attentive and conflict processing mechanisms, and are less tied to specific aspects of motor cognition. Theta frequency changes are indicative of the relative timing of motor execution over the motor cortex and the integration of visual and motor information over the parieto-occipital region. Overall, our result reflects the complexity of motor cognition, whereby a widespread network of brain areas need to share information and act in synchrony. Furthermore, attentive and predictive processes play a crucial role to filter out unnecessary information, to maintain an efficient energy-state and ultimately to make us successful in our actions with the world and with others.

Neural network for motor cognition

All three experiments in this thesis supported the strong functional link between motor and perceptual areas during action observation, and revealed a widespread neural network actively involved in both action observation and preparation. In line with previous research fMRI and MEG studies, the present results indicated the concurrent involvement of parieto-occipital areas, motor and premotor regions, supplementary motor and inferior frontal regions of the brain in the processing on observed actions (Caspers et al., 2010; Grosbras et al., 2012; Molenberghs et al., 2012a). Data from the two fMRI experiments demonstrated that this network is highly sensitive to the novel or repeated nature of action stimuli, by displaying a strong repetition suppression pattern. Visual inspection of Figure 3.5, 4.4, 5.2 and 5.3 indicates that all three experiments identified a highly similar neural network, regardless of neuroimaging methods or task differences between experiments. Overall, my data indicates that the processing of actions is a robust function of the brain, relying on an extensive neural network.

Attention & action observation

The main aim of this thesis was to explore how attention or context modulates the neural mechanisms involved in the processing of actions. The experiments presented here investigated three interesting questions, which aimed to model everyday situations. The first experiment investigated neural patterns linked to action observation under an attentionally demanding visual task. The second experiment examined how focusing our attention to one specific aspect of an action can modulate neural processing of actions. The final experiment explored how action observation is modulated by a concurrent motor plan. The results of all three experiments indicated that attention is a fundamental modulating factor of action related neural processes. While previous literature often failed to control attention we cannot hope to understand motor cognition better without systematically controlling this crucial factor.

In Chapter 3, results indicated that a widespread neural network is actively involved in the processing of actions even when attentional focus is on another visual task and the observed actions are task irrelevant. This result is in line with the *two process theory of attention* which claims an “automatic” and a “conscious control” mode of attention. Automatic processing is bottom-up, relying on the sensory stimulus and requires very limited if any attentional capacity, while consciously controlled processing is mainly top-down and relies heavily on attentional and neural resources (Styles, 2006). By applying a demanding attentional task, we investigated the relative position of action observation on the spectrum of automaticity. Our results suggest that action processing is a prioritised, basic function of the brain that shows a high level of automaticity. The information we can deduct from observing others act is highly important. Actions can warn us about dangerous situation or possible gains, we can learn essential skills by observing others, or actions can tell us -often unconsciously- about how other people think about us in a social situation. The accurate understanding of others’ actions is a valuable skill, and in the current literature problems with motor cognition and mirror neuron functioning are linked with serious disorders, such as autism or schizophrenia (Rizzolatti et al., 2009; Iacoboni & Dapretto, 2006; Buccino & Amore, 2008; McCormick et al., 2012). The results of the present thesis indicate that healthy individuals can monitor and process actions even while highly engaged in another task. An interesting niche for further research is to clarify how much, if any, of the processed information reaches conscious awareness.

Crucially, the results revealed an interaction effect between attentional load and the novel or repeated nature of observed actions. The processing of a novel action feature elicited more neural activation under a more demanding task compared to a low-load task, while the processing of a repeated stimulus feature was supressed more under high-load compared to low-load. It is likely that this pattern indicates a neural process that can act as an alert mechanism to sharpen the processing of any unexpected or novel action-stimulus while we are heavily engaged in a task. I posit that Chapter 3 illustrates the basic and most robust form of action processing, that relies on a semi-automatic brain mechanism that is in place to monitor changes in our environment which can be important to alter our behaviour.

In Chapter 4 we investigated the influence of task relevance on the processing of actions. Specifically, we were interested to see how focused attention on the acting agent, kinematics or action goals can modulate the neural pattern behind action processing. The data indicated that attentional focus enhanced neural activity in task-specific areas of the brain. Attending to the acting agent was linked to bilateral middle occipital area, including the fusiform gyrus. Attended kinematics increased activation in the right lateral prefrontal cortex around the insula and in the left inferior frontal gyrus. Attention to action goals showed additional neural processes in the right postcentral gyrus, right superior occipital gyrus, left middle occipital gyrus, and in the left superior parietal lobule. Importantly, the novel or repeated nature of the observed actions again proved to be an important modulating factor. Task relevance did not elevate the overall activity of corresponding brain regions, but enhanced the processing of novel stimuli and strongly supressed the processing of repeated action features, regardless of whether the feature in question was task-specific or task irrelevant. This neural pattern was consistent across the reported brain regions, suggesting a universal brain mechanism that is present in sensory, motor and frontal areas of the brain equally. A plausible function of such a mechanism is to boost neural activity in task-specific areas of the brain, to allow fast and precise discrimination between task-relevant sensory information.

Chapter 4 illustrates an important property of action processing: it shows signs of a holistic, integrated processing. Our data indicated that the whole action observation system is active during the processing of an action, even if only one feature of the action is task relevant. Novel and repeated action features were processed differently; however, the nature of what was novel or repeated between trials did not affect the overall neural pattern. The neural networks we have found in Chapter 3 and Chapter 4 are remarkably similar (Figure 3.5 and 4.4). These similarities further support the existence of a basic, semi-automatic mechanism related to action processing, a mechanism that is primarily involved to process actions holistically. In reality, actions cannot exist without acting agents, or goals without kinematics. There would be little importance for us in the natural word to analyse these action features purely on their own. My results suggest that the observation system processes actions in an integrated way, even if tasks required the processing of a single action feature. However, an interesting question for future research is to test the nature and the amount of cognitive load needed to successfully disrupt the robust processes behind action observation.

One can detect a possible conflict between Chapter 3 and 4. In Chapter 3 the results indicated that the less we attend to an action the higher the neural activity will be, while in Chapter 4 the results suggested greater neural activity with greater attentional focus. The important difference between the two experiments is context or the nature of the task. In Chapter 3, actions are never task relevant and so are no more than environmental noise that might or might not be important for us in general, whereas in Chapter 4 observed actions are task-relevant and crucially important for participants to attend. The similarity of the repetition suppression effect between the two experiments indicates that the basic neural processes are the same in both experiment, but what is relevant for the brain to analyse and prioritise is different. When actions are not the main focus of attention, they still carry potentially important information, thus the brain monitors any changes in those actions that are unexpected. I suggest that basic action observation processes, which rely on predictive mechanisms, are enhanced to detect any violation of predicted sensory states. In contrast, when actions are task relevant, the very same neural mechanisms are enhanced to process task-relevant sensory information specifically in specialised, task-related parts of the network. I reason that this apparent clash between the two experiments illustrates perfectly the flexible nature of action observation and emphasises the importance to control tasks and attentional conditions during experiments of motor cognition.

In Chapter 5, we investigated how concurrent motor plans modulate action observation, in light of these processes sharing neural resources. To explore neural patterns in a temporally detailed manner, we used MEG to map neural responses to observed actions. During the experimental paradigm, participants' attention was on the action they were preparing to execute, and observed actions were either task irrelevant (preparation condition) or minimally important (initiation condition) in the sense that they acted as a "go" cue for action execution. Based on the result of Chapter 3, the processing of observed action even when they are task-irrelevant was expected. However, the crucial issue here was how the same neural network can deal with the parallel processing of observed and planned actions. Additionally, the question arose how conflict between planned and observed actions would be present in frequency changes.

The data of Chapter 5 indicated that action preparation and observation can occur in parallel even if these two tasks share neural resources. Results showed again that the brain continues to process task-irrelevant actions, and revealed the strong modulatory effect of attentive and predictive forces. Both sensor level amplitude and frequency power changes were recorded, strictly tied to presentation of the observed actions. Traditional early neural responses around the 100ms and 170ms time points were clearly visible on sensor level amplitudes (Figure 5.4A). Importantly, conflict between planned and observed actions was registered in the very early processing stages in the form of elevated neural signal for sensory information in line with motor plans. Furthermore, beta frequency changes indicated increased power for congruent versus incongruent actions over parieto-occipital areas around action initiation. One explanation is that when there is increased need for neural resources (close in time to action execution) the processing of conflicting sensory stimuli at parieto-occipital sites is supressed. This result probably indicates a filtering mechanism that helps us to retain neural resources for the analysis of task relevant information while blocking out or inhibiting sensory stimuli that are irrelevant and in conflict with current behavioural goals. An alternative explanation is that the increased attentional focus on the observed action during the initiation condition interacts with predictive processes, resulting in an overall elevated neural activity for attended predicted sensory information. A similar pattern has recently reported over early visual areas (Kok et al., 2012) and in line with claims related to predictive processes (Feldman & Friston, 2010).

The data of the MEG experiment indicated elevated neural responses to observed actions that match prepared ones, thus probably represent expected sensory states. In Chapter 3, however, we reported elevated BOLD signals to actions that are novel or unexpected. Changes measured in the hemodynamic response usually occur 5-6 seconds after stimulus presentation (Huettel et al., 2009), while we only analysed the first 500ms after stimulus onset with MEG. The relative timing difference between the MEG and fMRI results make it difficult to determine whether these two neural activations reflect the same or different processes.

Additional MEG research is needed to extend our present knowledge about the later processing phase of action observation, as well as to examine how conflict monitoring and gating mechanisms present on neural processes. As I mentioned in Chapter 5, further analyses are planned on the MEG data. While presently we analysed theta, alpha and beta frequency ranges, the investigation of gamma frequency changes would be indicated based on current literature (Arnal & Giraud, 2012; Cheyne, 2013). Furthermore, more sophisticated analysis methods involving phase-locked frequency changes and identifying connectivity patterns would reveal more about the neural processes of motor cognition.

To summarise, my thesis highlighted different important aspects of attention on action observation. I argue that my results indicated the existence of a robust semi-automatic system that is involved in the processing of actions, even if they are task irrelevant. Attentional focus can modulate the neural pattern and enhance or attenuate the processing of a stimulus in task-specific regions of the brain. Theta, alpha and beta frequency oscillations play distinct roles in motor cognition, based on spatial and temporal locations in relations to observed and planned actions.

Predictive processes

The present thesis has not directly investigated the validity of predictive coding models in action observation, but many of my experiments showed results in line with those theories. According to Friston (2010), predictive processes provide a unified mechanism for the brain to optimise its performance and thus an individual's success in the ever-changing environment. The theory that the sensory brain evolved to infer the causes of changes in sensory inputs, or that the brain is an "inference machine" are ideas that reflect well how rudimentary predictive mechanisms are in the brain (Friston, 2005, 2010, Clark, 2013). A review of a wide range of experiments in Chapter 2 suggested that results are best explained by predictive models. Also, the present experiments displayed neural patterns that were in line with predictive processes. Chapters 3 and 4 described robust repetition suppression effects, a neural phenomenon that is strongly linked to predictive processes (Friston, 2005, 2006; Friston et al., 2010, 2011; Kovács et al., 2012; Larsson & Smith, 2012; Summerfield et al., 2008). Chapter 3 indicated the presence of repetition suppression tied to action observation, even when those actions were task irrelevant, and only limited attentional resources were available to process them. This indicates that whatever mechanisms are behind repetition suppression, they rely on basic brain mechanisms that require very little attentional resources. Predictive processes would be perfect candidates to explain our results and the neural mechanisms for repetition suppression.

Furthermore, results across the presented experiments are consistent with the theorised role of attention in predictive processes. According to the free-energy principle, attention should increase the relative precision of predictions, or in other words it should enhance the perceived difference between predicted and unpredicted sensory states (Friston, 2009; Feldman & Friston, 2010). In line with recent experimental results (Kok et al., 2012, Jiang et al., 2013), and the above theories, our results display exactly this pattern in Chapter 4, by showing an increased repetition suppression effect for attended action properties in task relevant brain regions. Furthermore, the results of

Chapter 5 revealed enhanced beta amplitudes for attended predicted stimuli versus attended but not predicted ones. Overall, these results show the joint effects of predictive and attentive processes on neural processes behind motor cognition.

Recent experiments have tried to disentangle predictive processes from attentional processes; however, the experiments in this thesis were not specifically set up to factorially modulate these neural forces. Importantly, attention is most often understood in the predictive context as whether a stimulus is behaviourally relevant or not (e.g.: Kok et al., 2012). The main focus here was to test the nature of attention on neural processes related to motor cognition, and thus it is important to emphasise the multifaceted nature of attention (Summerfield & Egner, 2009) in light of the present experiments (for interesting arguments on attention and predictive models see Bowman et al, 2013; Block & Siegel, 2013; Clark, 2013b). For example, in Chapter 3 salient changes within video clips could theoretically drive the enhanced repetition suppression result, even though the processing of those video clips was task irrelevant. In Chapter 4, a clear effect of task-relevance, controlling top-down allocation of attention was present. In Chapter 5, the effect of attention was less obvious. During the action preparation condition, action observation was task-irrelevant and stimuli could be ignored. In the action initiation condition, action-pictures were task relevant in the sense that they signalled that participants could start to execute actions, although the actual *content* of the presented images were irrelevant for the experimental task. Nonetheless, we found stronger neural sources for congruent versus incongruent actions during action initiation, a result that would be expected by the joint effect of attention and predictive mechanism. Overall, my experiments suggest that predictive models offer a valid theoretical model for motor cognition.

From the development of action understanding to brain architecture

Understanding actions is a primary function of our brain. Despite the number of existing theories on *how* we process actions, we are far from understanding let alone describing the complex neural processes that allow us to make sense of others' actions in the world. Importantly, it might not be possible to understand action perception on its own. The presented experiments highlighted the intricate nature of how action, perception, cognition, attention and prediction all intervene together to understand actions. I argue that predictive processes are the best existing theories to help us move forward and explore more about the neural processes underlying action understanding.

One exciting research area is how we acquire a system that is so effective that can translate the moving dots of point-light animations into higher-level understanding of intentions in a blink of the eye. There is a fast-growing research area investigating how human infants process and understand actions (Hunnius & Bekkering, 2014; Csibra et al., 2003; Bidet-Ildei et al., 2014; Frankenhuis et al., 203; Green et al., 2014; Grossmann et al., 2012; Henrik et al., 2014; Rotem-Kohavi et al., 2014, Southgate et al., 2009, 2010; Virji-Babul et al., 2012; Woodward & Gerson, 2014). It is argued that through actively experiencing actions and learning about the statistical regularities between actions and sensory information human infants gradually develop skills to understand and, importantly, to predict actions (for a recent review see: Hunnius & Bekkering, 2014). For example, recent literature reported oscillatory changes during action execution that revealed on-line predictive mechanisms while 9-months-old infants observe actions (Southgate et al., 2010). Furthermore, there has been work on network analysis based on EEG measures that show functional differences in the AON linked to infants' motor experience (Rotem-Kohavi et al., 2014). Despite the sophisticated and elegant behavioural techniques and the few neuroimaging experiments on the development of human action understanding, our knowledge is limited on this fascinating topic. To understand the development of the functional and neural link between action and perception helps us to understand how we develop the skills to understand actions around us, but also has much broader importance. Predictive coding models argue that these skills are reflective of the basic functions of our brain, and understanding them and their development is helping us to understand more about the nature of human cognition (Clark, 2013; Friston, 2010).

An interesting niche in recent years is to model internal processes to investigate predictive coding from the engineering or an evolutionary perspective. In every situation there are countless future states we can predict, but how does the brain choose what to predict? The healthy brain predicts what is most important for the individual to optimise their behaviour (Friston, 2010; Fiser et al., 2010). But to know what is the "most important" in a given situation requires learning of the regularities of the world (Fiser et al., 2010). Humans evolved to be curious to understand the cause and effect relationships of the world, and one theoretical model, *active sensing* aims to describe this process (Gordon & Ahissar, 2012; Ahissar & Arieli, 2001). As a first step, we learn how to use our body, how to orient our senses, how to focus, how to see, reach, move. Next, we start to interact with our environment; that is we learn the sensory-motor correlations and their regularities (Fiser et al., 2010). These assumptions lead to questions such as: How do we learn to control our body in the first place? What is the optimal way to move so we can learn quickly (Gordon & Ahissar, 2012)? When does our brain start to extract meaning and "predict" (Fiser & Aslin, 2002; Hunnius & Bekkering, 2014; Southgate et al., 2010)? What will happen if we are restricted to learn to use our senses? What is going wrong in the autistic brain, so a registration number can be more important than the fact that a car is approaching towards us with a high speed? Clearly, theoretical, computational and imaging work need to be combined to answer the many questions on "how" and "what" the brain predicts.

Finally, there are many interesting assumptions on the general architecture of the brain based on predictive models that have not yet been confirmed by experiments, but would be interesting to investigate in relation to action observation processes. In their review article, den Ouden and colleagues (2012) pointed out the heterogeneous nature of prediction error. Prediction error can manifest differently based on brain areas and functional specialisation. There are perceptual, cognitive and motivational prediction errors. We can also differentiate between cortical and subcortical prediction errors (de Ouden et al., 2012). Importantly, as we discussed in Chapter 5, cortical predictive mechanisms are strongly linked to neural oscillatory processes (Arnal & Giraud, 2012). Predictive coding theories posit asymmetrical hierarchical information passing between cortical layers, where prediction errors propagate forward and predictions propogate from higher to lower levels of the neural hierarchy (de Ouden et al., 2012, Summerfiled & Egner, 2009). These neural routes are supposedly linked to oscillatory changes. For example, predictions are linked to beta frequency changes, while prediction error to gamma oscillatory changes (Arnal & Giraud, 2012; Arnal et al., 2011; Buffalo et al., 2011). We are unaware of any research presently available to confirm these predictions linked to action observation. As mentioned, further experiments are planned on the dataset we reported in Chapter 5. Specifically, a more detailed analysis of oscillatory changes, their phase-locked properties and connectivity analysis on beta and gamma frequency bands would be indicated to test the postulated message-passing of predictive mechanisms. Generally, these planned analyses might be able to measure not just prediction errors, but “prediction signals”, which are so far rarely reported in the literature (for more on prediction signals see Koster-Hale & Saxe, 2013). Overall, I see that MEG research would be very beneficial to test the rapid brain processes behind action observation, with a possibility to test neural communication, functional networks, rhythmic brain activity, and to study the development of motor cognition in a non-invasive way.

Correlation between magnetic and hemodynamic measures

The present thesis contains both fMRI and MEG data on action processing, thus it is natural to ask how these different techniques correlate with each other, and whether we can draw conclusions between the results. Potentially, the combination of fMRI and MEG should allow a superb temporal and spatial resolution, however the exact correlation between these two measures are yet unresolved in the literature (for an excellent summary on this problem see Poline et al., 2010). Local power increases and decreases can both result in elevated BOLD responses (Winterer et al., 2007). Invasive neural recordings point to a complex correlation in which the BOLD response positively correlates with high-frequency oscillations (30-150 Hz) and negatively correlates with low-frequency (8-30 Hz) oscillatory power changes (e.g.: Zumer et al., 2010). Furthermore, Kujala and colleagues (2014) show that this relationship also varies across cortical areas. During my experiments I did not focus on investigating the relationship between fMRI and MEG. The nature of the tasks between experiments was very different, focusing on different experimental questions. Mainly, during the MEG task my main focus was on the first 500 ms after action observation, while fMRI lacks this temporal resolution. In my thesis I refrained from drawing any conclusions between the relationships between the two neuroimaging modalities, however it is an interesting question that would worth further investigation in the future.

Motor cognition, perception, & attention

I started this thesis by emphasising the link between action and perception. For considerable time, perception and action were viewed as an "input-output" pair with linked, although separate and dissociable, neural processes (Hurley, 1998). Nowadays, terms like "action-oriented predictive processes" (Clark, 2013), "active inference" (Friston, 2009) or "action-effect anticipation" (Waszak et al., 2012), along with their theoretical models, posit that action and perception are deeply united. According to Clark, theories of predictive processes go as far as depicting "perception, cognition, and action as profoundly unified and, in important respects, *continuous*" (Clark, 2013, p.187; italics added). The presented experiments set out to investigate action observation, but I argue they did more: they inevitably let us glimpse the basic neural mechanisms of the brain.

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